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INFLUENCE OF GRAZING, DUNGING AND TRAMPLING ON SHORT-TERM DYNAMICS OF GRASSLANDS IN MOUNTAIN WOODED PASTURES

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Influence of grazing, dunging and trampling on short-term dynamics of grasslands in mountain wooded pastures

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Summary

Wooded pastures are a traditional landscape of the Swiss Jura Mountains. Influenced by the combined action of grazing and forest management, they represent a form of multiple uses of natural resources. Cattle summer grazing plays a main role in vegetation dynamics of such ecosystem by inducing three types of disturbances: herbage removal, dung deposition and trampling. The main objective of this thesis was to assess the successional processes involving herbaceous vegetation in relation to cattle activity (herbage removal, dung and urine deposition, trampling and gap creation). To achieve this objective both experimental and observational methods were applied at various spatial scales.

To assess spatial and seasonal pattern of cattle activities at large scale, we estimated the intensity of herbage removal, dung deposition and trampling after each of three grazing periods on a grid of 393 square cells of 25 m covering an entire rotational paddock. Spearman's rank correlations after accounting for spatial autocorrelation revealed a lack of positive correlations between cattle activities, suggesting that the spatial pattern of cattle habitat use depends on each cattle activity. The spatial patterns became more homogeneous through the season especially for herbage removal, whereas no important change was observed in trampling patterns between grazing periods. Multivariate analysis showed that cattle activities depend on different environmental factors, that the importance of management-induced versus natural structures was highest for herbage removal, and that dunging patterns were dominated by large-scale, herbage removal by medium-scale, and trampling by fine-scale spatial structures. Systematic differences in the spatial and seasonal patterns of cattle activities may result in complex interactions with vegetation. We conclude that in heterogeneous environments, such as many sylvo-pastoral ecosystems, spatially explicit models of vegetation dynamics need to consider dunging, trampling and grazing separately, even at landscape scale.

An experimental approach was chosen to explore the effects of cattle activity on vegetation dynamics at fine scale. We selected on two sites three plant communities depending on various light conditions but with similar soil and elevation. In both sites experimental areas were fenced to prevent large herbivores disturbances and a total 88 plots of 4 m^2 were defined. A set of controlled factors simulating the three cattle activities was applied on plots in fenced areas: (1) repeated mowing - three levels; (2) intensive trampling - two levels; (3) manuring with a liquid mixture of dung and urine - three levels. The three factors were combined into treatments. Inside exclosures, all treatments were applied homogeneously to the entire surface of each plot during the summer period of three or four years. Additionally, plots outside the fenced areas represented reference plots with regular cattle pasturing. Vegetation response was recorded twice a year in spring and in autumn with a point-intercept frequency measurement. Multivariate analyses of vegetation data in the first year showed a clear seasonal shift and significant differences induced by treatments. Abandoned and manured plots showed the largest deviation from the cattle-grazed reference plots. 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. Results over the whole experimental period (3 or 4 years) showed that effects of treatments on vegetation structure were important and similar in the three communities depending on various light conditions. By contrast, plant succession induced by treatments, as well as the importance of each treatment to explain species variation, differed among the three communities. Results showed very interesting dynamic properties of each community. High shade conditions induced slower dynamics than that one observed in open or low closed areas where communities presented resilience again disturbance. The high relevance of potential plant height and plant life form to explain vegetation dynamics again disturbances was confirmed by our observations. Our experiments showed clearly that cattle activities induced various dynamics in the herbaceous layer of pastures at species and functional levels. The results revealed a high complexity in species response to disturbances and their interactions. In reality, this complexity is even higher if one considers crossed effects of gap creation by heavy trampling, cattle selectivity and heterogeneous soil conditions occurring at a very fine scale. These phenomena are probably a key to understanding plant coexistence in perennial grasslands.

The effect of the treatments simulating cattle activities on the structure and potential activities of soil microbial communities were also explored and compared to effects of soil properties and plant composition or biomass. At the end of the experiment, physiological profiles of microbial communities (Biolog Ecoplates^{TM}) were measured in plots exposed to two light conditions (shady or sunny). Furthermore soil chemical properties (pH, total organic carbon, total nitrogen and total phosphorus), plant species composition and plant biomass were also measured. Results showed first that, despite differences in plant communities and soil properties, the metabolic potential of the microbial community in the sunny and in the shady situations were similar. Moreover, treatments affected the microbial community and effects were more pronounced in the sunny than in the shady situation. In both cases soil microbial activity was mostly affected by repeated mowing. By contrast, fertilising was not a significant factor. The main difference between light situations was that in sunny plots the vegetation explained a high proportion of variation of the microbial community descriptors while no significant variation appeared under shady condition. By contrast the soil variables explained a significant proportion of the variation of the microbial community descriptors in shady plots while no significant variation appeared under sunny condition. We conclude that the three components of cattle activity influence soil microbial communities and that this influence depends on the light conditions within the wooded pasture.

Plant colonisation of artificial gaps under the different treatments simulating cattle activities was also investigated during 3 years. Results suggested that at 1-m^2 scale, gap creation has almost no impact on the number of species even if this disturbance destroyed about 40 % of the vegetation. Impact of this disturbance on the number of species is perceptible only at the scale of the gap (in this case few dm^2). Colonisation of the gap affected the relative contribution of species in the community and this effect persisted up to the end of the observation, especially in the centre of the gap. The list of species involved in gap colonisation was a subset of the species pool around the gap and only four new species appeared. Small seed, unspecialised seed dispersal, persistent seed bank and high vegetation spread were attributes characterising species favoured in the gap. There was a very clear edge effect supported by a very high similarity between species composition at the edge of the gap and in the surrounding vegetation. Our treatments simulating cattle activities did not clearly play a primary role in gap revegetation. It seems that constraints imposed by gap environment were more important than disturbances induced by treatments. Nevertheless, differences between treatments appeared, but with secondary importance. Gap creation combined with cattle activities induce complex interactions participating in the high biodiversity of pasture.

A cell-grid method was used to survey seasonal changes in the plant communities under natural cattle activities. We defined four permanent plots in four typical herbaceous communities of a wooded pasture. Plant communities were: an eutrophic grazed meadow, a temporary refused meadow, an underwood herb community and an oligotrophic lawn. Permanent plots consisted in 1-m^2 grids subdivided into 100 square cells of 1 dm^2. In each cell of each plot and every month from May to September, we estimated dominance and grazing occurrence of all species. Our results showed that seasonal changes in species composition were very strong and scale-dependent. Changes at plot scale were mainly driven by a seasonal shift. Changes at cell scale suggested high small-scale dynamics of species. Despite high changes at cell scale, the structure of the community did not change and local species richness did not show any trend. We found no correlation between the turnover at cell scale and cattle activity. We conclude that dynamics and internal species turnover of the community at fine scale and short time seem more driven by internal characteristics of the community than by disturbances induced by cattle. At seasonal scale, plant communities may be stable in their structure despite fluctuations in their texture.

We investigated also at dm^2 and monthly scale the vegetation dynamics induced by dung deposition. Results suggest that in a first step at very short-term time scale (a few days) dung patches increase plant biodiversity. At this stage vegetation height is still low and there is a high nutrient input. This induces favourable conditions for many species, some of them being not able to survive when height increases, provoking concurrence for light. In a second step the dung patches protect the vegetation around them against grazing activity. This enables established species to grow without disturbance and to get higher than the surrounding vegetation. At this stage vegetation near the dung may slowly change. However, these changes are not accompanied by an important change in the floristic composition. We conclude that dung deposition by cattle plays an important role in grassland ecosystems by changing the equilibrium between plant species and by maintaining favoured species in the community.

Conclusively from all results of the thesis, we defined six general plant species response groups linked to cattle activities and proposed a qualitative model of vegetation dynamics in wooded pastures using plant functional groups. Finally we present some implications of our results for management practices and suggest some perspectives for researches in the future.

Keywords: Biodiversity; Cattle activity; C-S-R strategy; Dung deposition; Fertilising; Field experiments; Gap; Grazing; Herbage removal; Light conditions; Multivariate analyses; Plant community; Plant functional traits; Plant species mobility; Seasonal changes; Spatial monitoring; Spatial and temporal scale; Sylvopastoral ecosystem; Swiss Jura Mountains; Trampling; Vegetation dynamics.

Résumé

Les pâturages boisés sont un paysage traditionnel du Jura suisse. Ils résultent d'un multiusage où interviennent principalement les exploitants agricoles et les forestiers. La présence du bétail durant la période de végétation (mai à octobre) joue un rôle clé dans ce type d'écosystème en induisant trois types de perturbations: le broutage, le dépôt de bouses et le piétinement. Le principal objectif de cette thèse est de comprendre les processus dynamiques induits dans la végétation herbacée par les activités du bétail (broutage, bouses, piétinement et création de trouées). Pour atteindre cet objectif, des approches observationnelles et expérimentales ont été utilisées à différentes échelles spatiales.

Pour comprendre la distribution spatiale et saisonnière des activités du bétail, nous avons estimé l'intensité de broutage, le nombre de bouses déposées et le piétinement après trois périodes de présence du bétail dans un parc. Les observations ont été effectuées selon une grille de 393 cellules de 25 m de côté couvrant l'entier du parc. Les corrélations de rangs de Spearman tenant compte de l'autocorrélation spatiale ont révélé une absence de corrélations positives entre les trois activités du bétail, suggérant que la distribution spatiale des activités du bétail dépendaient de chaque activité. Durant la saison, la distribution spatiale du broutage est devenue de plus en plus homogène, alors que celle du piétinement a très peu varié. Des analyses multivariées ont montré (1) que les activités du bétail dépendaient de différents facteurs environnementaux, (2) que pour expliquer la distribution du broutage, les structures induites par la gestion (barrières, points d'eau) étaient plus importantes que les structures naturelles alors que l'inverse était vrai pour les deux autres activités, (3) et que la distribution des bouses était dominée par des structures spatiales à large l'échelle, alors que le broutage s'expliquait par des structures à échelle moyenne et le piétinement par des structures à échelle fine. Des différences systématiques dans les distributions spatiales et saisonnières des activités du bétail peuvent donc conduire à des interactions complexes avec la végétation. Dans un environnement hétérogène, comme le sont les écosystèmes sylvopastoraux, des modèles spatialement explicites de la dynamique de la végétation doivent considérer séparément le broutage, le dépôt de bouses et le piétinement.

Nous avons choisi une approche expérimentale pour explorer les effets des activités du bétail sur la végétation herbacée à échelle fine. Dans deux sites, nous avons sélectionné trois types de communauté végétale dépendants de conditions de lumière différentes mais sur un sol et à une altitude similaires. Les sites expérimentaux ont été clôturés pour que le bétail n'interfère pas dans les expériences et un total de 88 carrés permanents de 4 m^2 ont été définis. Sur les carrés permanents, nous avons simulé les trois activités du bétail: (1) fauche répétée avec trois niveaux; (2) piétinement intensif avec deux niveaux; (3) engraissement avec du purin selon trois niveaux. Ces trois facteurs ont été combinés en différents traitements. Durant

3 ou 4 ans, les traitements ont été appliqués de façon homogène sur la surface de chaque carré permanent durant les périodes estivales. De plus, en dehors des zones clôturées, des carrés permanents ont été définis pour observer l'évolution de la végétation en présence d'une activité naturelle du bétail. La réponse de la végétation aux traitements a été suivie deux fois par an, au printemps et en automne, avec la méthode des points-quadrats. Des analyses multivariées sur les données de végétation de la première année d'observation ont montré un changement saisonnier clair et des différences significatives induites par les traitements. Les carrés permanents sans aucun traitement et uniquement engraissés ont montré les plus grands changements par rapport aux carrés permanents dans des conditions d'activité naturelle du bétail. Le broutage, simulé par une fauche fréquente, était le facteur le plus important pour maintenir la texture de la végétation. Les effets saisonniers des traitements étaient partiellement effacés au second printemps, démontrant une inattendue résilience de la communauté végétale, probablement due aux caractéristiques des plantes et à la baisse de la compétition suivant la perturbation de la neige en hiver. Les résultats sur l'ensemble de la durée des expériences (3 ou 4 ans) montrent que les effets des traitements sur la biomasse et sur la hauteur de la végétation ont été similaires pour les trois types de communautés végétales dépendants de conditions de lumière différentes. Contrairement à cela, la succession végétale induite par les traitements et l'importance de chaque traitement pour expliquer cette succession différaient d'une communauté à l'autre. Chaque communauté présentait des propriétés dynamiques très intéressantes. En condition de fort ombrage, les traitements ont induit une dynamique plus lente que celle observée dans des milieux plus ouverts, dans lesquels les communautés ont montré une résilience par rapport aux perturbations. La dynamique engendrée par les perturbations pouvait être principalement expliquée par la hauteur potentielle des plantes ainsi que par les grandes catégories taxonomiques (graminées, légumineuse, ligneux, etc.). Nos expériences ont donc démontré clairement que les trois activités du bétail génèrent des dynamiques différentes dans la végétation herbacée des pâtures à l'échelle des espèces et des groupes fonctionnels. Nos résultats ont révélé une très grande complexité avec des espèces réagissant de manière multiple en fonction des perturbations et de leurs interactions. Par ailleurs, la complexité est encore supérieure en conditions naturelles dans lesquelles les trouées formées par un piétinement important (qui n'était pas simulé dans nos expériences) induisent une dynamique différente et où les conditions du sol varient rapidement à petite échelle.

L'effet des traitements simulant les activités du bétail sur les communautés bactériennes a aussi été exploré. De plus, nous avons comparé l'effet des traitements sur les communautés bactériennes avec les effets des propriétés du sol et de la végétation. À la fin des expériences (c.f. ci-dessus), des profils de communautés bactériennes (Biolog Ecolpate™) ont été mesurés pour les carrés permanents qui étaient dans deux conditions de lumière (peu d'ombre et très ombragé). Les propriétés du sol (pH, carbone organique total, azote total et phosphore total), la composition floristique et la biomasse végétale ont aussi été déterminées. Les résultats ont montré premièrement que malgré d'importantes différences dans la composition floristique et dans les

propriétés du sol, le potentiel métabolique de la communauté bactérienne était très similaire dans les deux conditions de lumière. Dans les deux cas, l'activité bactérienne était affectée par la fauche répétée et la fertilisation n'avait pas d'effet significatif. La principale différence entre les deux conditions de lumière était que pour les carrés permanents avec le plus de soleil, la végétation expliquait une grande proportion de la variation de la communauté bactérienne alors qu'aucune relation significative apparaissait à l'ombre. Les trois perturbations induites par l'activité du bétail influencent donc les communautés microbiennes du sol et l'importance de ces facteurs dépend des conditions de lumière à l'intérieur des pâturages boisés.

La colonisation de trouées artificielles en fonction de l'effet des traitements simulant l'activité du bétail a aussi été étudiée. Les résultats ont démontré qu'à l'échelle du mètre carré les trouées n'avaient presque pas d'influence sur le nombre d'espèces même si cette perturbation détruisait 40 % de la végétation. L'impact de cette perturbation sur le nombre d'espèces n'était perceptible qu'à l'échelle de la trouée (quelques dm^2). La colonisation des trouées a affecté la contribution relative des espèces dans la communauté et cet effet a persisté jusqu'à la fin de l'expérience (3 ans) principalement au centre de la trouée. La composition spécifique de la trouée était une liste appauvrie des espèces présentes autour de celle-ci et seulement quatre nouvelles espèces sont apparues. Les caractéristiques des plantes favorisées par la trouée étaient un faible poids des graines, un mécanisme de dispersion des graines non spécialisé, une banque grainière persistante et une grande propagation latérale. Un effet de bord important a été observé. Il y avait une très grande similarité entre les espèces présentes dans la trouée et les espèces directement sur les bords de la trouée. Nos traitements simulant l'activité du bétail n'ont pas un joué un rôle prépondérant dans la recolonisation des trouées. Il semble que les contraintes imposées par la trouée sont plus importantes que celles induites par les traitements. Néanmoins, des différences entre les traitements sont apparues de manière secondaire. Les trouées combinées avec l'activité du bétail induisent donc des interactions complexes avec la végétation participant ainsi au maintien de la biodiversité importante des pâtures.

Pour suivre l'évolution de la végétation en présence de l'activité naturelle du bétail, nous avons suivi l'évolution saisonnière de la végétation à l'aide d'une grille de cellules. Nous avons défini quatre carrés permanents dans quatre communautés herbacées caractéristiques des pâturages boisés: un pré pâturé eutrophe, un refus temporaire, un sous-bois et une pelouse oligotrophe. Les carrés permanents consistaient en des grilles de 1 m^2 subdivisé en 100 cellules carrées de 1 dm^2. Une fois par mois entre mai et septembre, nous avons estimé, dans chaque cellule de chaque carré, la dominance et la présence de trace de broutage pour toutes les espèces présentes. Nos résultats ont montré que les changements saisonniers étaient très importants et dépendants de l'échelle. Les changements à l'échelle du carré permanent étaient principalement d'ordre phénologique. Par contre à l'échelle de la cellule, les changements étaient beaucoup plus importants suggérant une très grande dynamique des espèces à échelle fine. Malgré ces changements importants à l'échelle de la cellule, la structure spatiale de la communauté ne variait pas et le nombre d'espèces par cellule ne montrait aucune tendance. Nous n'avons pas

trouvé de corrélation entre le turnover à l'échelle de la cellule et l'importance de l'activité du bétail. La dynamique interne des communautés végétales à échelle fine semble donc plus influencée par les caractéristiques intrinsèques de la communauté que par les perturbations du bétail. De plus, à l'échelle de la saison, les communautés peuvent être stables dans leur structure en dépit de fortes variations dans leur texture.

Nous avons aussi exploré à l'échelle du dm^2 et du mois, la dynamique de la végétation induite par les bouses. Nos observations ont démontré que dans un premier temps à très court terme (quelques jours) les bouses généraient une augmentation de la biodiversité. Durant cette étape, la végétation était toujours basse et il y avait un grand apport de nutriments. Des conditions favorables pour de nombreuses espèces étaient ainsi créées. Dans un second temps, le bétail évitait de brouter autour des bouses. Cela permettait aux espèces présentes de croître sans perturbation et de devenir plus grandes que la végétation alentour. Durant cette étape, la végétation autour de la bouse a légèrement changé. Cependant ces changements étaient principalement d'ordre quantitatif et n'étaient pas accompagnés par des changements importants de la composition floristique. Le dépôt de bouses joue donc un rôle important dans les pâtures en changeant l'équilibre entre les espèces et en maintenant ainsi certaines espèces dans la communauté.

En conclusion, à partir de l'ensemble des résultats de cette thèse, nous avons défini six groupes d'espèces réagissant de manière différente aux activités du bétail et nous proposons un modèle qualitatif de la dynamique de la végétation en pâturage boisé basé sur des groupes fonctionnels d'espèces. Finalement nous discutons de quelques implications de nos résultats pour la gestion des pâturages boisés et proposons quelques pistes pour de futures recherches.

Mot-clés: Activité du bétail; Analyses multivariées; Biodiversité; Broutage; Caractéristiques des plantes; Changements saisonniers; Communauté végétale; Conditions de lumière; Dépôt de bouses; Dynamiques de la végétation; Echelles spatiales et temporelles; Ecosystèmes sylvopastoraux; Expériences en champs; Fertilisation; Jura suisse; Mobilité des plantes; Piétinement; Stratégies C-S-R; Suivi spatial.

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CHAPTER 1

General introduction

1. General introduction

This general introduction will firstly present the ecological context of this thesis with an overview on wooded pastures in the Swiss Jura Mountains, showing their originality in terms of management and vegetation structure. Secondly, it will focus on ecological questions and concepts directly linked to the topic of this thesis: (1) relations between cattle activity and herbaceous vegetation, (2) plant succession, vegetation processes, disturbance and stress and (3) plant functional classification. Finally, it will introduce the main objectives and the outline of this dissertation.

1.1. *Wooded pastures*

Seminatural, silvo-pastoral ecosystems, such as wooded pastures, woodland pastures or grazed forests, form traditional landscapes in Europe (Etienne 1996). Influenced by a combined action of cattle grazing and forest management, the wooded pastures represent a form of multiple use of natural resources. This is particularly interesting when considering the efforts and challenges of a sustainable management of mountain areas. Wooded pastures must not be mistaken for agroforestry systems, where all trees are planted and grass is sown. In typical wooded pastures, the regeneration of both grassland and woodland is natural. Most of these silvo-pastoral ecosystems in Europe suffered a dramatic decline during the last century, due to changes in agricultural management towards local intensification or extensification. Nevertheless, in certain regions like in the Swiss Jura Mountains (Figure 1.1), wooded pastures are still the most abundant type of man-made landscape (Rieben 1957; Gallandat et al. 1995).

Wooded pastures in the Swiss Jura Mountains (photos are presented in Appendix Ia) occur principally between 800 m and 1400 m a.s.l. They occupy a transition zone between the cultivated areas close to the villages and the forest, normally at the foot of the Swiss Jura Mountains hills as well as on the ridges near the tree line (Gillet and Gallandat 1996a). Wooded pastures tend to develop on moderate to steep, sunny slopes. Climate in the Swiss Jura Mountains is predominantly oceanic with a mean of annual rainfall of about 1600 mm at 1200 m a.s.l. (with more than 400 mm snow precipitation)

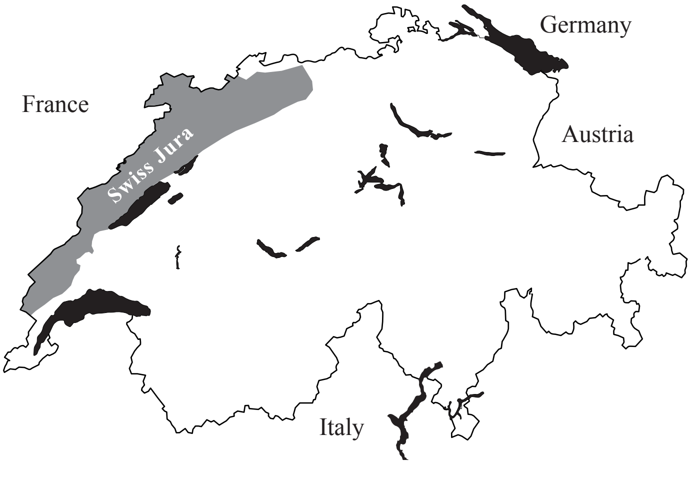

Figure 1.1: Geographical situation of the Swiss Jura Mountains.

and a mean annual temperature of 7°C. Mean day temperature is below 0°C on more than 60 days per year at this altitude and the ground is generally covered with snow from November to April.

Like in other temperate mountains regions the climate induces a reduced (Dullinger et al. 2003) cattle management limited to the summer period. Therefore, cattle is present on the pastureland from the end of May till the end of September. Cattle herds are mainly composed of heifers, but dairy cows can be seen on about half of the pastures and in some areas horses can be the principal domestic animal. Live stock density ranges from 0.5 to 1.5 adult bovine-unit/ha (Gillet and Gallandat 1996a), which is low compared with intensive grazing systems. For a farm-unit, surface occupied by pastures ranges from about 30 ha to about 300 ha. Two systems of grazing are applied in this type of wooded pastures (Gillet and Gallandat 1996a): (1) free range: the animals spend the whole summer season roaming freely through the pastures; (2) grazing rotation: the pasture is subdivided in paddocks; the animals pass from one paddock to another according to a variable rotation period (between 2 and 7 rotations per season, corresponding to a stay in each paddock of 10 to 80 days). More and more wooded pastures are now managed according to the rotation grazing system.

Generally, pastures receive fertiliser based on farm manure and commercial PK fertilisers (Meisser 1993). In addition, mineral nitrate is often used on pastures grazed in rotation by dairy cows. For the maintenance of the pasture unpalatable herbs (*Cirsium* sp., *Gentiana lutea*, *Rumex* sp.) and shrubs (*Rubus* sp., *Rosa* sp.) are partially cleared more or less regularly using mechanical or chemical means, in order to prevent loss of grazing area.

Foresters intervene in wooded pastures mainly to remove dying or affected trees and to check on re-growth. In general, the wood is not of high quality and does not cover the costs of removing it. The stumps are usually left on place. This creates together with the presence of thorny bushes and bramble (*Rubus* sp.) a favourable microenvironment, facilitating the re-growth of young trees. If natural regeneration fails, new saplings may be planted, usually around the stump, and fenced for protection against cattle. The forester's personal experience and local tradition play an important role in planning spatial distribution of trees (groups of trees against isolated ones) (Gillet and Gallandat 1996a).

From a socio-economic point of view, the main users of wooded pastures are farmers, even if in some regions revenues generated from forestry activities may be quite significant. Besides the farmers and foresters, a wide variety of occasional users become more and more important: walkers, skiers, horse riders, cyclists, picnickers, etc. The importance of this landscape for the tourist economy is considerable, although difficult to measure.

Vegetation of wooded pasture can be structurally defined as a complex mosaic of trees, shrubs and open grassland. This structure causes a very high vegetation heterogeneity and biodiversity, which is even more pronounced by a heterogeneous soil mosaic (Gobat et al. 1989; Havlicek et al. 1998). To describe this complex vegetation structure, Gillet and Gallandat (1996b) distinguish three organization levels (Figure 1.2):

- Level 1 consists of elementary plant communities, which are one-layered, floristically, physiognomically and ecologically homogeneous vegetation units (*Synusiae* (Barkman 1973) of trees,

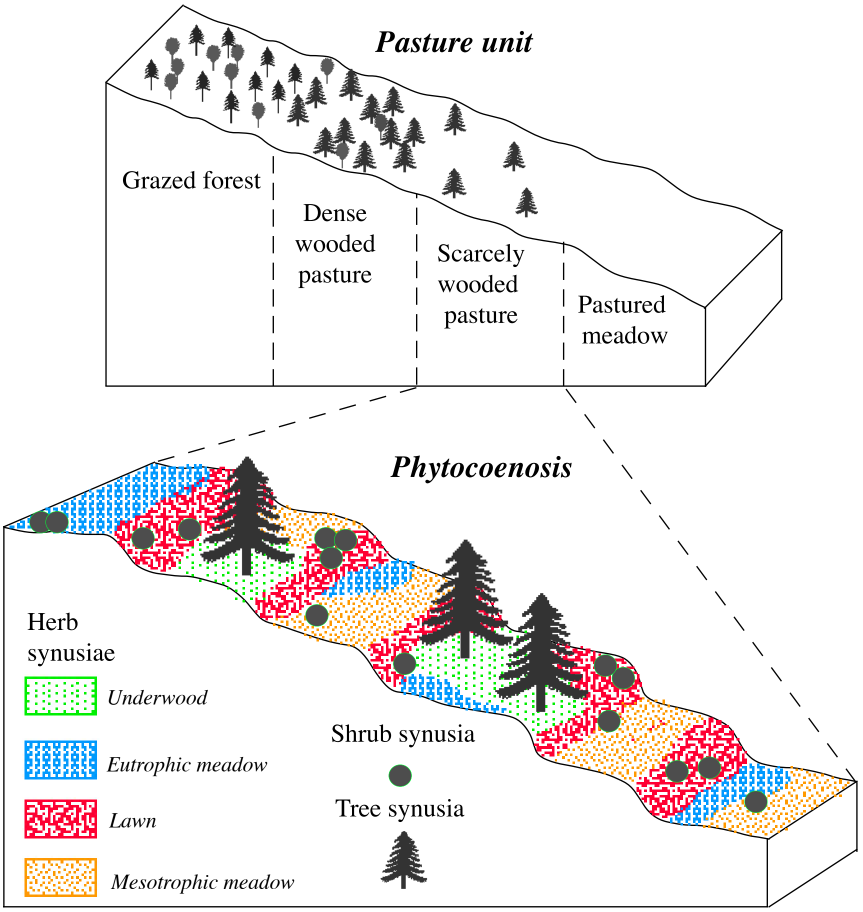

Figure 1.2: The different vegetation organisation levels of wooded pastures (adapted from Gillet and Gallandat 1996b).

shrubs, herbs and mosses). These communities are directly linked to uniform environmental conditions (microclimate, microtopography, soil, biotic factors).

- Level 2 (*Phytocoenosis* (Barkman 1973)) consists of complex structures of *synusiae*, which are functionally strongly linked both in space (mosaics, stratification) and time (seasonal aspects, regeneration cycles) (Figure 1.3).
- Level 3 consists of a mosaic of *phytocoenoses* (from non-wooded pastures to grazed forest), which interact through the system of grazing (paddocks, pasture units).

In a study including a comprehensive vegetation sample of Swiss Jura Mountains wooded pastures, Gallandat et al. (1995) described 96 types of synusiae (16 of tree, 15 of shrub, 54 of herb and 11 of epigeic moss vegetation). Furthermore, they established qualitative models to describe relations in space and time between synusiae of a phytoceonosis (Figure 1.4). Relations were deduced from a complex set of both natural (geo-morphology, soil and climate) and human factors (tree cover, grazing intensity and fertilisation) and based on a synchronic vegetation description.

Due to economical constraints, mountain agricultural practices changed during the last decades. Maximising productivity and simplifying management was promoted, by

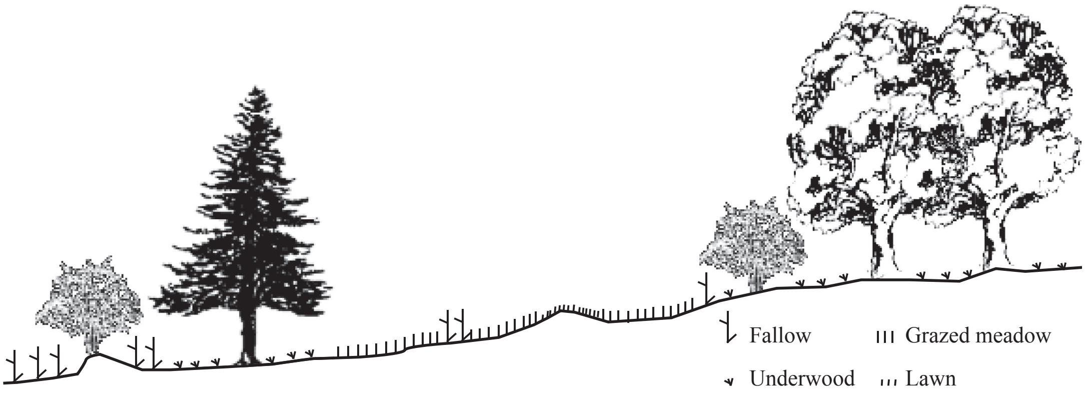

Figure 1.3: Simplified spatial organisation of the complex of synusiae in a phytocoenosis. Example of a scarcely wooded pasture (adapted from Gallandat et al. 1995).

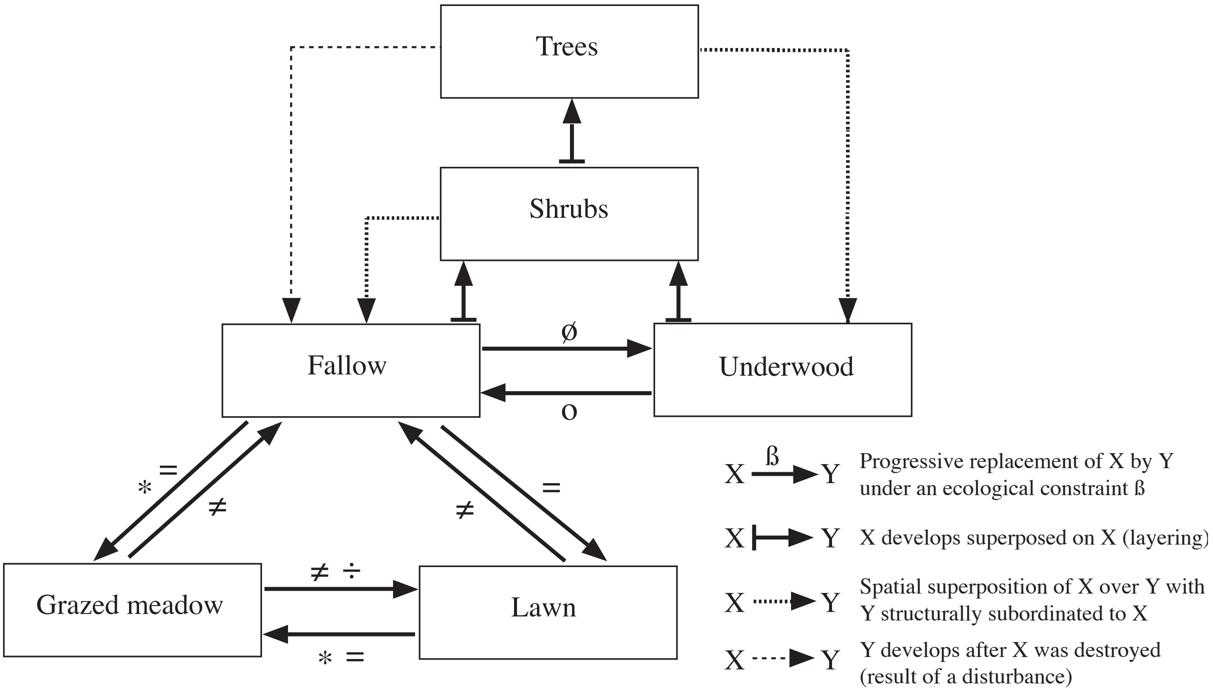

Figure 1.4: Formal structure (qualitative model of organisation) for a wooded pasture (adapted from Gallandat and Gillet 1999). Ecological constraints: o: light increase; ø: light decrease; *: soil nutrients increase; ÷: soil nutrients decrease; =: trampling, browsing (grazing increase); ≠: grazing decrease.

separating forestry and cattle management. Moreover, the number of heifers going on summer pastures in Switzerland decreased from about 280'000 in 1975 to about 200'000 in 2000 (Swiss Federal Statistical Office). This led to more intensive and concentrated low-wooded grazing areas. Vast areas of former pastures overgrew with shrubs and young trees. Fortunately the situation in the Swiss Jura Mountains is not critical yet and is not too late to conserve this attractive landscape with a high ecological value.

Integrated management planning of wooded pastures requires an intensive collaboration between agronomists, foresters and ecologists (Rieben 1957; Wettstein 1983; Gmür and Wettstein 1986; Gmür et al. 1989; Perrenoud et al. 2003). In this ecosystem, the question of management type and intensity is fundamental. The current political and ecological context motivates exploring new forms of use (Etienne 1996). Strategic objectives of management may aim to the conservation of the state of wooded pastures, or to more or less severe interventions, even through re-creation of wooded pastures starting from forests or grasslands. Successful management, in particular for biodiversity conservation, requires further traditional scientific experimentation and is generally not yet founded on specific scientific tests, but based on anecdotal evidence or, at best, on empirical studies (Rook et al. 2004).

1.2. Cattle activity and herbaceous vegetation

Spatial patterns of vegetation in pastures are strongly directed by human and cattle activity (Olff and Ritchie 1998; Olff et al. 1999). The role of grazing by large herbivores in ecosystem processes and particularly their relation to vegetation structure and processes was the topic of numerous recent studies with a wide variety of objectives: e.g. relations between grazing distribution pattern and vegetation or landscape structures (Senft et al. 1987; Bailey et al. 1996; Parsons and Dumont 2003), effects of grazing on plant community composition (Schläpfer et al. 1998; Jutila 1999; Krahulec et al. 2001), effects of grazing on tree regeneration (Hester et al. 1996, Humphrey and Swaine 1997), grazing and primary productivity (McNaughton 1985), the role of herbivore in controlling plant species richness (Collins et al. 1998; Olff and Ritchie 1998; Poschlod et al. 1998; Bartolomé et al. 2000; Rook et al. 2004), the impact of different herbivores on vegetation dynamics (Damhoureyeh and Hartnett 1997; Bakker and Olff 2003), the impact of herbivores on the nitrogen cycle in grasslands (Berry et al. 2003; Bakker et al. 2004), the role of grazing in nature conservation and extensive land use in Europe (van Wieren 1995), mechanisms by which large grazers establish and maintain heterogeneity and structural diversity in the vegetation (Bullock et al. 1995; Olff et al. 1999; Adler et al. 2001; Bakker et al. 2004), plant population and livestock movement (Malo and Suarez 1995; Fisher et al. 1996), the identification of plant functional groups related to grazing (Noy-Meir et al. 1989; McIntyre and Lavorel 2001), dynamic modeling of the relation between herbivores and vegetation (Bergez et al. 1999; Gillet et al. 2002).

Most authors are interested in the global effect of cattle (or other large herbivores) activity and consider grazing as a single variable, depending on the overall stocking rate. However, it seems clear that if interested in the internal vegetation dynamics of a pasture, cattle activity must be considered as a source of various types of disturbance or stress (Schläpfer et al 1998; Bakker and Olff 2003; Rook et al. 2004). Consequently, it is possible to subdivide cattle activity into three categories of disturbance or stress: herbage removal, dunging and trampling. Moreover, heavy trampling may create gaps.

1.2.1. Herbage removal

Herbage removal – or grazing *sensu stricto* – is the main biotic factor affecting vegetation structure and dynamics in pastures (Rook et al. 2004) and has been investigated in many experimental studies (e.g. Belsky 1992; Diaz et al. 1992; Milchunas and Lauenroth 1993; Cooper and Huffaker 1997; Schläpfer et al. 1998; Birch et al. 2000). Grazing changes the arrangement of photosynthetic structures in communities with consequences on different scales. On a broad scale, growth forms of the component species are of major importance for predicting community responses to physical factors and to disturbances (Pickett and White 1985). On a finer scale, the plant form is influenced by a trade-off between competition and convergence, and thus reflects the plants niche. External biotic factors result in convergent adaptations of target populations, linked in this way by common requirements. Given a particular intensity of grazing pressure, some plant populations may be unable to persist, whereas others may continue to exist, either because the individuals manage to capture sufficient light while maintaining their original growth forms, or because they substantially modify their original growth forms (Gómez Sal et al. 1986).

Field experiments in Mediterranean pastures (Hadar et al. 1999) showed grazing being a selective agent, favouring small grasses, geophytes and species with early flowering. Selective grazing by cattle was studied by Guevara et al. (1996) in an experiment on the response of perennial grasses to rotation and continuous grazing systems. Diaz et al. (1992) considered grazing as a disturbance and applied multivariate ordination and classification techniques to define vegetation traits, following a morphology-based approach at three levels (spatial structure of the vegetation, identification of morphological plant groups and quantification of morphological shifts). Hulme et al. (1999) investigated vegetation changes in acidic grasslands using three treatments (normal, heavy and light grazing) over seven years. They emphasised the need to take into account both the initial composition of the vegetation (species present) and the overall productivity of the site.

1.2.2. Dunging

Dunging – or, more widely, fertilising – is also considered as an important factor affecting vegetation changes in herbaceous or dwarf-shrub communities (Sougnez 1965; Bakker and Olff 2003). Statistical comparisons between primary productivity and species richness across various community types generally lead to a “hump-shaped” model, with a peak of richness at a low to intermediate level of productivity (Grime 1973a and b). Other studies showed consistently unimodal relationships (Moore and Keddy 1989), especially in plant community comparisons (Grace 1999). Thus, fertilisation effects in plant communities based on field experiments often conclude on a negative linear correlation between the relative aboveground net primary production and the relative species density. However, considerable variation often characterises the magnitude of responses (Gough et al. 2000). Initial species composition is a key factor in the community response. This response might be particularly strong when different life forms or functional groups co-exist. In a short term, the initial floristic composition determines which species remain present, but in the longer scale the species composition is determined more by the environmental regime (kind and intensity of fertilising) than by initial conditions (Hill and Carey 1997).

Many authors studied effects of dung deposition on the soil fertility and on plant communities. The deposition of the dung represents a potential source of N and other nutrients (Shepherd et al. 2000; Aarons et al. 2004). MacDiarmid and Watkin (1972) showed a significant increase of N, P and K around dung patches. This increase could be measured till 15 cm around the dung patches (MacDiarmid and Watkin 1972; Deenen and

Middelkoop 1992). Twelve months after dung application, Williams and Haynes (1995) observed soil organic C, nitrate and phosphate still being higher in dung patches compared to control patches. Some residual effect of organic C was still measurable three years after cattle dung application.

Dung plays an important role in the dynamics of plant communities in pastures. Initially cattle dung is detrimental to herbage growth, because of smothering. Being covered for several weeks by the dung patch, the affected plants probably die from a lack of light (Williams and Haynes 1995). This smothering is compensated by an increased plant growth around the dung patches (Borghesio et al. 1999). The effect decreases with distance, but may extend as far as 40 cm from the edge of the patch (MacDiarmid and Watkin 1971). Furthermore, many authors showed the importance of dung for seed dispersal, germination and soil seed bank composition, which induces also changes in vegetation composition (Welch 1985; Akbar et al. 1995; Malo and Suarez 1995; Dai 2000; Bakker and Olff 2003). Dai (1998) showed that patch size of some plant species in alvar limestone grasslands were similar to the average size of a cattle dung patch, suggesting a correlation between species and dung patches.

1.2.3. Trampling

Trampling affects the vegetation through detaching or destroying plant material with hoof action and by influencing the water regime in firming the soil (Abdelmagid et al. 1987). By contrast to herbage removal, biomass is in this case stays on the ground and nutrients then return to the soil. In experimental studies, trampling is often considered as a disturbance. Vegetation changes in various community types have been interpreted according to the concept of resistance (ability to resist the 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 different components of stability (Cole 1995b). Plant morphological characteristics (vegetation stature, erectness, life form) explain more of the variation in response to trampling than the site characteristics do (altitude, overstorey canopy cover, total groundlayer vegetation cover). Trampling can also be regarded as a constraint, if its regularly repeated action does not induce severe changes in species assemblage and if species are adapted to this stress factor. In this case, one can experiment the response of the same community type to different trampling intensities and frequencies, independently of other biotic factors (Guthery and Bingham 1996).

1.2.4. Gap creation

Heavy trampling can create gaps. For a floodplain meadow occupied by cattle, mole and rabbits, Bakker and Olff (2003) conclude that gaps are almost exclusively created by animals. In that case rabbit and mole burrowing activity mainly caused gaps. Gap creation is a major disturbance factor participating in the dynamics of a wide range of plant communities, like forests (e.g. Hubbel et al. 1999; Wright et al. 2003) or grasslands (e.g. Williams 1992; Lavorel et al. 1994; Vandvik 2004). By removing biomass, this disturbance reduces competition intensity and allows poor competitor species to persist in the community, if they colonise the gap first (e.g. Hobbs and Hobbs 1987; Tilman 1994). Moreover, Suding and Goldberg (2001) pointed out that beyond removing biomass, gap creation could change the abiotic and biotic environment in many different ways: soil compaction, microtopography, herbivores, diseases, mycorrhizae, and many others. Suding (2001) concluded that gap creation might affect species competitive hierarchy, possibly due to changes in the environment, where the interactions occur and not only due to competitive reduction. By contrast with forest vegetation, where most gap colonists are of seed origin (Brokaw and Busing 2000 but see Pontailler et al. 1997), colonists of gaps in perennial grasslands can be of seed or clonal origin (Bullock et al. 1995). The high proportion of species with clonal reproduction in grasslands (Klimes et al. 1997; Tamm et al. 2001) points to a high possibility for adult plant to colonise gaps by clonal growth. Furthermore, many studies have shown a high small-scale turnover and spatial dynamic of plant species, even in undisturbed vegetation (e.g. van der Maarel and Sykes 1993; Otsus and Zobel 2002). Proportion between seed-derived and clonal colonisation varies according to gap size. Extended gap size increased the density and size of seed-derived plants (Bullock et al. 1995; Rogers and Hartnett 2001; Vandvik 2004). It is thus clear that the ability of species to colonise gaps, depends of regenerative traits. Trait attributes may be advantageous in closed canopy, but are not necessarily an advantage for gap colonisation. Consequently, plant species often occur with a different relative frequency in recently colonised gaps, than in the surrounding vegetation (Martinsen et al. 1990; Bullock et al. 1995). It is evident that gap colonisation is potentially an important source of vegetation change in grasslands. These communities can be seen as patchworks of microsites in different stages of re-vegetation (Vandvik 2004). At landscape and long time scale, this small scale disturbances appear effective in maintaining a high plant diversity as a result of the interplay of differences in regeneration niches, lottery for establishment and the incidence of different conditions in time and space (Lavorel et al. 1994).

1.2.5. Spatial pattern of herbage removal, dunging and trampling

There is evidence that the three types of activities are spatially heterogeneous and not congruent at landscape and very fine scale (Rook et al. 2004).

At landscape scale, according to Rice et al. (1983), the selection of grazing locations by cattle depends on herbage density, water availability, relief, slope, elevation, aspect, natural and artificial barriers, herd social interactions, prior experience and climate. The spatial pattern of foraging is the best-studied attribute of cattle activity (Senft et al. 1987; Coughenour 1991; Bailey et al. 1996; Rook et al. 2004). Cattle preferentially graze certain plant communities (Roath and Krueger 1982). These preferences seem to be the main cause of the distribution of cattle in a paddock (Van Rees and Hutson 1983; Senft et al. 1985; Putman et al. 1987). The choice of the community type and consequently cattle distribution is expected to be highly influenced by the nutritive value of plant species (Osuji 1974; Anderson and Kothmann 1980). Pinchak et al. (1991) concluded that apart from water source and physiographic complexity, forage characteristic is a good predictor of cattle habitat use. Loehle and Rittenhouse (1982) found it unrealistic to predict habitat use from forage quality exclusively. They suggested that, particularly in large pastures, other factors such as distance from fences or water availability could affect cattle behaviour. At the landscape scale, abiotic factors act as constraints for the biotic factors, operating at the finer scale (Bailey et al. 1996).

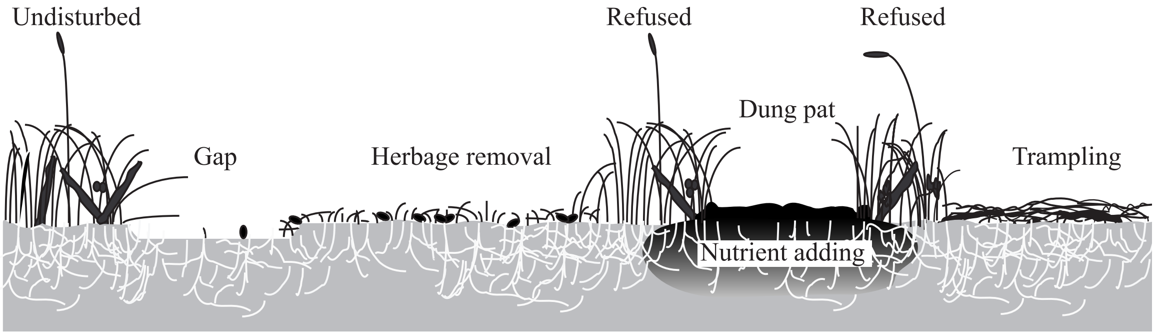

Figure 1.5: Schematic profile of fine scale vegetation heterogeneity induced by cattle activities.

The spatial distribution of faeces and urine from cattle is not uniform and their concentration is often higher in areas of special attraction, such as around water sources, gates, fences, shade and shelter belts (Petersen et al. 1956; Marsh and Campling 1970; Peterson and Gerrish 1996; White et al. 2001). In mountain regions, cattle faeces distribution patterns are significantly associated with slope, aspect, hydrological position and season (Tate et al. 2003). Daily faecal load is higher in flat areas (Costa et al. 1990) and is lower during the wet season compared to the dry season. Observations from dairy cows in an intensive, rotationally stocked pasture showed the number of defecations and urinations being highly correlated with the time spent in those areas (White et al. 2001). Manure concentration was higher around the water tank, especially during warm-weather periods.

The distribution of trampling effects not only depends on cattle behaviour, but also on slope and soil characteristics, such as texture, water content, etc. On steeper ground grazed by sheep and red deer, Hester and Baillie (1998) found that at low densities, the impact of trampling on vegetation is more important than the effect of herbage removal.

At a very fine scale (less than 1 m^2, bite and feeding station *sensu* Bailey et al. 1996), nutrients adding by dung and urine deposition, are not evenly distributed over the pasture, but applied in small areas at high concentrations (MacDiarmid and Watkin 1972). Dung patches induced also at this scale, reduction of the herbage attractiveness during the first months or years after deposition (Edwards and Hollis 1982) and consequently provoke a heterogeneous pattern of herbage removal. Finally, effects of trampling are higher on preferential cattle paths, on slope and on soil with high water content. Pastures can therefore be seen as a fine patchwork of various disturbances or as a combination of disturbances from cattle activities (Figure 1.5 and photos in Appendix Ia), which induce various vegetation dynamics. This spatial heterogeneity at various scales of the three activities causes a very complex pattern of disturbances on the vegetation, which may change from year to year.

1.3. Plant succession, vegetation processes, disturbance and stress

Plant succession is the progressive replacement of communities or species through time (Clements 1916; Lepart and Escarre 1983). Since the mid-1970s two major conceptual trends have dominated research in vegetation dynamics science (Glenn-Lewin et al. 1992): (1) a shift away from holistic explanations of successional phenomena (Clements 1916; Margalef 1968; Odum 1969) towards reductionist and mechanistic approaches, emphasising direct causes of vegetation change; (2) a shift away from equilibrium towards non-equilibrium paradigms (Picket and White 1985). The present paradigm rather focuses on inductive forecasting, than on deductive predicting. Succession is regarded as a population process, emphasising life histories and competitive interactions of the component species within fluctuating environmental conditions, rather than the emerging properties of communities (Peet and Christensen 1980; Picket et al. 1987). The role of disturbances and other stochastic processes is often asserted to explain divergent successional patterns (Glenn-Lewin 1980; Picket and White 1985).

Following Grime (2001), vegetation dynamics can be predicted and explained by recognising the importance of habitat productivity, the frequency and severity of biomass destruction during the evolution and in the current ecology of plant species. Grime (2001) classified external factors acting on vegetation dynamics into two categories. The first, defined as stress, consists of the phenomena restricting photosynthetic production, such as shortages of light, water and mineral nutrients or sub-optimal temperatures. The second, defined as disturbance, is associated with partial or total destruction of the plant biomass and arises from the activities of herbivores, pathogens, man (trampling, mowing, and ploughing) and from other phenomena, such as wind-damage, frosting, droughting, soil erosion and fire. The difference between stress and disturbance (*sensu* Grime) is, however, discussed controversially in ecological literature. Most of the experimental studies implicitly or explicitly consider biotic factors, like grazing, trampling or dunging, as disturbances. However, they might better be considered as stress factors, when acting permanently or regularly on adapted plant communities (van der Maarel 1993). These concepts are strongly scale-dependent (Pickett et al. 1989) and the same factor can act as a disturbance (accidentally destroying biomass) at the individual level and at short-term or as a stress factor or constraint (permanently limiting biomass production) at the community level and on longer terms.

Interspecific competition is often considered as a key process in vegetation dynamics at the community level depending strongly on nutrient availability (Grime 1987; Tilman 1988; Aerts 1999). In nutrient-rich environments, competition is mainly for light. Plant communities are therefore dominated by fast-growing perennials with a tall stature, a rather uniform vertical distribution of the leaf area and a high turnover of leaves and roots (growth rate strategy). In nutrient-poor environments, competition is mainly for nutrients and plant communities are dominated by traits reducing nutrient losses (nutrient retention strategy). A positive feedback occurs between species dominance and nutrient availability, thereby promoting ecosystem stability.

How can up to 40 plant species coexist on 1 m^2 of grassland? This is a key question in modern plant ecology. Braakhekke (1980) described three different ways of coexistence: (1) true coexistence, where functional differences between species enable to exist simultaneously in a homogeneous environment; (2) non-equilibrium coexistence, where continuous immigration and extinction take place in a homogeneous environment and (3) non-coexistence equilibrium, where species occur in different microhabitats within the same community. Grime (2001) described coexistence in relation to horizontal, vertical and temporal variation in the environment and discussed it with his model of competitors, stress tolerators and ruderals. Gigon and Leutert (1996) proposed the dynamic keyhole-key model to explain coexistence. In this model the plant species corresponds to the key and the microsites to the keyholes, which are mostly biogenic (excreta, gaps, feeding place). Where species diversity and microsite diversity match, coexistence can occur. For productive meadows, both theoretical (Palmer 1994) and empirical studies (Kull and Zobel 1991; Güsewell et al. 1998; Schläpfer et al. 1998) suggest the most important factor responsible for the long-term maintenance of species richness is regular removal of above-ground biomass, either by mowing or grazing. Klimes and Klimesova (2002) concluded that the usually dominating taller plants are selectively suppressed by mowing. Thereby plant coexistence is promoted potentially.

The stability of a plant community can be defined from four different points of view (Burrows 1990; van der Maarel 1993): constancy (no change in species composition and structural characteristics), persistence (survival of populations over a period of time), inertia (ability of the community to recover from disturbances) and resilience (the speed at which the community returns to its initial state). These aspects are scale-dependent, both in space and time. A fluctuation is defined by van der Maarel (1993) as any change in the environment absorbed by the community and not experienced as a disturbance. Mechanisms of small-scale fluctuations within plant communities can be different of mechanisms of large-scale successions (Watt 1947; Ritter and Mathieu 1972). Van der Maarel and Sykes (1993) showed that fluctuation might be detected at a small scale, but not on a larger one. This led them to the concept of cumulative species richness as a result of a small-scale turnover (carrousel model). Tilman (1997) showed in his invasibility experiment local biotic interactions and recruitment dynamics jointly determining diversity, species composition and species abundance in natural grassland communities. He stressed on the importance of a metapopulation-like perspective over a purely interspecific-interaction perspective or a purely regional perspective.

1.4. Plant functional groups and types

Following Colasanti et al. (2001) species belonging to the same functional group must share a single important attribute, which confers the similarity of function within the community (e.g. species with symbiotic atmospheric nitrogen fixation). A species may simultaneously be a member of several functional groups and interspecific differences may exist, both within and between such groups. In contrast, species comprising a functional type share the same collection of attributes. These, acting together, enable that type to function as no other can, even if the latter happens to exhibit some (but not all) of the same attributes. As the type is the higher level of organisation, each species can be a member of only one type[a].

Grouping species into functional types to describe and compare different structural states of plant communities has many advantages and complements usefully the species-based description of communities: (1) it reduces the number of components describing the community; (2) it allows a focus on the biological traits explaining dynamic processes; (3) it allows generalisations and world wide comparisons. For example, taxonomically distant species have convergent forms and behave as if they have similar roles

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[a] The difference between plant functional groups and plant functional types is not commonly agreed in the plant functional traits literature. This terminology is generally used more or less exchangeably.

and similar structural positions in the network of matter-energy processes. Additionally, communities from distant though ecologically similar sites may be different in floristic composition, but very similar in structure (Diaz et al. 1992). Other studies showed the existence of morphological differences among populations within the same species (Dirzo 1984; Schlichting 1986).

Many different classifications have been proposed so far, based on eco-physiological (life forms: Raunkiaer 1934), morphological (growth forms: Noble and Slatyer 1980; Barkman 1988; Noble and Gitay 1996), demographic (adaptive strategies, regeneration traits: van Steenis 1956; Grime 2001; Rameau 1987) or sociological (Julve 1989) criteria. However, for many authors a universal classification into functional groups does not exist or is irrelevant (Hadar et al. 1999). The trend is to replace *a priori* functional groups by *a posteriori* biological trait syndromes derived from experimental studies and based on response to disturbance (Diaz et al 1992; Lavorel et al. 1997; McIntyre et al. 1999; Lavorel and Garnier 2002; see Rusch et al. 2003 for an overview). Groups define by this approach are called “species response groups”. The main problem with this approach is to deal with the simultaneous analysis of data organised in three tables: (1) species composition (species by sample matrix), (2) environmental gradients (environment by sample matrix) and (3) functional attributes (species by attributes matrix). So far, no standard statistical method is recognised and many approaches have been published (Dolédec et al. 1996; Legendre et al. 1997; Lavorel et al. 1998; McIntyre and Lavorel 2001; Pillar and Sosinski 2003; Nygaard and Ejrnæs 2004). Recently Pausas and Lavorel (2003) and Suding et al. (2003) pointed up the importance to consider plant functional classification in a hierarchical way, focussing on the mechanisms acting at different levels of organisation.

The relevance of biological traits to characterise vegetation dynamics in response to natural and land use disturbances is now well established (e.g. McIntyre et al. 1999; Jauffret and Lavorel 2003; Rodiriguez et al. 2003 but see Vesk et al. 2004) and can be seen as a promising tool for new management practices (Gondard et al. 2003). Moreover, plant functional types can be used in dynamic modelling (Colasanti et al. 2001; Gillet et al. 2002). In that way plant functional types permit to construct relatively simple model of vegetation dynamics.

1.5. General objectives and outline

For a long time, wooded pastures have been ignored by phytosociologists and plant ecologists, because of their complex and heterogeneous structure, partially due to human multiple land-use. The research programme PATUBOIS (Gallandat et al. 1995) at the University of Neuchâtel revealed that this kind of complex ecosystem, if analysed with appropriate new tools, may serve as a model-systems to understand complex patterns and processes in semi-natural vegetation (§ 1.1). This programme provided large-scale records on silvo-pastoral ecosystems of the Swiss Jura Mountains, including useful phytoecological, agronomic and forestry data. This first general study was to be completed by precise experimental investigations on vegetation dynamics.

Many studies addressed the question of grazing, trampling or fertilising effects onto grassland, heathland or woodland communities (§ 1.2), but never considered the relative impact of these biotic factors

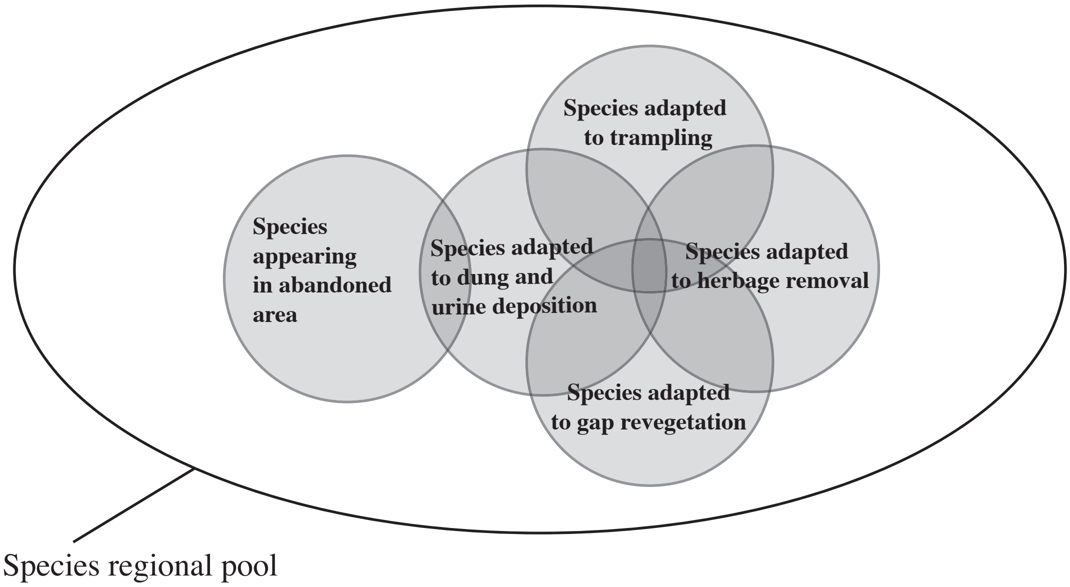

Figure 1.6: Schema of hypothetical plant functional types. In grey: species of wooded pastures.

and their mutual interactions for structuring the vegetation of silvo-pastoral ecosystems. Focussing on patterns and processes at short term and on synusia level, the present work will address these questions.

At a larger spatial scale, the balance between these combined factors induced by cattle activity may vary depending on the location within the pastoral unit and on the type of phytocoenosis, as well as on frequency, intensity and season of grazing. Additionally, site conditions, such as soil configuration, nutrient status or microclimate need to be examined. Thus, it will be examined how biotic factors and site conditions interact, in order to build up a dynamic scheme of the herbaceous vegetation within the context of silvo-pastoral ecosystems.

Dynamic modelling of silvo-pastoral ecosystems is recent and bases generally on lumped entities (tree, sward, livestock, ...) and simplified rules. PATUMOD (Gillet et al. 2002) was the first model designed to simulate *synusiae* replacement inside *phytocoenoses* of wooded pastures. This spatially implicit dynamic model at the *phytocoenosis* level needs now to be refined with sound experimental data, as well as to be complemented with a functional approach at the *synusia* level. Results from this work could then be used to develop a model of plant functional group dynamics inside herbaceous communities, built up and parameterised with the results of enclosure and exclosure experiments. Ultimately, this model should be integrated as a submodel in a more general model, to be developed in related projects.

The primary aim of this thesis was to assess the successional processes involving herbaceous vegetation within wooded pastures of the Swiss Jura Mountains in relation to cattle activity (herbage removal, dunging, trampling and gap creation) in various environmental conditions and degrees of tree cover.

General hypotheses were:

- Herbage removal, dunging, trampling and gap creation by cattle activity have various effects on vegetation dynamics
- These dynamics can be described

in term of plant functional types or groups (Figure 1.6).

- These dynamics vary according to the different community types building the mosaic of the herb layer.

The following chapters of this thesis are organised as follows (see Table 1.1 for an overview presenting the main questions):

Chapter 2 presents results of an observational study on spatial and seasonal patterns of herbage removal, dunging and trampling. Patterns are related to natural and management induced structure. The spatial aspect of these patterns is analysed.

Chapter 3 groups the results of exclosure experiments. The effects of simulated impacts of cattle activities (herbage removal, dunging and trampling) on vegetation dynamics of various plant communities at seasonal (§ 3.1) and year (§ 3.2) scale are described. Effects of simulated cattle activities on microbiological communities are also discussed (§ 3.3). Finally, recolonisation of artificial gap and role of cattle activities in this dynamic are explored (§ 3.4).

Chapter 4 presents observational studies on 1 dm^2 scale dynamics in grasslands. The spatial and temporal stability of some communities in pastured surfaces (§ 4.1) and the dung pats effects on vegetation are described (§ 4.2).

Finally **Chapter 5** integrates all results of the preceding chapters to get general overview of the relation between cattle activities and vegetation dynamics. Implications of the results for management of wooded pastures are also discussed and research perspectives proposed.

Table 1.1: Organisation of this thesis. Topics, main questions and approaches used to solve the addressed questions.

Topics	**Main questions**	**Approaches**	**Chapter**
Spatial pattern of cattle activities	How are the cattle activities related to landscape structures?	Observations on an entire rotational paddock (grain = 25 m x 25 m).	2
Effects of cattle activities on vegetation dynamics	How do herbage removal, dunging and trampling affect vegetation dynamics at a seasonal scale?	Exclosure experiments with controlled treatments, simulating cattle activities applied on plots of 2 m x 2 m.	3.1
	How do herbage removal, dunging and trampling affect vegetation dynamics at year scale?		3.2
	How do herbage removal, dunging and trampling affect microbial community at year scale?		3.3
	How gaps are colonised? How do herbage removal, dunging and trampling affect this colonisation?		3.4
	How do herbage removal and trampling affect vegetation dynamics at a very fine scale?	Observations in the field with natural cattle activites (grain = 1 dm x 1 dm).	4.1
	How do dung patches affect vegetation dynamics at very fine scale?		4.2

Warning

Each chapter or subchapter of this thesis is in a paper form and was written to be read independently from the others. Two are already published (§ 3.1 and § 4.1); four are at present submitted (§ 2.1, § 3.3, § 3.4 and § 4.2) and one is manuscript (§ 3.2). I apologise for redundancy particularly in introduction and method sections.

Moreover, Appendix I is included in the CD-ROM, attached at the end of this document. This CD-ROM includs:

- *Photos presenting wooded pastures and field work (Appendix Ia).*
- *For each paper already published, a pdf-file of the reprint (Appendix Ib).*
- *Posters and presentations related to this work, presented at different congresses (Appendix Ic).*

Details on Appendix I are presented in page 175.

CHAPTER 2

Patterns of cattle activity

2.1. Spatial and seasonal patterns of cattle habitat use in a mountain wooded pasture

F. Kohler, F. Gillet, S. Reust, H.H. Wagner, J.-M. Gobat and A. Buttler

2.1.1. Introduction

One of the greatest challenges in ecology today is to determine the causes and consequences of spatial heterogeneity in ecosystem structure and function. Sylvopastoral ecosystems, which are widespread around the world, are made of a mosaic of woodland and grassland with a complex spatial structure (Etienne 1996). The understanding of how this landscape structure affects cattle activity and what feedback effect cattle activity has on landscape structure is a key to successful management of these ecosystems.

In a heterogeneous range system, the overall stocking rate does not reflect local differences in grazing pressure. At low stocking rates, cattle will preferentially graze easily accessible areas with abundant high-quality forage, while other areas are under-utilised. At high stocking rates, the depletion of the preferred grazing areas forces the animals to graze the pasture more homogeneously. Hence, the patchiness of a pasture depends not only on the natural resource variability and the overall stocking rate, but also on the distribution of stocking density over time (Verweij 1995). Many management schemes apply a rotational system of smaller paddocks in order to achieve a more homogeneous use of resources. Within each rotational unit, a seasonal change from selective to more uniform grazing is to be expected. The installing of fences, salt and watering places for a paddock system introduces additional landscape elements that are likely to affect the grazing pattern beyond the effect of the temporal increase in stocking density.

Vegetation is the key component of the system and cattle activity is the most important factor for structuring vegetation in sylvopastoral ecosystems (Olff and Ritchie 1998). At a fine spatial scale (bite and feeding station *sensu* Bailey et al. 1996), cattle may influence vegetation through three main activities: (1) herbage removal (herbivory, foraging or grazing), (2) dung and urine deposition, and (3) trampling. These three activities have different impacts on the vegetation, creating fine-scale mosaics in the herb layer (Kohler et al. 2004a and §3.1).

Understanding the spatial patterns of habitat use by large herbivores, as well as their effects on vegetation dynamics, is an important topic for ecosystem management. The majority of models of rangeland vegetation dynamics are implemented at a landscape scale (Weber et al. 1998; Hahn et al. 1999; Van Oene et al. 1999; Gillet et al. 2002). They generally consider grazing pressure as an emergent behaviour of the three primary activities which can be assessed through mapping either foraging or dung deposition and depends on the overall stocking rate. There is evidence, however, that the spatial patterns of the three activities are not congruent and may depend on different factors, as will be discussed in the following paragraphs.

According to Rice et al. (1983), the selection of grazing locations by cattle depends on herbage density, water availability, relief, slope, elevation, aspect, natural and artificial barriers, herd social interactions, prior experience, and climate. The spatial pattern of foraging is the best studied attribute of cattle activity (Senft et al. 1987; Coughenour 1991; Bailey et al. 1996). Cattle preferentially graze certain plant communities (Roath and Krueger 1982) and this preference seems to be the main cause of the distribution of cattle in a paddock (Van Rees and Hutson 1983; Senft et al. 1985; Putman et al. 1987). The choice of the community type and consequently cattle distribution are expected to be highly influenced by the nutritive value of plant species (Osuji 1974; Anderson and Kothmann 1980) and Pinchak et al. (1991) concluded that apart from water source and physiographic complexity, forage characteristic is a good predictor of cattle habitat use. Loehle and Rittenhouse (1982) found that it is unrealistic to predict habitat use from forage quality only. They concluded that, particularly in large pastures, other factors such as distance from fences or water could affect cattle behaviour. At the landscape scale, abiotic factors act as constraints for the biotic factors operating at a finer scale (Bailey et al. 1996).

The spatial distribution of faeces and urine from cattle is not uniform and their concentration is often higher in areas of special attraction, such as around water sources, gates, fences, shade and shelter belts (Petersen et al. 1956, Marsh and Campling 1970; Peterson and Gerrish 1996; White et al. 2001). In mountain regions, cattle faeces distribution patterns are significantly associated with slope, aspect, hydrological position and season (Tate et al. 2003): daily faecal load is higher in flat areas (Costa et al. 1990) and is lower during the wet season compared to the dry season. Observations from dairy cows in an intensive, rotationally stocked pasture showed that the number of defecations and urinations were highly correlated with the time spent in those areas (White et al. 2001); manure concentration was higher around the water tank, especially during warm-weather periods.

The distribution of trampling effects depends not only on cattle behaviour, but also on slope and soil characteristics such as texture, water content, etc.. On steeper ground grazed by sheep and red deer, Hester and Baillie (1998) showed that at low densities, the impact of trampling on vegetation was more important than the effect of herbage removal.

So far, the relationships between these different patterns of habitat use by large herbivores are poorly understood. Such patterns are difficult to study because each pasture or paddock is a functional unit whose elements are directly linked by the process of cattle activity. Consequently, the patterns can only be described and explained if an entire paddock or pasture is studied. Such an exhaustive coverage is data-intensive and puts important constraints on the nature of data that can be collected over this spatial extent. In addition, statistical analysis and modelling are likely to run into problems of spatial autocorrelation, as the observations are inherently dependent. Spatially-structured multivariate responses are preferably analysed using constrained ordination (Borcard et al. 1992), by partialling out the variation explained by environmental variables alone (ecological dependence), spatial variables alone (spatial autocorrelation) and the shared variation due to spatially-dependent environmental descriptors (spatial dependence).

Among the various habitat characteristics identified as potential predictors of cattle effects, one may distinguish between those that are mostly of natural origin (topography, soil, vegetation, microclimate), and those that are primarily induced by management decisions (position of fences, gates, salt or water sources). This distinction between ‘natural structures’ and ‘management-induced structures’, even if not absolute, is important in the perspective of ecosystem management, the latter being more easily controllable.

Thus, our purpose was to provide an exhaustive description of spatial and seasonal patterns of grazing, dunging and trampling for an entire rotational paddock of a wooded pasture at a landscape scale (25-m resolution), and to explain the observed patterns by the response of cattle to natural and management-induced structures of the environment, while accounting for spatial dependence and autocorrelation.

This paper addresses the following questions: How do spatial patterns of cattle habitat use vary with the attribute of cattle activity in a mountainous wooded pasture? Do these patterns change during the year? What are the relationships between the cattle effects and the local site conditions? What is the respective role of natural, management-induced and spatial structures in explaining the patterns of cattle habitat use? What is the importance of spatial dependence and spatial autocorrelation for each response variable?

We focused on three working hypotheses: (1) At the landscape scale, the spatial pattern of cattle habitat use depends on cattle activity: especially herbivory and dung deposition are expected to occur in different locations. (2) The spatial pattern of each cattle activity weakens from the beginning to the end of the season. (3) Each cattle activity depends on different environmental conditions.

Thus, we assess whether the assumption of ‘grazing pressure’ as a single emerging property of cattle activity is a valid simplification for modelling the mutual interactions between cattle and vegetation at a landscape scale. This question is of great importance for the development of decision support models aimed at a sustainable management of heterogeneous and extensive range systems.

2.1.2. Methods

2.1.2.1. Study site

The study was conducted in the Jura Mountains of northwestern Switzerland at Orvin, Métairie d’Evilard (47°09’ N, 7°10’ W). The climate is predominantly 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.

We chose a paddock of 23.2 ha which provided a typical example of an extensively managed wooded pasture of the Jura Mountains (Perrenoud et al. 2003). Elevation varies from about 1170 m a.s.l. in the South of the paddock to 1250 m in the North. Aspect is South-East. The study area contains a great diversity of habitats, from open grassland to forest, with flat or sloping ground and a heterogeneous soil mosaic (Calcisols, Cambisols, Leptosols, Luvisols, according to Deckers et al. 1998). This landscape is the result of centuries of mixed land use combining cattle grazing and forestry. The climax vegetation is a beech-fir forest. The dominant tree species are *Fagus sylvatica*, *Acer pseudoplatanus* and *Picea abies*. The herb layer is a mosaic of various grazed meadows (dominated by *Festuca nigrescens* and *Alchemilla monticola*), short-grass, tall-grass and understorey communities. The management is extensive with a rotational grazing system during the summer period only. During the grazing season of 2001, 120 heifers (49.2 Adult Bovine Units) stayed three times in the paddock: 13 days in June, 10 days in July and 19 days in August and September. The stocking rate was equivalent to 2.12 cows/ha throughout the grazing periods. The herd was a mix of Holstein and Swiss Brown breeds belonging to various owners.

2.1.2.2. Sampling design

In order to get complete spatial information, we subdivided the paddock into a grid of square cells of 25 m. The valid paddock area within cells along the edge was calculated in ArcGIS 8.2 (ESRI Corp.), and only cells covering at least 100 m^2 of the paddock were retained for analysis (n = 393).

Attributes of cattle activity

Immediately after every rotational grazing period, thus three times in one year, we estimated the effects of three cattle activities for each cell.

(1) For herbage removal, we applied a global index of foraging intensity of the herb layer, measured as an ordinal variable with three levels (1: between 0 % and 10 % of shoot biomass removed; 2: between 10 % and 50 % removed; 3: more than 50 % removed). Field estimation of the biomass removed was based on vegetation height and direct traces of grazing. This three-level descriptor is a good compromise between precision and efficiency. For quantitative analyses, each observed level was replaced by its central value (i.e., 1 replaced by 0.05, 2 by 0.30 and 3 by 0.75).

(2) We counted the number of dung pats in each cell. This number was divided by the valid paddock area (between 100 and 625 m^2) and multiplied by 100 to get the dung density in terms of the average number of faeces on 100 m^2.

(3) We estimated the trampling effect by the percent of bare soil and flattened vegetation due to trampling, in intervals of 10 % with two additional intervals at 5 % and 95 %. This estimate reflected the most visible effects of trampling on the herb layer, which depend both on cattle frequentation and on the sensitivity of the soil-vegetation complex.

Note that these variables, especially the dung density and the trampling effect, were partially cumulative between rotations, so that the effects of cattle activity remained visible from one rotation to the next. It was impossible to observe only the fresh impact after each grazing period. On the other hand, herbage removal was not purely cumulative due to regrowth of shoots, and a considerable proportion of dung pats disappeared between rotations, probably due to rain and to a high decomposition rate.

Environmental descriptors

To describe 'management-induced structures' (two continuous variables), we computed the distance from the centre of each cell to the nearest watering place and to the nearest fence with ArcGIS 8.2 (ESRI Corp.).

We collected six ecological descriptors of 'natural structures' at the cell scale as well. Tree cover, shrub cover and rock outcrops were estimated in the field using intervals of 10 %. The annual fodder potential of the herb layer (quantitative variable) was calculated from the pastoral value of vegetation units, deduced from a vegetation map (Gillet and Gallandat 1996b; Perrenoud et al. 2003). The average slope for each cell was calculated from a digital elevation model with a cell size of 25 m x 25 m (DHM25©, 1994, Swiss Federal Office of Topography) using the standard routine in ArcView 3.3 (ESRI Corp.). We quantified the degree of openness in vegetation structure (*VO*) inside a moving window of 75 m x 75 m (3 x 3 cells). To this purpose, woodland cover *W* was derived for each cell i from the observation of a recent aerial orthophotograph (woodland cover lower than 1 %: *W* = 0; woodland cover between 1 % and 20 %, isolated trees: *W* = 1; woodland cover between 20 %and 70 %, clumped trees: *W* = 2; woodland cover greater than 70 %, forest structure: *W* = 3). Vegetation openness *VO* was calculated for each cell as following:

$$VO = 1 - \frac{\sum_{i=1}^{9} W_i}{27}$$

2.1.2.3. Statistical analysis

We first plotted the data for each attribute of cattle activity. Maps were drawn with ArcView 3.3 (ESRI Corp.). To compare the variability of the different attributes observed after each rotation in the whole paddock, the coefficient of variation was calculated (n = 393 cells).

To assess spatial autocorrelation in cattle effects, we calculated correlograms for each attribute at each rotation, using the R 4.0 package (Casgrain and Legendre 2001) and choosing Moran's *I* as autocorrelation statistic with 30 equidistant classes of distance.

Correlations between all variables (attributes of cattle activity, management-induced and natural structures) were estimated using Spearman's coefficient in order to gauge the strength and the direction of the bivariate relationships. We corrected the significance tests for the rank correlations by using the procedure of Dutilleul (1993) implemented in the Mod_t_test program (Legendre 2001) to allow for the underlying spatial autocorrelation.

In order to analyse the variation of cattle activities in relation to local environmental conditions, Redundancy Analysis (RDA) was performed using the vegan library in R 1.9.0 (R Development Core Team 2004). All seasonal variables describing the effects of cattle activity (3 x 3 = 9 response variables, n = 393 cells) were included in the response matrix after applying a square-root transformation and a range standardization, where each seasonal value was divided by the maximum value observed for the same attribute over the three rotations. This response matrix was constrained by a second dataset describing management-induced and natural structures (eight quantitative explanatory variables, n = 393 cells).

In addition, three RDAs were performed to assess the relative importance of small-, medium- and large-scale spatial structures for each cattle activity using three subsets of the total response matrix, each with three seasonal variables. A spatial explanatory matrix was constructed with the principal coordinates of neighbour matrices (PCNM method, Borcard and Legendre 2002). This method uses eigenvectors of the principal coordinate analysis (PCoA) of a truncated matrix of geographic distance among cells as spatial descriptors and permits to detect patterns at a wide range of scales. Eigenvectors (PCNMs) were calculated with the Spacemaker program (Borcard and Legendre 2001). The highest value retained for geographic distance was 36 m, including the eight nearest neighbours of each cell; any value higher than 36 m was replaced by 144 m (4 x 36). 223 PCNMs were thus calculated. To avoid overfitting in the regression model due to the large number of explanatory variables, we performed a forward selection retaining for each attribute of cattle activity only the significant PCNMs based on a Monte Carlo test ($P < 0.01$). If the geographic coordinates *x* and *y* appeared as significant explanatory variables, we included them first as covariables in the model to detrend the data, as recommended by Borcard and Legendre (2002). Following Legendre and Borcard (2003), we grouped the selected PCNMs in three sets of spatial variables according to their scale in terms of wave length: fine-scale (0-50 m), medium-scale (50-150 m) and large-scale structures (150-700 m). We then performed a series of partial redundancy analyses (Legendre and Legendre 1998) with each of these three sets of variables and the *x* and *y* coordinates to assess the importance of each spatial scale in explaining the attributes of cattle activity.

In order to assess the importance of management-induced and natural landscape structure separately for each cattle activity, all spatial structure was accounted for using partial RDA. For this analysis, we used three sets of explanatory variables: (1) management-induced structures (two variables), (2) natural structures (six variables) and (3) spatial structure (significant PCNMs together with *x* and *y* coordinates). This analysis permitted to extract the variation in the response dataset explained by each independent dataset and shared by the three datasets (see Borcard et al. 1992 and Økland and Eilertsen 1994 for details). Partial RDAs and permutation tests were computed with CANOCO 4.5 (ter Braak and Smilauer 2002).

2.1.3. Results

2.1.3.1. Spatial patterns of grazing, dunging and trampling

Our indirect observations revealed that cattle activities were quite variable through space and time (Figure 2.1.1). Only herbage removal at the third rotation was relatively homogeneous, with most cells reaching the maximum values, indicating that by the end of the season, cattle had intensively grazed almost the whole area. Nevertheless, the paddock was completely visited at each rotation, with all cells showing at least one cattle effect.

For all attributes of cattle activity, we observed positive spatial autocorrelation at shorter distances (Figure 2.1.2). For herbage removal during the first rotation, there was a significant positive autocorrelation from 0 m to 138 m and a significant negative autocorrelation from 299 m to 460 m. The feeding activity was intense near the border of the paddock (Figure 2.1.1). At the second rotation, the structure was similar, but during the third rotation it was replaced by a very homogenous pattern with only one significant positive autocorrelation from 23 m to 46 m. The coefficient of variation decreased dramatically from the first to the last rotation (Table 2.1.1).

All Spearman's correlations were significantly positive between following rotations, but not between the first and the third (Table 2.2.2). For the dunging pattern after the first rotation, we found significant positive autocorrelation from 23 m to 253 m and significant negative autocorrelation from 345 m to 460 m. The distribution was almost the same for the second rotation. For the third rotation, autocorrelation occurred at shorter distances (positive: 0 m to 184 m; negative: 253 m to 460 m) but the correlogram was similar (Figure 2.1.2). We observed an increase of the dung density during the season, which was localized principally in places where it was already high, so that the coefficient of variation decreased only slightly (Table 2.1.1). This spatial pattern was very similar between successive rotations, with high correlation coefficients (Table 2.1.2).

The structure of the trampling pattern did

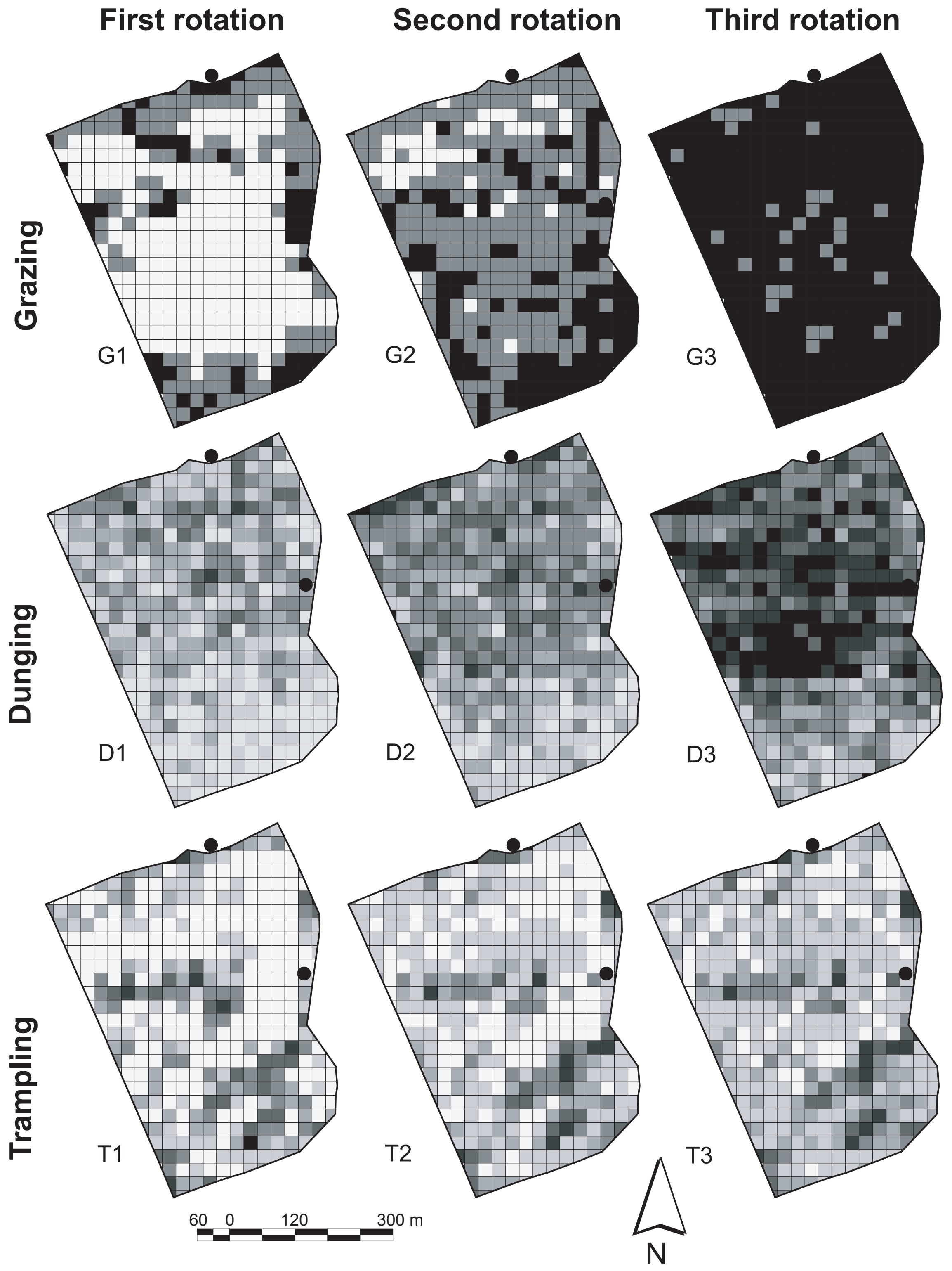

Figure 2.1.1: Maps of cattle activity assessed by its three attributes at the three rotations. The paddock is subdivided into 393 cells. Darker shading corresponds to higher values of the variable for each activity in all rotations. Black points indicate the two watering places.

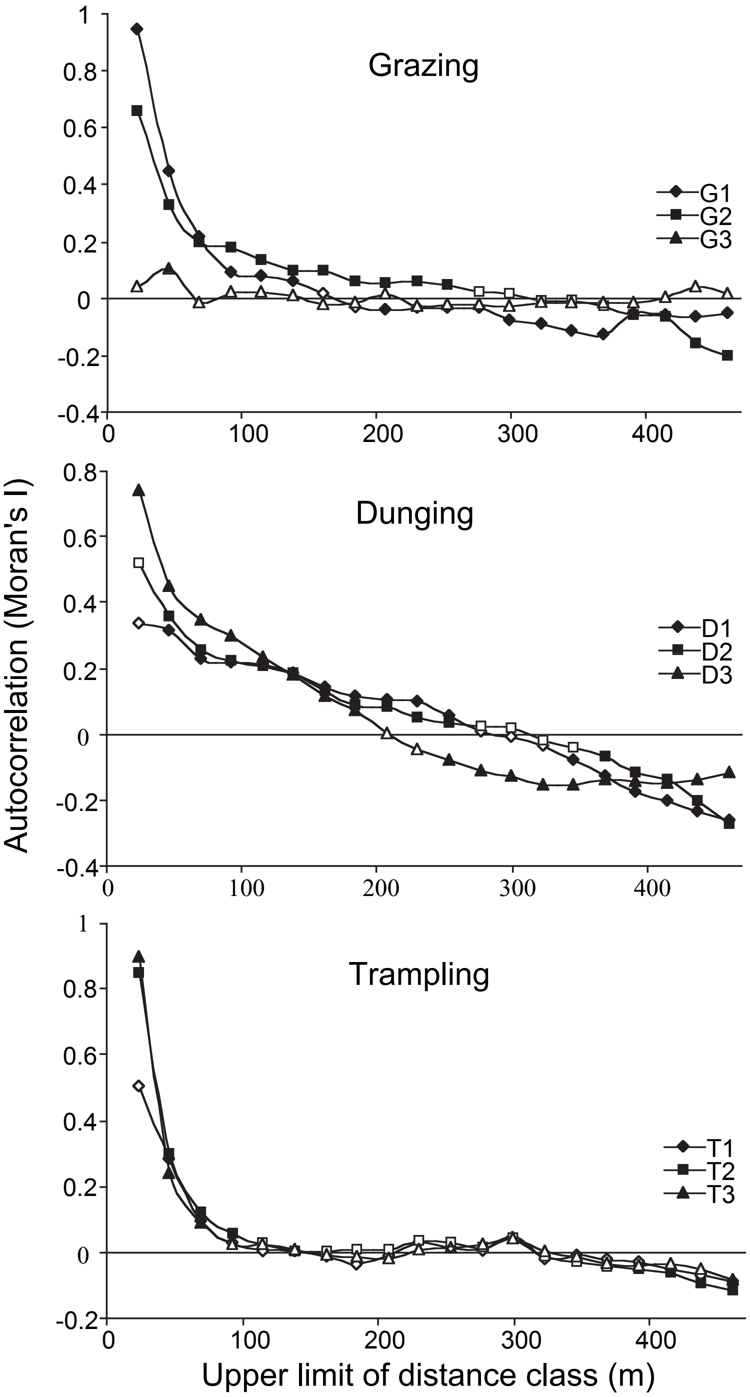

Figure 2.1.2: Correlograms of Moran's *I* of the three attributes describing cattle activity at each rotation. Solid black symbols indicate significant correlations after regular Bonferroni correction ($P < 0.05/30$). Diamond: first rotation, square: second rotation, triangle: third rotation. G: herbage removal; D: dung density; T: trampling effect; 1, 2, 3: rotation.

not change through the season, with significant positive autocorrelation at short distances (0 m to 69 m) and negative autocorrelation from 415 m to 460 m, which were significant mainly at the second rotation. Indeed, Table 2.1.2 shows a highly significant positive correlation between each pair of rotations: the trampling effect was always located in the same place during the season (Figure 2.1.1). Contrary to grazing and dunging, the coefficient of variation of trampling increased

Table 2.1.1: Mean and coefficient of variation (CV) of each attribute of cattle activity measured after each rotation (n = 393 cells).

Attribute	Rotation 1	Rotation 2	Rotation 3	
Herbage removal (percent)	22.2	40.8	71.6	Mean
	1.083	0.579	0.167	CV
Dunging (number of faeces on 100 m^2)	2.24	3.52	6.51	Mean
	0.688	0.563	0.551	CV
Trampling effect (percent)	13.1	13.1	16.2	Mean
	0.935	0.961	0.745	CV

Table 2.1.2: Correlations between rotations for each attribute of cattle activity (n = 393 cells). The *P*-value of the Spearman's rank correlation coefficient (rs) was corrected for spatial autocorrelation by Dutilleul's procedure (* $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$). G: herbage removal; D: dung density; T: trampling effect; 1, 2, 3: rotation.

Grazing	r_s	Dunging	r_s	Trampling	r_s
G1 vs. G2	0.261***	D1 vs. D2	0.788***	T1 vs. T2	0.742***
G2 vs. G3	0.173**	D2 vs. D3	0.669***	T2 vs. T3	0.848***
G1 vs. G3	0.107	D1 vs. D3	0.434**	T1 vs. T3	0.642***

slightly between the first and the second rotation before decreasing at the third rotation (Table 2.1.1).

2.1.3.2. Correlations among attributes of cattle activity

The different patterns of cattle habitat use were not generally correlated and whenever a correlation occurred, it was negative (Table 2.1.3). There were only two significant negative correlations after accounting for spatial autocorrelation: at the second rotation between dunging and grazing, and at the third rotation between dunging and trampling.

2.1.3.3. Correlations between cattle attributes and environmental variables

Even after accounting for spatial autocorrelation, Spearman's correlations between attributes of cattle activity and local environmental descriptors were often significant (Table 2.1.4), except with herbage removal, for which only few rank correlations were found.

Negative correlations between herbivory and distance to the fence were observed at the first and the second rotations. At the third rotation, tree cover was negatively and fodder potential positively correlated with this activity.

Many strong correlations were observed between dung density and natural structures. For each rotation, significant negative correlations occurred with slope and rock outcrops and positive correlations with fodder potential and vegetation openness. At the third rotation, significant negative correlations were

Table 2.1.3: Correlations between attributes of cattle activity for each rotation (n = 393 cells). The *P*-value of the Spearman's rank correlation coefficient (rs) was corrected for spatial autocorrelation by Dutilleul's procedure (* $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$). G: herbage removal; D: dung density; T: trampling effect; 1, 2, 3: rotation.

Rotation 1	r_s	Rotation 2	r_s	Rotation 3	r_s
D1 vs. T1	0.012	D2 vs. T2	-0.166	D3 vs. T3	**-0.201***
D1 vs. G1	-0.165	D2 vs. G2	**-0.347***	D3 vs. G3	-0.100
T1 vs. G1	0.099	T2 vs. G2	0.012	T3 vs. G3	-0.028

Table 2.1.4: Correlations between attributes of cattle activity and environmental variables (n = 393 cells). The *P*-value of the Spearman's rank correlation coefficient (rs) was corrected for spatial autocorrelation by Dutilleul's procedure (* $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$). VO: vegetation openness; Tcov: tree cover; Scov: shrub cover; Fpot: fodder potential; Rock: percentage of rock outcrops; DW: distance to the nearest watering place; DF: distance to the nearest fence; G: herbage removal; D: dung density; T: trampling effect; 1, 2, 3: rotation.

	Natural structures						**Management-induced structures**	
	VO	**Tcov**	**Scov**	**Fpot**	**Rock**	**Slope**	**DW**	**DF**
G1	-0.006	0.006	0.032	-0.051	0.213	0.192	-0.032	**-0.544****
G2	-0.293	0.035	0.154	-0.002	0.196	0.365	0.201	**-0.189***
G3	0.127	**-0.149****	0.001	**0.110***	-0.071	0.095	0.021	-0.158
D1	**0.401***	-0.067	-0.229	**0.152***	**-0.265***	**-0.476***	-0.382	0.184
D2	**0.486***	-0.156	-0.208	**0.232****	**-0.277****	**-0.537***	-0.317	**0.177***
D3	**0.372***	**-0.202****	**-0.220***	**0.244*****	**-0.366****	**-0.498***	-0.260	0.318
T1	**-0.491*****	**0.636*****	**0.290*****	**-0.462*****	**0.475*****	0.191	0.152	-0.051
T2	**-0.494*****	**0.499*****	**0.273****	**-0.380*****	**0.370****	0.247	0.181	-0.029
T3	**-0.439*****	**0.465****	**0.219****	**-0.351*****	**0.366****	0.213	0.119	-0.017

found with tree and shrub cover. Concerning management-induced structures, no significant correlation was found between dunging and the distance to the nearest watering place after accounting for spatial autocorrelation, but a significant positive correlation appeared with the distance to the fence at the second rotation.

Trampling effect was highly positively correlated with tree cover, shrub cover and rock outcrops across the whole season. Conversely, it was negatively correlated with fodder potential and vegetation openness.

2.1.3.4. Redundancy analysis with environmental variables

In the RDA biplot, one observes a clear disjunction of the three sets of response variables on the first two axes (Figure 2.1.3).

Axis 1 is closely related to vegetation openness and axis 2 to distance to the fence. The eight explanatory variables explained 32.2 % of the variation of the nine response variables. Monte Carlo permutation tests were significant for the first axis ($P = 0.001$), the second axis ($P = 0.001$) and the overall model ($P = 0.001$).

For herbage removal, the three seasonal variables differed more in their response to landscape structure than for the other attributes. The factors influencing this activity seemed to change during the season. The quite homogeneous distribution of herbage removal at the third rotation explained that this response variable G3 was close to the origin of the ordination biplot. The distance to the fence appeared rather important in explaining grazing activity, even if this influence decreased from the first to the last rotation.

The three seasonal dunging variables showed a similar response to landscape structures, as indicated by their similar position in the biplot. They were mainly negatively correlated with slope and rock outcrops.

Trampling patterns were mainly influenced by the natural structures. As for dung density, the three seasonal trampling variables had similar position in the biplot. They were positively correlated with tree cover and negatively correlated with vegetation openness and fodder potential.

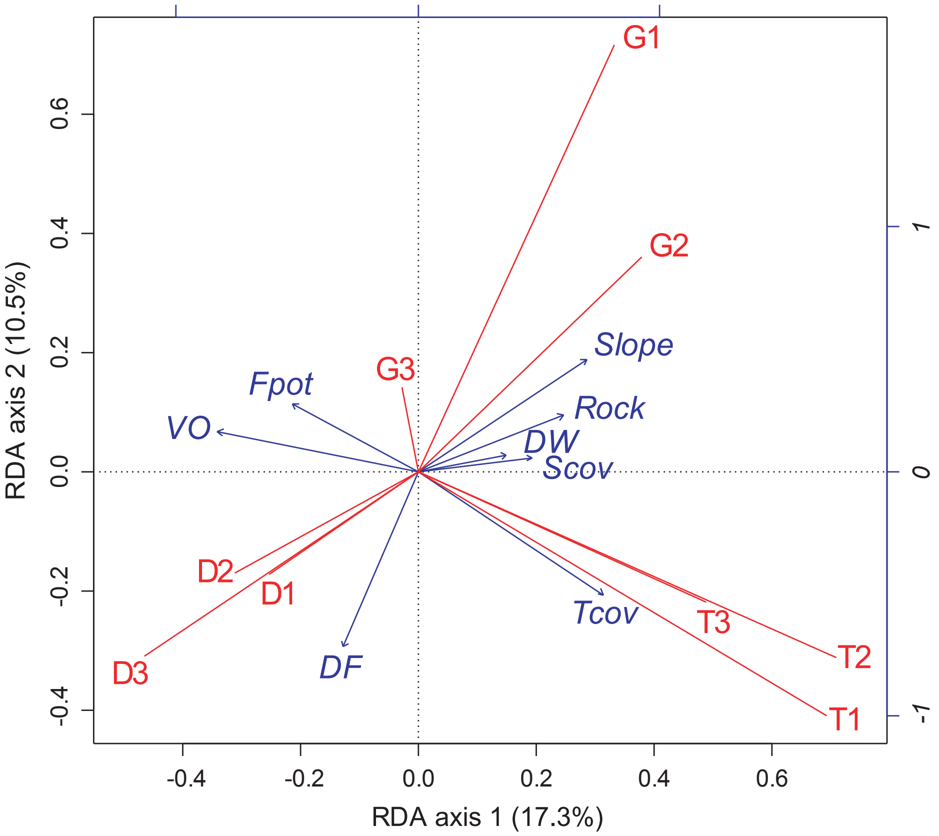

Figure 2.1.3: Correlation biplot of axes 1 and 2 of RDA on the three attributes describing cattle activity at each rotation constrained by eight environmental variables (italic labels and scale). *Fpot*: fodder potential; *Tcov*: tree cover; *Scov*: shrub cover; *Rock*: percentage of rock outcrops; *VO*: vegetation openness; *DW*: distance to the nearest watering place; *DF*: distance to the nearest fence; G: herbage removal; D: dung density; T: trampling effect; 1, 2, 3: rotation.

2.1.3.5. Partial redundancy analysis with spatial structure

For herbage removal, coordinates *x* and *y* as well as 24 PCNMs were significant after the forward selection (Table 2.1.5). Four variables were retained for large-scale, 16 for medium-scale and four for fine-scale structures. Examples of spatial structure for these three scale categories are presented in Figure 2.1.4.

The three sets and the spatial coordinates explained 48.7 % of the variation of the grazing dataset (Figure 2.1.5). The medium scale set explained most of this variation, followed by large scale, geographic coordinates and fine scale sets.

For explaining the density of dung pats, geographic coordinates *x* and *y* as well as 12 PCNMs were significant after the forward selection (Table 2.1.5). Two variables were retained for large-scale, eight for medium-scale and two for fine-scale structures. The four spatial sets explained 48.3 % of the variation of the dunging data (Figure 2.1.5). Geographic coordinates explained most of this variation indicating a topographical gradient, followed by large scale, medium scale and fine scale sets.

For trampling, only the *y* coordinate and 14 PCNMs were significant after the forward selection (Table 2.1.5). Two variables were retained for large-scale, 10 for medium-scale and two for fine-scale structures. The three spatial sets and the *y* coordinate explained 33.8 % of the variation of the trampling

Table 2.1.5: Selected PCNMs after the forward selection ($P < 0.01$) for each attribute of cattle activity.

	Large scale PCNMs	Middle scale PCNMs	Fine scale PCNMs
Grazing (herbage removal)	1, 3, 5, 6	9, 10, 11, 12, 18, 20, 21, 29, 36, 38, 43, 46, 47, 50, 58, 67	71, 85, 103, 134
Dunging (dung density)	2, 3	9, 16, 17, 23, 32, 36, 55, 65	91, 104
Trampling effect	4, 7	15, 16, 17, 21, 26, 29, 42, 43, 57, 60	73, 97

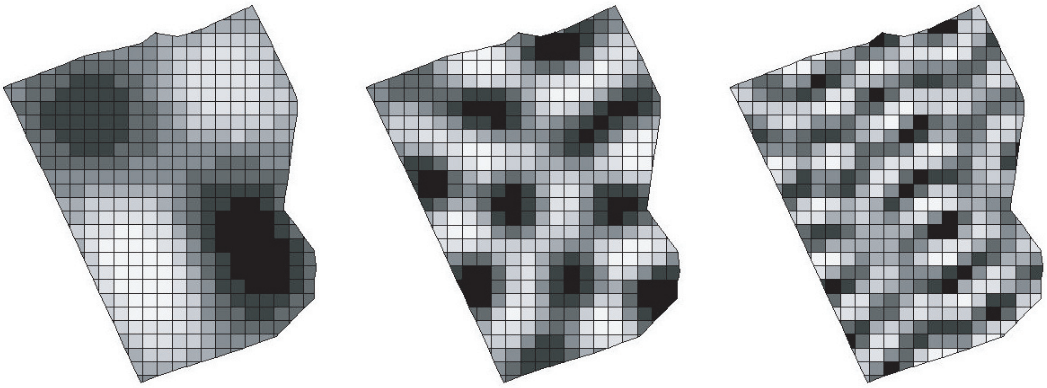

Figure 2.1.4: Examples of spatial structures used as explanatory matrices in the RDAs based on principal coordinates of neighbour matrices: PCNM 4 (large scale), PCNM 32 (medium scale) and PCNM 104 (fine scale).

dataset (Figure 2.1.5). The medium-scale set explained most of this variation, followed by the *y* coordinate, large-scale and fine-scale structures.

As PCNM extracts independent axes, there was no shared variation between the three sets of spatial variables, and the selected PCMNs were almost linearly independent of the *x* and *y* coordinates.

2.1.3.6. Partial canonical analysis with spatial structure and landscape characteristics

RDA revealed the importance of spatial structure in explaining herbage removal (48.7 % of explained variation). The variation explained by spatial structure alone (27.3 %) may reflect some contagious biological process (in this case cattle behaviour) without any relation with environmental components included in the analysis (spatial autocorrelation sensu Legendre 1993). Management-induced structures were more important (16.4 %) than natural structures (15.6 %). The shared variation (spatial dependence sensu Legendre 1993) between spatial variables and the two other sets was high (Figure 2.1.6). This common variation was partly a consequence of the relation between cattle activities and spatially structured environmental conditions, but the relation may not be causal (Borcard et al. 1992). It is unlikely that an external space-structuring process did influence both management-induced structure, natural structure and grazing in the same way. Thus we can suppose a causal relationship between the management-induced structure or the natural structure and grazing. The shared variation can be explained by autocorrelation in the two matrices, too (Legendre and Legendre 1998). It

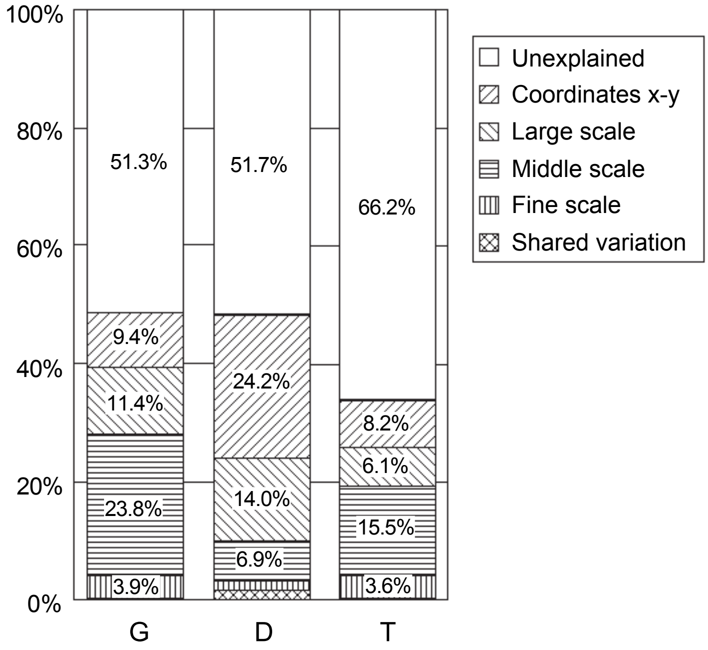

Figure 2.1.5: Variation partitioning with partial RDA for each attribute of cattle activity (three rotations) with the significant PCNMs grouped into three scale classes. Variations lower than 2 % are drawn but not labelled. G: herbage removal; D: dung density; T: trampling effect.

is the case here. The shared variation between natural and management-induced structure is not represented in Figure 2.1.6 because it was negative (-0.4 %), due to a strong direct effect of the two sets on the response variables and a strong correlation between the sets (Legendre and Legendre 1998).

For explaining the density of dung pats, the most important set was the spatial structure (48.3 %). The variation explained by spatial structure alone was 16.5 %. The second set was the natural structure, which explained 32.1 % of the variation. Finally, management-induced structure explained 14.8 %. Almost all the variation of the landscape characteristics was shared with spatial structure (Figure 2.1.6).

The effect of trampling was principally influenced by the natural structures, which explained 39.4 % of the variation. Management-induced structures explained

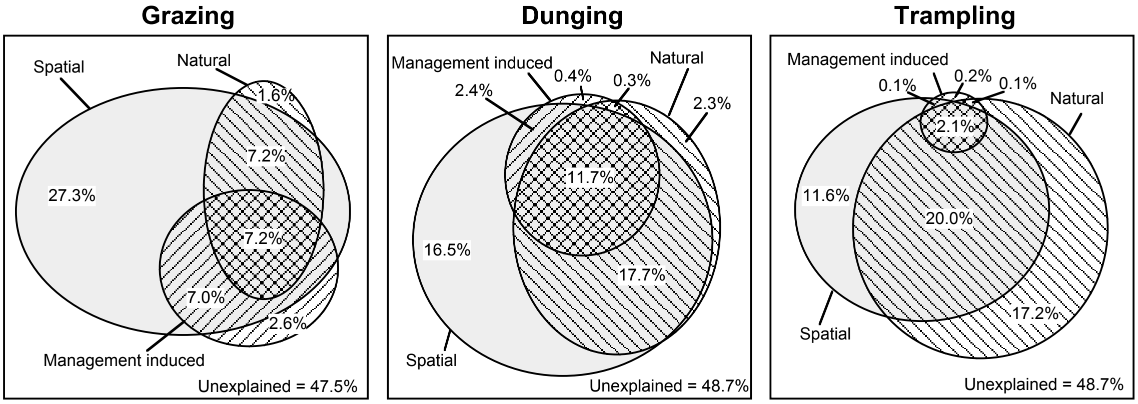

Figure 2.1.6: Variation partitioning with partial RDA on each cattle activity (three rotations) with spatial structure, management-induced structure and natural structure (only significant variables). G: herbage removal; D: dung density; T: trampling effect.

only 2.5 % of the variation. With 33.8 % of explained variation, spatial effects were less important than natural structures (Figure 2.1.6).

2.1.4. Discussion

Our first hypothesis that the pattern of habitat use differs strongly between activities was supported by the data. Areas with a lot of dung pats did not correspond to the most or least trampled or grazed areas. This is consistent with the findings by Cook (1966), comparing the number of dung pats and the forage use by cattle, and by Hester and Baillie (1998), for trampling and herbage removal by sheep.

Second, we expected that the spatial pattern of each cattle activity weakens through the season. The distribution of cattle activities was generally similar for the successive rotations, with an increasing use of the paddock, involving a more homogeneous pattern. This was true principally for foraging, less so for dunging, but not for trampling. Changes within each activity across time were less important than differences between activities. The temporal correlations may also be due to the fact that the observed effects were partly cumulative.

Results of correlation and ordination analyses supported our third hypothesis that the three attributes of cattle activity depend on different environmental conditions. The relative importance of management-induced and natural structures for explaining patterns was very different between cattle activities.

Results about foraging activity suggested that at the beginning of the season, when resources were abundant everywhere, heifers explored the perimeter of the paddock and grazed preferably near the fence, and later chose places with high fodder potential. At the first rotation, the main factor explaining herbage removal was clearly the distance to the fence. This observation confirms that of Owens et al. (1991), who showed the importance of management-induced structure to explain the utilization of a paddock. The forage quality, negatively correlated with tree cover (Miller and Krueger 1976), seemed to play a role only at the third rotation, when almost all the paddock area was grazed. Contrary to many authors (e.g., Roath and Krueger 1982; Pinchak et al. 1991), we found that distance to water was not the main predictor, possibly because of the small area of the paddock. Hart et al. (1993) showed that uniformity of herbage removal was higher in a small pasture area than in a larger area because the travel distance to water was shorter.

In contrast, dung deposition occurred mostly in flat and open areas towards the centre of the paddock. The dung density was influenced by both management-induced and natural structures. Concerning natural structures, dunging activity was linked to flat and open areas without rock outcrops and with low tree and shrub covers. Concerning management-induced structures, dunging was linked to a large distance to the fence. These results show the high number of factors influencing dung pat distribution. As shown by Costa et al. (1990), the slope seems to be the main factor. Flat areas correspond to resting places (Peterson and Woolfolk 1955; Senft et al. 1985; Jewell 2002) and dung drop occurs mainly at the end of the rest. Other factors like low cover of trees or low percentage of rock outcrops are linked to resting places, too. The positive correlation with the distance to the fence during the second rotation can be explained by the preference for resting areas with low human disturbance (cars or hikers), as fences are often installed along roads and footpaths.

Trampling effect was mainly observed under the trees and in rocky areas with poor forage quality. For this attribute of cattle activity, there was a clear influence of natural structure and no influence of management-induced structure. Areas with high tree cover correspond to refuge places during rain or heat periods (Mitlohner et al. 2001). Furthermore, the understorey vegetation is sparse and the trampling effect is thus more important and visible. A high percentage of rock outcrops corresponds generally to a low soil thickness, which is more easily affected by trampling. Thus, the observed trampling pattern may be influenced more by site conditions than by cattle distribution.

Spatial analysis showed the importance of autocorrelation and revealed systematic differences in the patterns of the three cattle activities. All distributions were significantly autocorrelated for short distances, showing a contagious process: cattle evaluate environment at a coarser scale than 25 m. The gregarious behaviour of heifers could explain this pattern. Social links are high and these herbivores are rarely observed in groups less than ten individuals with the same activity (Roath and Krueger 1982; Pratt et al. 1986). Shiyomi and Tsuiki (1999) showed that the spatial pattern of a cattle herd was not random but aggregated. Moreover, these authors showed that the aggregation rate of the herd varied with the activity: it was lower for resting state than for feeding state and highest for moving state. This can explain the difference of variation explained by the three categories of scale between the three cattle activities. Thus, the fact that heifers move as a herd has a great importance on the distribution of cattle activity and on the contagious process described in the correlograms. High values for variation explained by large- and medium-scale spatial structures in partial RDA confirmed this conclusion. Patterns did not seem to be at the same scale for the three effects: the two analyses suggested that the dunging pattern was more coarse-grained than the others. Further analyses in the framework of multiscale ordination, or the spatial partitioning of ordination results (Wagner 2003, 2004), may provide a more detailed description and interpretation of the spatial structure caused by the social behaviour of the animals (spatial autocorrelation) and by their response to landscape characteristics (spatial dependence).

Spatial autocorrelation can be explained by cattle behaviour or by hidden environmental variables. In our study we observed that this autocorrelation was different between activities, but we can only make hypotheses on the mechanisms. Knowledge about cattle behaviour is low in this type of ecosystem characterized by high heterogeneity. Further investigations on cattle behaviour, taking into account differences among breeds (hill climbers and bottom dwellers), age and nursing status (Bailey et al. 2001), as well as the influence of the range system, are necessary to know how to manage this ecosystem.

If the observed patterns of habitat use are repeated over many years, the spatial segregation at the landscape scale may have important ecosystem implications (Jewell 2002). In particular, the spatial segregation of feeding and excretion activities should lead to a transfer of nutrients from the feeding places to the resting places, with trampling effects concentrated in intermediate situations, i.e. moving places. Indeed, our trial period can be considered a normal year in respect to climatic and management conditions. However one can expect some deviation from these patterns in warm and dry periods, as suggested by results from intensive pasture systems (White et al. 2001), where heterogeneity of the spatial distribution of faeces and urine was increased. A more precise assessment of nutrient transfer and its implication on grass growth and leaching requires a modelling approach (McGechan and Topp 2004).

2.1.5. Conclusion

In heterogeneous wooded pastures, the relative independence between grazing, dunging and trampling patterns may lead to various and changing local combinations of biotic constraints and disturbances affecting vegetation dynamics. By exhibiting different spatial and seasonal patterns of habitat use, cattle maintain complex interactions with vegetation and thus contribute to its variability and its heterogeneity at a landscape scale. Natural structures are linked to soil conditions, which are highly heterogeneous in this landscape. There is evidence that the three cattle activities, which are influenced by the natural landscape structure, maintain and reinforce this heterogeneous structure, particularly shrub cover, tree cover and fodder potential. The importance of this positive feedback effect depends on cattle pressure or stocking rate. We suppose that with a high grazing pressure, activities become less influenced by natural structures and create a rather homogeneous open landscape. In the opposite case, with a low pressure, the landscape will become a homogeneous closed forest. An intermediate, optimal grazing pressure is expected to maintain this typical landscape structure with its high plant biodiversity. Dynamic, spatially explicit models calibrated with experimental data are needed to specify such an optimal grazing pressure. Even if management-induced structures seem less important than natural and spatial structures in a highly heterogeneous environment except for herbage removal, one may not neglect these factors. By considering natural structures when paddock limits and watering places are defined, the efficiency of management-induced structures as tools for managing cattle habitat use may be increased.

In conclusion, our results show that it is necessary to distinguish the three components of cattle activity in spatially explicit dynamic models of sylvopastoral ecosystems. More generally, these results show the importance of considering the activities when mapping organism distribution.

Acknowledgments

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Note:

- *Maps of the paddock and the different variables are included in Appendix Ia*

CHAPTER 3

Simulated effects of cattle activity

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

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3.1.1. Introduction

Spatial patterns of vegetation in pasture is strongly directed by human and cattle activities (Olff and Ritchie 1998, Olff et al. 1999). The effect of cattle on vegetation can be subdivided into three categories of stress factors (*sensu* Grime 2001): herbage removal, dunging and trampling. Many studies have addressed effects of grazing (e.g. Milchunas and Lauenroth 1993, Schläpfer et al. 1998, Birch et al. 2000, Cingoliani et al. 2003), trampling (Cole 1995b, Guthery and Bingham 1996, Kobayashi et al. 1997), dung deposition (Malo and Suarez 1995, Dai 2000), or manuring or fertilizing (Gough et al. 2000) on grassland, heathland or woodland communities. Grazing is the main biotic factor affecting vegetation structure and dynamics in pastures (Olff et al. 1999, Bokdam and Gleichman 2000). It changes the arrangement of above-ground 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 (1995b) 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 1973a, Moore and 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 and 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 and Gleichman 2000). Moreover, there is very poor information on the influence of these factors at seasonal scale. Studies about grazing effect generally have a temporal resolution of one or more years (e.g. Bokdam and Gleichman 2000, Marriott et al. 2002) or are synchronic (e.g. Mitlacher et al. 2002, Vandvik and Birks 2002, Huebner and 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 strong 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 datasets before and after treatments; (4) at the seasonal scale, morphological traits of species are important to explain community dynamics.

3.1.2. Methods

3.1.2.1. Study site

This 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^{o}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 typical dystrochrept (Soil Taxonomy) or 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, unfertilised, extensively grazed *Cynosurion* meadow. Dominant species of this community were *Festuca nigrescens*, *Anthoxanthum odoratum*, *Trifolium repens* and *Alchemilla monticola* (see Appendix II 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-units/ha.

3.1.2.2. Experimental design

In the exclosure, controlled treatments were applied, simulating herbage removal, trampling and dunging by cattle. The experimental area was fenced to prevent the large herbivores from interfering with the treatments, but activities of small herbivores were not controlled. 40 plots (2 m x 2 m) separated by a 1-m pathway were arranged on a 5 x 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 drillings. 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, which 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) and 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).

3.1.2.3. 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 was assessed using point-intercept frequency measurements (Goodall 1953; Daget and 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 points/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.

3.1.2.4. 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 and Wagner 2001) and field observations.

3.1.2.5. 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 and 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 and Legendre 1998, Casgrain and 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 relevé 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.

3.1.3. Results

3.1.3.1. Seasonal shift

The PCA with spring and autumn records of the first year (Figure 3.1.1) 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* subsp. *albiflorus*, which disappeared in the autumn records, while *Agrostis capillaris* appeared (see Appendix II). 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.

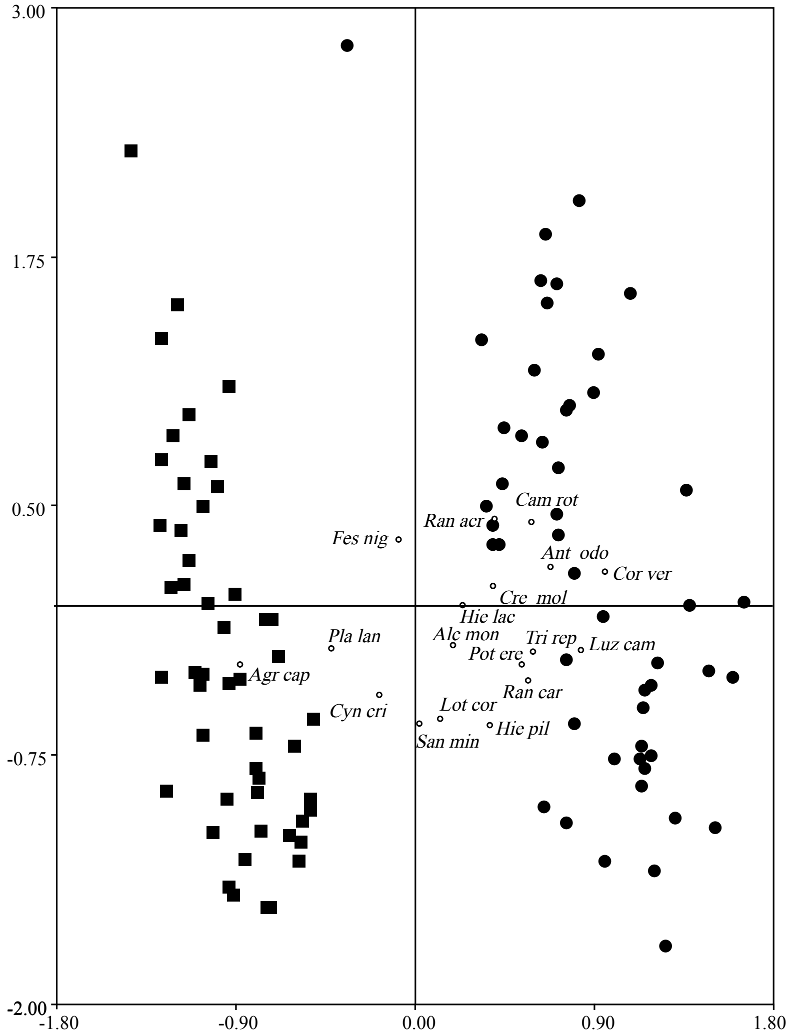

Figure 3.1.1: Scatter diagram of the PCA of vegetation records made in spring (●) and in autumn (■). Explained variation: axis 1: 26.3 %, axis 2: 10.9 %. Species-arrows are represented by the end point of their vector. Only species with frequency > 90 % are presented: *Agr cap = Agrostis capillaris; Alc mon = Alchemilla monticola; Ant odo = Anthoxanthum odoratum; Cam rot = Campanula rotondifolia; Cre mol = Crepis mollis; Cro ver = Crocus vernus subsp. albiflorus; Cyn cri = Cynosurus cristatus; Fes nig = Festuca nigrescens; Hie lac = Hieracium lactucella; Hie pil = Hieracium pillosella; Lot cor = Lotus corniculatus; Luz cam = Luzula campestris ; Pla lan = Plantago lanceolata; Pot ere = Potentilla erecta; Ran acr = Ranunculus acris subsp. friesianus; Ran car = Ranunculus carinthiacus; San min = Sanguisorba minor; Tri rep = Trifolium repens.*

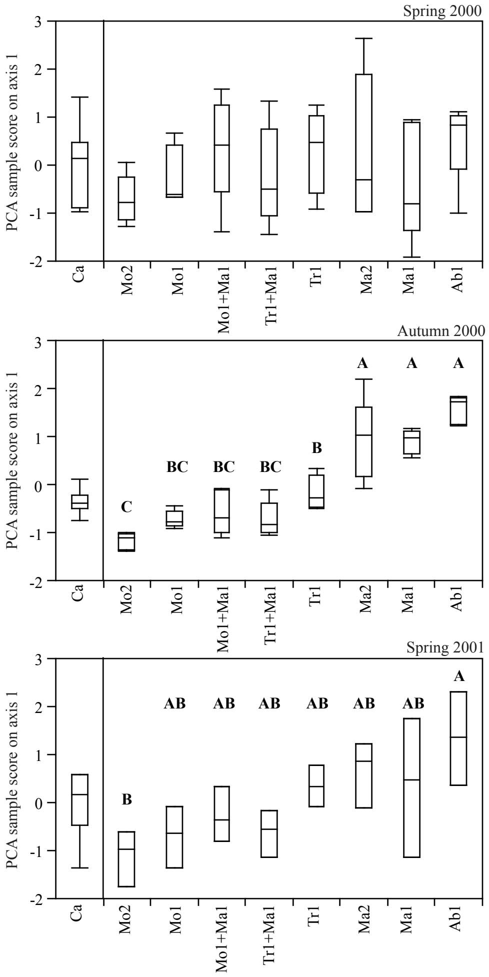

Figure 3.1.2: Coordinates of records made in the previous spring, in the autumn of the first year and in spring of the following year, on the first ordination axis of each PCA, grouped by treatments. Plots with cattle activity were considered as passive samples. For autumn 2000 and spring 2001, significant 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.

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* subsp. *albiflorus*, *Coeloglossum viride*, *Primula veris*, *Orchis mascula*, *Gentiana acaulis*).

3.1.3.2. 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 <

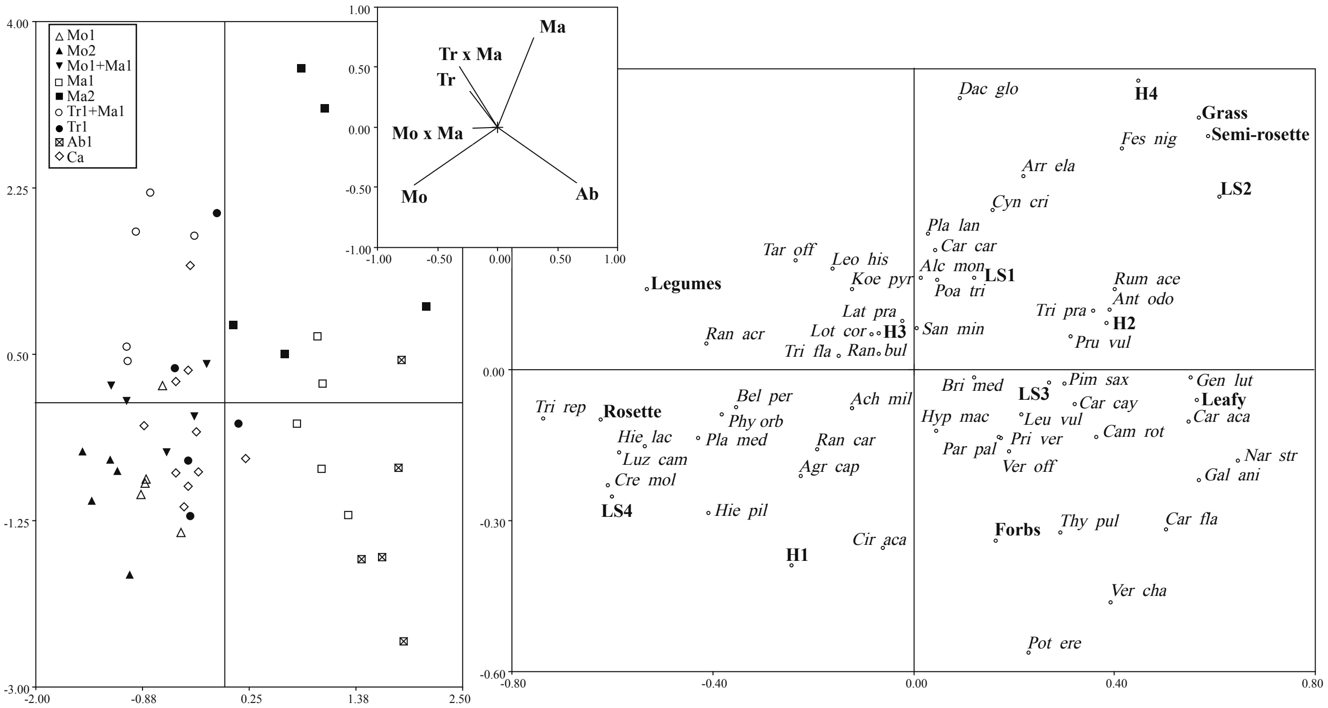

Figure 3.1.3: Scatter diagram of the RDA of vegetation records made in autumn (for details see text). Symbols for records indicate the treatment. Plots with cattle activity are considered as passive samples. For clarity species-arrows are represented by the end point of their vector. Plant traits are 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 subsp. millefolium; Arr ela = Arrhenahterum elatius subsp. elatius; Bel per = Bellis perennis; Bri med = Briza media subsp. media; Car aca = Carlina acaulis subsp. 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 subsp. 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 subsp. trivialis; Pri ver: Primula veris subsp. 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 Figure 3.3.1.

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 ($P = 0.52$) (Figure 3.1.2). 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. 3.1.2): (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 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 the RDA using the autumn data set (Figure 3.1.3) were significant in the forward selection (rank of explained variance: Mowing > Trampling > Manuring > Abandoning). Interactions (Manuring x Trampling and Mowing x Manuring) were not significant. The Monte Carlo permutation test was significant for the first ($P = 0.001$), the second ($P = 0.004$), and

Table 3.1.1: 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

the third axis (P = 0.015). The explanatory variables explained 35 % of the variation of the species matrix. Axis 1 was correlated to 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 3.1.1).

3.1.4. 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 and Fabian 1999). In our study, these life-history traits were modifying the community structure (Figure 3.1.1) 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 difference appeared between groups before treatments (Figure 3.1.2). 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 and 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.

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 fine scale. As in long-term studies on grazing effects (Lavorel et al. 1999a, 1999b), 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 (1995b) 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 (Figure 3.1.3) 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 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 ones 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 (Figure 3.1.2 and 3.1.3). 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 temporarily competition processes that are different from those under cattle pressure.

This seasonal approach clearly shows that cattle affect 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 in 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 and 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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Note:

- *Map of the geographical situation of Le Haut des Joux, diagram of the experimental design and photos of the field, treatments and vegetation measurements are included in Appendix Ia*
- *Pdf file of the printed version in the Journal of Vegetation Science is included in Appendix Ib*

3.2. Simulated effects of cattle activity on vegetation dynamics in mountain wooded pastures

F. Kohler, F. Gillet, J.-M. Gobat and A. Buttler

3.2.1. Introduction

Cattle activity greatly influences plant species composition, productivity and richness of grazing pasture ecosystems (Olff and Ritchie 1998; Olff et al. 1999; Bakker et al. 2004). The effect of cattle on the vegetation can be subdivided into three categories of disturbances: herbage removal, dunging and trampling. The effect of herbage removal or grazing *sensu stricto* on plants is principally the loss of above-ground biomass and consequently a change in light competition between species (Grime 2001). Furthermore, herbage removal induces an exportation of biomass, linked with a loss of soil nutrients. Trampling affects the vegetation through detaching or killing plant material by hoof action and by influencing water regime in firming the soil (Abdelmagid et al. 1987). By contrast to herbage removal, biomass remains on the ground and nutrients return to the soil. Moreover, heavy trampling may create gaps, which induce particular vegetation dynamics (Bullock et al. 1995). Finally, fertilization by dung pats and urine deposition stimulates plant growth.

There is evidence that these three types of activities are not spatially congruent at landscape scale and at very fine scale (Rook et al. 2004). At landscape scale cattle have, for example, favourite resting and dunging areas, which may be different from their preferred grazing area (Bokdam and Gleichman 2000). At very fine scale (less than 1 m^2, bite and feeding station *sensu* Bailey et al. 1996), nutrient adding by dung and urine deposition, is not evenly distributed over the pasture, but applied in small areas in high concentrations (MacDiarmid and Watkin 1972). On this very fine scale, dung patches induce also a reduction of the herbage attractiveness during the first months or years after deposition (Edwards and Hollis 1982) and consequently creates a heterogeneous pattern of herbage removal. Finally, effects of trampling are higher on preferential cattle pathways. The spatial heterogeneity at various scales of the three cattle activities induces a very complex pattern of disturbances on vegetation, which can even change from one year to another. Pastures can therefore be considered as a fine patchwork of various disturbances or a combination of disturbances from different cattle activities, which induce various vegetation dynamics. Kohler et al. (2004a and § 3.1) showed, these three disturbances having various effects on plant species abundances at seasonal scale. In wooded pastures of the Swiss Jura Mountains, where the study was conducted, complexity is increased by disturbances acting on a great variety of herb communities depending on various soil types and on the amount of shade caused by trees and shrubs (Gallandat and Gillet 1999). The principal aim of the present study is then to assess plant succession appearing with each disturbance or with combinations of these disturbances in various plant communities. Due to the variation of the spatial pattern of disturbances at fine scale from year to year, we were not interested in the succession appearing on a long-run, but in short-term succession (some years).

Furthermore, our research addressed the hypothesis if plant functional response types can be used as indicators of these vegetation dynamics. Functional classification of plants is used to overcome the limitations of species based conclusions, restricted by phytogeographical boundaries (Pillar and Sosinski 2003). Plant functional groups are defined as groups of species with similar responses to a given environmental factor. They are characterised by a set of common biological attributes correlating in their behaviour. The idea is that "soft" attributes, which are easily measurable structural traits, can be used as surrogates of "hard" attributes (i.e.purely functional traits, such as respiration, photosynthesis, competitive ability, etc.), generally hardly measurable (Hodgson et al. 1999; McIntyre et al. 1999; Lavorel and Garnier 2002, but see Walker and Langridge 2002). The relevance of biological traits to characterise vegetation dynamics in response to natural and land use disturbances is now well recognised (e.g. McIntyre et al. 1999, Gondard et al. 2003, Jauffret and Lavorel 2003, Rodriguez et al. 2003 but see Vesk et al. 2004). Moreover, functional response to grazing is well documented (e.g. Hadar et al. 1999, Barabaro et al. 2000, Diaz et al. 2001, Bullock et al. 2001, McIntyre and Lavorel 2001). Nevertheless, these studies consider grazing as a general disturbance combining the three cattle activities (dunging, trampling and herbage removal). In addition, they generally compare the vegetation state with different stocking rates or with presence or absence of grazing. None of these studies considers the relative impact of the three activities or their interactions in structuring the vegetation of pastures. Therefore, there is poor information on the functional internal dynamic of pastures linked with cattle activity.

The objective of this study was (1) to assess separately or in combination, the effects of treatments simulating cattle activities (repeated mowing, manuring and trampling) on three communities depending on various light conditions, in a 3 or 4 years exclosure experiment and (2) to assess these dynamics at functional level by determining relevant plant traits and by testing the efficiency of the C-S-R plant strategy theory (Grime 1974, Grime 2001, Colasanti et al. 2001).

Our general working hypotheses were: (1) our treatments induce quantitative divergence of the communities; (2) these changes get more and more important with elapsed time; (3) light conditions influence the plant succession induced by the treatments; and (4) have an impact on species richness, biomass and vegetation height; (5) plant traits of species can be used to describe vegetation dynamics influenced by the treatments; (6) treatments will induce various trajectories of communities in the C-S-R space.

3.2.2. Material and Methods

3.2.2.1. Study sites

This study was conducted in two sites of the Jura Mountains in NW Switzerland: site A is located at Le Haut des Joux (Les Ponts-de-Martel NE, 46°38' N, 6°38' W) and site B at La Métairie d'Évilard (Orvin BE, 47°09' N, 7°10' W). Site A is at an altitude of 1240 m a.s.l. and site B at 1210 m a.s.l. In both locations 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 and the mean daily temperature is below 0°C on more than 60 days per year. Both sites are typical wooded pastures containing a great diversity of habitats, from open grassland to forest patches. The climax vegetation is a *Fagus-Abies* forest.

The experiments were carried out in three typical communities (one in site A and two in site B) building a mosaic of herb layer in wooded pasture. In site A, the chosen community is the most widespread in open areas. This dense short-grass community is an unfertilized, extensively grazed *Cynosurion* meadow ("Site A - Grazed Meadow" or A-GM in this paper) dominated by *Festuca nigrescens*, *Agrostis capillaris*, *Trifolium repens* and *Alchemilla monticola*. In the site B, both chosen communities are influenced by the shade of *Fagus sylvatica* trees. The first community occurred at about 10 m from the edges of the thickets and suffered a moderate effect of shade (Table 3.2.1). Like in site A, this dense short-grass community is an unfertilized, extensively grazed *Cynosurion* meadow ("Site B - Grazed Meadow" or B-GM in this paper). Species composition was similar to A-GM, but due to shade effects biomass production was lower (Table 3.2.1). The second community occurred along the shaded edges of the thickets. This "forest-edge herb community" ("Site B – Forest-edge" or B-FE in this paper) was dominated by *Festuca nigrescens*, *Luzula sylvatica*, *Anemone nemorosa* and *Geranium sylvaticum*. On the contrary to both other communities, vegetation was rather sparse. The three chosen communities grow in various light conditions, but were similar regarding the soil conditions (see Table 3.2.1 for details). In each case soil was a Cambisol (Dekers et al. 1998) on a calcareous substratum. All communities were in equilibrium with decades of extensive cattle activity during the summer months. Management is a grazing rotation system with heifers (the animals pass from one paddock to another according to a variable period of rotation). The stock density is ranging from 0.6 to 0.9 adult-bovine-units/ha.

3.3.2.2. Experimental designs

Controlled treatments were applied, simulating herbage removal, trampling and dunging by cattle. In both sites, the experimental areas were fenced to prevent large herbivores from interfering with the treatments. The fences did not exclude small grazer, such as voles, but such grazing is not a significant factor at the sites. Three factors were introduced to be

Table 3.2.1: General description of the three communities at the beginning of the experiment (except for the dry-weight of biomass measured at the end of the experiment). Means (± standard errors) are presented. For soil chemical values, means were calculated from 30 samples for A-GM and from 15 samples for B-GM and B-FE. Samples were cores with a diameter of 6 cm and a length of 10 cm (corresponding to the thickness of the A horizon). Water pH, total nitrogen (N) and total organic carbon (C) were measured with standard methods (Anderson and Ingram 1993).

Sites	Community type	Abbrev.	Plant species richness per plot	Total plant species richness	Dry-weight of biomass (g DM/m^2)	Percentage of potential sun hours[a]	Soil depth (cm)	pH (H_2O)	N (%)	C (%)	C/N
A	Grazed meadow	A-GM	32.0 ± 0.6	57	431 ± 17	100 ± 0	27 ± 0.9	5.1 ± 0.04	0.77 ± 0.02	7.9 ± 0.2	10.4 ± 0.1
B	Grazed meadow	B-GM	31.8 ± 0.5	63	221 ± 16	60 ± 0.7	26 ± 1.1	5.1 ± 0.05	0.56 ± 0.02	6.4 ± 0.2	11.4 ± 0.3
B	Forest-edge	B-FE	27.5 ± 0.9	66	99 ± 7	20 ± 1.1	27 ± 1.6	5.2 ± 0.06	0.53 ± 0.02	6.4 ± 0.3	12.1 ± 0.2

[a] Percentage of potential sun hours per day in the station compared to an open area, estimated from 30 measurements per community type, with a solar compass (Herzog Forsttechnik AG, Switzerland) for the vegetation period (May to October).

combined into treatments:

1. Repeated mowing with a lawn mower (Mo) at three levels: Mo0 = no mowing; Mo1 = once in a month; Mo2 = twice a month.
2. Trampling (Tr) with wooden shoes (1000 footsteps per m^2 with approx. 70 kg per footstep on 35 cm^2, representing a mean pressure of 2 kg/cm^2) at two levels: Tr0 = no trampling; Tr1 = once in a month.
3. Manuring (Ma) with a liquid mixture of dung and urine given once in a month at three levels: Ma0 = no manuring; Ma1 = 0.5 l/m^2; Ma2 = 2 l/m^2. Ma1 simulates a normal cattle activity, Ma2 an intensive cattle activity. The liquid mixture came from cattle living in the study area, containing possibly seeds from species already present in the study area.

The experimental design was slightly different in both sites. In the exclosure area of site A, 24 plots (of 2 m x 2 m) were arranged on a 3 x 8 grid. In the pasture around the exclosure area, six additional plots were established. In this site, the different levels of Mo and Ma were tested. From the 18 possible factor combinations, only eight were retained and randomly allocated in the 24 plots of the exclosure experiment with three replicates, giving:

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

In the exclosure area of site B, for both chosen communities, 24 plots (of 1.8 m x 1.8 m) were arranged on a line parallel to the edge of the thickets and divided into three blocks of eight plots. In the pasture around the exclosure area, six additional plots per community type were established. In this case, we excluded both low level treatments Mo1 and Ma1 to establish in both communities a balanced factorial design with three replicates at eight different treatments:

- Three single treatments:
  Mo2(+Ma0+Tr0); Tr1(+Mo0+Ma0);
  Ma2(+Mo0+Tr0).
- Three coupled treatments:
  Mo2+Tr1(+Ma0); Ma2+Tr1(+Mo0)
  and Mo2+Ma2(+Tr0).
- One tripled treatment: Mo2+Ma2+Tr1
- Abandoned plots with no intervention:
  Ab = Mo0+Ma0+Tr0.

The eight treatments were allocated randomly within each of the three blocks in both communities.

Experiments started in 2000 in site A and in 2001 in site B. For each community type, the plots were as similar as possible with respect to floristic composition, canopy structure and biomass. The soil homogeneity was checked by surface drilling. All treatments were applied homogeneously to the entire surface of each plot, from the end of May to the end of September 2000 for site A and in 2001 and 2002 in both sites. These periods corresponded to the presence of cattle on this pastureland. Apart from these periods, the vegetation was not artificially disturbed. Plots outside the fenced area represented reference plots with regular, uncontrolled cattle activity (Ca).

3.2.2.3. Vegetation data

Records were made in a central subplot of 1 m^2, leaving a buffer strip of 50 cm (site A) or 40 cm (site B) around each plot. Absolute and relative cover of vascular plant species were assessed using point-intercept frequency measurements (Goodall 1953; Daget and Poissonet 1969). The number of contacts of green parts with a vertical needle was counted, considering only the first hit for each species. A threshold of 120 points/m^2 was retained, allowing efficient measurements. Because rare species are often missed with this method (Buttler 1992), a complete list of all species within each subplot was recorded additionally. To species without any contact in the point-intercept frequency measurements, but present in the subplot, a minimum value of 1 occurrence was attributed. To consider seasonal changes, records were made at the end of spring and at the beginning of autumn in 2000 in site A and in 2001 and 2002 in both sites. Plots were recorded a last time at the end of the experiments in spring 2003.

Vegetation height was estimated with an automated rising plate meter and above-ground biomass was measured at the end of the experiment in June 2003. The 1 m^2 central subplot was cut near the ground level and the dry weight of the plant material was measured after 48 hours at 60°C.

3.2.2.4. Plant functional traits and C-S-R plant strategy

Plant functional traits were used to detect general trend in trait promotion or inhibition by treatments. We selected twelve traits describing plant morphology, regeneration strategy and life history. The traits were quantitative variables ("maximum plant height", "seed mass", "seed length", "begin of flowering", "duration of flowering") or categorical variables ("life-form", "canopy structure", "lateral spread", "seed bank longevity", "seed dispersal mode", "pollen vector", "reproduction type"). See Table 3.2.2 for details and data sources. These traits are widely used and easily accessible in database or literature. For categorical variables, attribute classes are large to allow trait plasticity (Dyer et al. 2001) and to include a sufficient number of species. Moreover, species were allocated to one of the nineteen C-S-R types following Biostress (2003) and Klotz et al. (2002).

3.2.2.5. Statistical analyses

Univariate responses (e.g. turnover, biomass) were analysed by fitting multiple linear regression models. The three factors (mowing, trampling and manuring) and their interactions (when they were simulated) served as explanatory variables and were 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. For site B, overall differences among blocks were removed in all analysis. Moreover, data from plots with natural cattle activity were excluded for these analyses, because they had not been included into the experimental design. Calculations were performed with R 1.9.1 (R Development Core Team 2004).

To measure the temporal multivariate response of a plant community, principal response curves (PRCs) (van den Brink and ter Braak 1999, ter Braak and Smilauer 2002) were used (see Frampton et al. 2000 or Vandvik 2004 for ecological examples). This recently developed method derived from partial redundancy analysis permits analysing the effect over time of one or more treatments relatively 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. In this case, each treatment (in total eight per community) were coded independently as binary variables and the plots with natural cattle activity were added and chosen as references. As raw data, species absolute cover was used. Because Redundancy Analysis (RDA) is not

Table 3.2.2: Plant traits. Trait description, data source and missing values (total number of species included in the analysis = 59).

Traits	Variable category type	Data source	Missing values
Life-form	Categorical (grasses, sedges, forbs, legumes, shrubs and trees)	Klotz et al. 2001	-
Maximum plant height (cm)	Quantitative	Lauber and Wagner 2001	-
Canopy structure	Categorical (rosette, semi-rosette and leafy stem)	Klotz et al. 2001	-
Lateral spread[a]	Categorical (none, low (< 10 cm) and high (≥ 10 cm)))	Klimes et al. 1997	-
Seed mass (mg)	Quantitative	Klotz et al. 2002	5 (8 %)
Seed length (mm)	Quantitative	Klotz et al. 2002	5 (8 %)
Seed bank[b]	Categorical (transient, persistent)	Thompson et al. 1997	7 (12 %)
Dispersal mode	Categorical (anemochore, zoochore and unspecialized)	Klotz et al. 2002	-
Pollen vector	Categorical (wind, insects)	Klotz et al. 2002	1 (2 %)
Reproduction type	Categorical ("only by seed", "mostly by seed and rarely vegetatively", "by seed and vegetatively" and "mostly vegetatively, rarely by seed")	Klotz et al. 2002	-
Begin of flowering (month)	Quantitative	Lauber and Wagner 2001	-
Duration of flowering (month)	Quantitative	Lauber and Wagner 2001	-

[a] Lateral spread: None: CLOPLA1(1, 2, 4, 12, 16-19), Low: CLOPLA1(6, 7, 9, 13, 15), High: CLOPLA1(3, 5, 8, 10, 11, 14). CLOPLA1 is the database of Klimes et al. (1997) and the numbers refer to types of clonal growth.

[b] Seed bank: Transient: «transient» in more than 80 % of all records. Persistent: «Short or long term persistence» in more than 20 % of all records. Following data of Thompson et al. (1997).

appropriate to analyse a vegetation matrix with a high quantity of zeros (Legendre and Legendre 1998), data matrix was transformed with the Hellinger transformation (Legendre and Gallagher 2001). Moreover, for site B differences among blocks were removed. To evaluate the statistical significance of each PRC, Monte Carlo permutation tests were calculated by permuting the whole time series freely within each plot. PRCs were performed using CANOCO 4.5 (ter Braak and Smilauer 2002).

To measure the variation explained by the factors at each sampling date, separate RDAs on the species absolute cover matrix after the Hellinger transformation (Legendre and Gallagher 2001) were calculated separately for each community. Explanatory variables were built with four 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. Abandoned: Ab0 (mowing, trampling and/or manuring) = 0, Ab1 = 1. Interactions between explanatory variables were also included in the model, when simulated (CANOCO option). Moreover, to assess the importance of each factor or interaction, separate RDAs were calculated with each explanatory variable separately. For site B, overall differences among blocks were removed in each analysis and as in the linear models (see above), data from the plots with natural cattle activity were excluded. To test the statistical significance of each RDA, Monte Carlo permutation tests were calculated. For site B, plots were permuted freely within each block.

To observe general trends in species composition after 2 years of treatments, all records of the fifth session were grouped and analysed with two different sets of variables: (1) the conditions of light coded as three binary variables; (2) the treatments coded as in the separate RDAs (see above). Partial RDA (Borcard et al. 1992) was then used to extract the variation in the species data set, explained by both sets of explanatory variables. Rare species with only one record and plots with natural cattle activity were excluded (see above). Species data were transformed with the Hellinger transformation and site effects (A or B) were removed. To examine the relationship between species and treatments, inter-species correlations and species scores divided by standard deviation were chosen (CANOCO options). To test the statistical significance of the RDA, Monte Carlo permutation tests were calculated by permuting freely the plots within each light condition.

To explore the relation between plant traits and treatments, species response groups (*sensu* McIntyre and Lavorel 2001) were related directly to species traits. This was calculated using RDA results of all records of the fifth session, constrained by the factors and their interactions (see above). Variations explained by the sites and the light conditions were removed. On the first two axes, the relationship between explanatory variables and the response variable (species) was found by calculating the angle between the arrows. Groups of species were then identified by classifying each species into a response group, by relating the explanatory variable with the highest relationship (the least angle). To obtain a sufficient number of species in each group, species relating to explanatory variables with similar behaviour were aggregated. Species contributing less (i.e. the length of the arrow) than the equilibrium contribution (Legendre and Legendre 1998) in the first two axes, were excluded.

To relate directly these groups with the functional traits, we used classification trees (Breiman et al. 1984). This method, recently introduced in ecology (De'Ath and Fabricius 2000), permits to explain the variation of a single categorical response variable (in this case species response groups) by explanatory variables, which can be categorical and/or numeric (in this case plant traits, which were categorical or numeric) and which can show missing values. The tree is constructed by repeated splitting of the data, defined by a simple rule, based on a single explanatory variable. At each split, the data is partitioned into two mutually exclusive groups, each as homogeneous as possible. The splitting procedure is then applied to each group separately. The objective is to partition the response into homogeneous groups, but also to keep the tree reasonably small. To explore the relation between species response groups and plant traits, we selected the best trees with a minimum number of 5 species in any node and a minimum number of 2 species in any terminal leaf. Calculations and graphs were performed with the *mvpart* library of R 1.9.1 (R Development Core Team 2004).

Finally, we calculated the C-S-R signature for each plot following Colasanti (2000): (1) each species was assigned to one of the nineteen C-S-R types; (2) within each type present, the sum of the relative cover of all the occurrences was calculated; (3) the sum of each type was assigned to C, S or R, depending on the type (example for CSR type: 33 % for C, 33 % for S and 33 % for R or for C/CR type: 75 % for C, 0 % for S and 25 % for R), inducing for each vegetation record three values and the sum C + S + R = 1. For each of the three values, differences between the first and last records were analysed by fitting multiple linear models (see above).

3.2.3. Results

3.2.3.1. Effects of treatments on plant diversity and structure

The study is based on a total of 510 records. We observed 71 species in A-GM, 71 in B-GM and 77 in B-FE, which corresponded to a total of 111 different species. In B-GM, repeated mowing had a significant effect on difference between species richness at the first and the last records (Table 3.2.3). This factor induced an increase or a low decrease of the species richness. Ma2 plots lost on average 10 species in A-GM and 8 in B-GM, while about 1.7 species was won in Mo1 plots in A-GM and 0.7 in Mo2+Ma2 plots in B-GM. Repeated mowing had also a significant effect on the turnover in both GMs (Table 3.2.3). In A-GM, the most stable plots were Mo1 plots with on average 37 % of species turnover, while the maximum of change was observed in Ma2 plots (63 %). In B-GM the minimum (18 %) of changes was found for Mo2+Ma2+Tr1 plots while the maximum (40 %) appeared in Ma2 plots. In B-FE, trampling had a significant effect on species richness (Table 3.2.3). This factor induced a decrease of the species richness. In B-FE, Mo2+Tr1 plots lost about 4 species, whereas Mo2+Ma2 won 2. For the turnover, trampling had also a significant effect. In this case Mo2+Ma2+Tr1 plots,

Table 3.2.3: ANOVA tables computed for multiple linear regression models of effects of factors and their interactions on difference in species number, turnover, biomass and height (N = 24). For A-GM, which is unbalanced, type I sum of squares was chosen and factors were included in the model in the order presented in the table from left to right. For site B, block effects were removed. The turnover was calculated as the Jaccard distance (1 – Jaccard similarity) on presence-absence data. F: F-value, *P*: *P*-value. ***: *P* < 0.001, **: *P* < 0.01, *: *P* < 0.05, •: *P* < 0.1, ns: not significant.

		Mo		Ma		Tr		MoxMa		MoxTr		MaxTr		MoxMaxTr		Treatments into mean ascending order Italicised: negative values
		F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	
Difference in species number between first and last records	*A-GM*	3.0	•	3.1	•	0.2	ns	0.5	ns	-	-	1.2	ns	-	-	*Ma2 < Tr1 < Ab < Ma1+Tr1 < Ma1 < Mo2 < Mo1+Ma1* < Mo1
	B-GM	13.6	**	0.5	ns	0.7	ns	2.0	ns	3.5	•	1.0	ns	0.7	ns	*Ma2 < Ab < Ma2+Tr1 < Tr1 < Mo2+Tr1 < Mo2+Ma2+Tr1* < Mo2 < Mo2+Ma2
	B-FE	<0.1	ns	0.2	ns	5.1	*	1.3	ns	1.0	ns	0.2	ns	0.3	ns	*Mo2+Tr1<Ma2+Tr1<Tr1<Mo2+Ma2+Tr1* < Ma2 < Ab < Mo2 < Mo2+Ma2
Turnover between first and last records	*A-GM*	11.3	**	10.4	**	0.2	ns	2.6	ns	-	-	0.4	ns	-	-	Mo1 < Mo1+Ma1 < Mo2 < Tr1 < Ab < Ma1 < Ma1+Tr1 < Ma2
	B-GM	16.2	**	4.5	•	0.9	ns	0.9	ns	0.4	ns	2.4	ns	0.4	ns	Mo2+Ma2+Tr1 < Mo2 < Mo2+Tr1 < Ab < Mo2+Ma2 < Tr1 < Ma2+Tr1 < Ma2
	B-FE	2.5	ns	3.5	•	6.6	*	0.1	ns	0.2	ns	2.5	ns	1.0	ns	Ma2 < Tr1 < Mo2 < Ab < Mo2+Ma2 < Mo2+Tr1 < Ma2+Tr1 < Mo2+Ma2+Tr1
Biomass	*A-GM*	16.0	***	7.3	*	0.1	ns	2.9	ns	-	-	0.3	ns	-	-	Mo1 < Mo2 < Tr1 < Ab < Mo1+Ma1 <Ma1+Tr1 < Ma1 < Ma2
	B-GM	6.3	*	10.9	**	<0.1	ns	0.8	ns	1.8	ns	0.8	ns	0.6	ns	Mo2+Tr1 < Mo2 < Tr1 < Mo2+Ma2+Tr1 < Ab < Mo2+Ma2 < Ma2 < Ma2+Tr1
	B-FE	10.5	**	3.6	•	4.4	•	0.1	ns	<0.1	ns	0.7	ns	<0.1	ns	Mo2+Tr1 < Mo2 < Mo2+Ma2+Tr1 < Tr1 < Mo2+Ma2 < Ma2+Tr1 < Ab < Ma2
Height	*A-GM*	21.7	***	2.0	ns	0.7	ns	0.2	ns	-	-	0.8	ns	-	-	Mo1 < Mo2 < Mo1+Ma1 < Tr1 < Ab < Ma1+Tr1 < Ma2 < Ma1
	B-GM	42.7	***	19.2	***	5.2	*	3.4	•	2.2	ns	2.0	ns	<0.1	ns	Mo2+Tr1 < Mo2 < Tr1 < Mo2+Ma2 < Mo2+Ma2+Tr1 < Ab < Ma2+Tr1 < Ma2
	B-FE	43.8	***	3.6	•	26.3	***	0.7	ns	5.4	*	0.4	ns	0.1	ns	Mo2+Tr1 < Mo2+Ma2+Tr1 < Mo2 < Tr1 < Ma2+Tr1 < Mo2+Ma2 < Ab < Ma2

which presented the lowest changes in B-FE, showed the highest values with a turnover of 41 %. At the opposite Ma2 plots were the most stable with a turnover of 24 %.

There was also a great significant impact of factors on vegetation biomass and vegetation height in the three communities (Table 3.2.3). In A-GM, maximum biomass and height were found in Ma2 plots (means = 517 g DM/m^2 and 23 cm) and minimum in Mo1 plots (means = 329 g DM/m^2 and 14 cm). In B-GM, biomass was maximal in Ma2+Tr1 plots with on average 307 g DM/m^2 and the highest mean for the height was 18 cm in Ma2 plots. Minimum for biomass (mean = 163 g DM/m^2) and height (mean = 8 cm) was observed for Mo2+Tr1 plots. In B-FE, maximum mean was found in the Ma2 plots for the biomass (144 g DM/m^2) and for the height (14 cm). Minima were observed in B-GM for Mo2+Tr1 plots (mean = 61 g DM/m^2 and 5 cm).

3.2.3.2. Plant succession induced by treatments

For the principal response curve (PRC) in A-GM, differences between treatments and references (natural cattle activity) over time accounted for 44.4 % of the variation and were highly significant (Figure 3.2.1A). On the first axis, which was also highly significant (Figure 3.2.1A), Ma2 and Mo2 showed larger deviations from the reference. Ab, Ma1, Tr1 and Ma1+Tr1 plots showed a similar picture, but with a less pronounced trend than Ma2. Species with positive weight (e.g. *Agrostis capillaris* and *Dactylis glomerata*) are expected to increase with these treatments. At the opposite, we found all treatments including repeated mowing. With these treatments, species like *Hieracium pilosella* or *Luzula campestris* increased. In B-GM, differences between treatments and references over time accounted for 38.2 % of the variation and were highly significant (Figure 3.2.1B). The first axis, which was also highly significant (Figure 3.2.1B), showed changes in species composition induced by treatments. Ma2 showed, like in A-GM, the largest deviation from the reference. Abandoned plots showed the same, but less important trend. Species with positive weight (e.g. *Agrostis capillaris* and *Veronica chamaedrys*) are linked with these two treatments. At the opposite, we found all treatments including repeated mowing with a low deviation from the control. These treatments, which deviated from the reference at the first autumn, were newly similar to the reference at the second spring. For all these treatments species such as *Trifolium pratense* or *Luzula campestris* increased. Tr1 and Ma2+Tr1 treatments showed an intermediate behaviour. In B-FE, differences between treatments and reference over time accounted for 28.3 % of the variation and were significant (Figure 3.2.1C). In this case the first axis was not significant. Nevertheless, the diagram indicates a different pattern than in both GMs. Treatments showed large deviations above and below the reference. Above, we found Ab linked with species such as *Luzula sylvatica* and *Geranium sylvaticum*. At the end, Ma2 showed a similar picture, but very less pronounced trend. At the opposite, we found all treatments including trampling. *Agrostis capillaris*, which was linked to Ma2 and Ab in both GMs, increased with trampling in this case. Mo2 and Mo2+Ma2 showed seasonal variations and were at the end similar to plots with natural cattle activity.

In both GMs, the effect of all factors and their interactions was significant already in the first autumn (Figure 3.2.2A and B). There was a decrease of the explained variation in the following spring. After that, the variation increased till the end of the experiment with

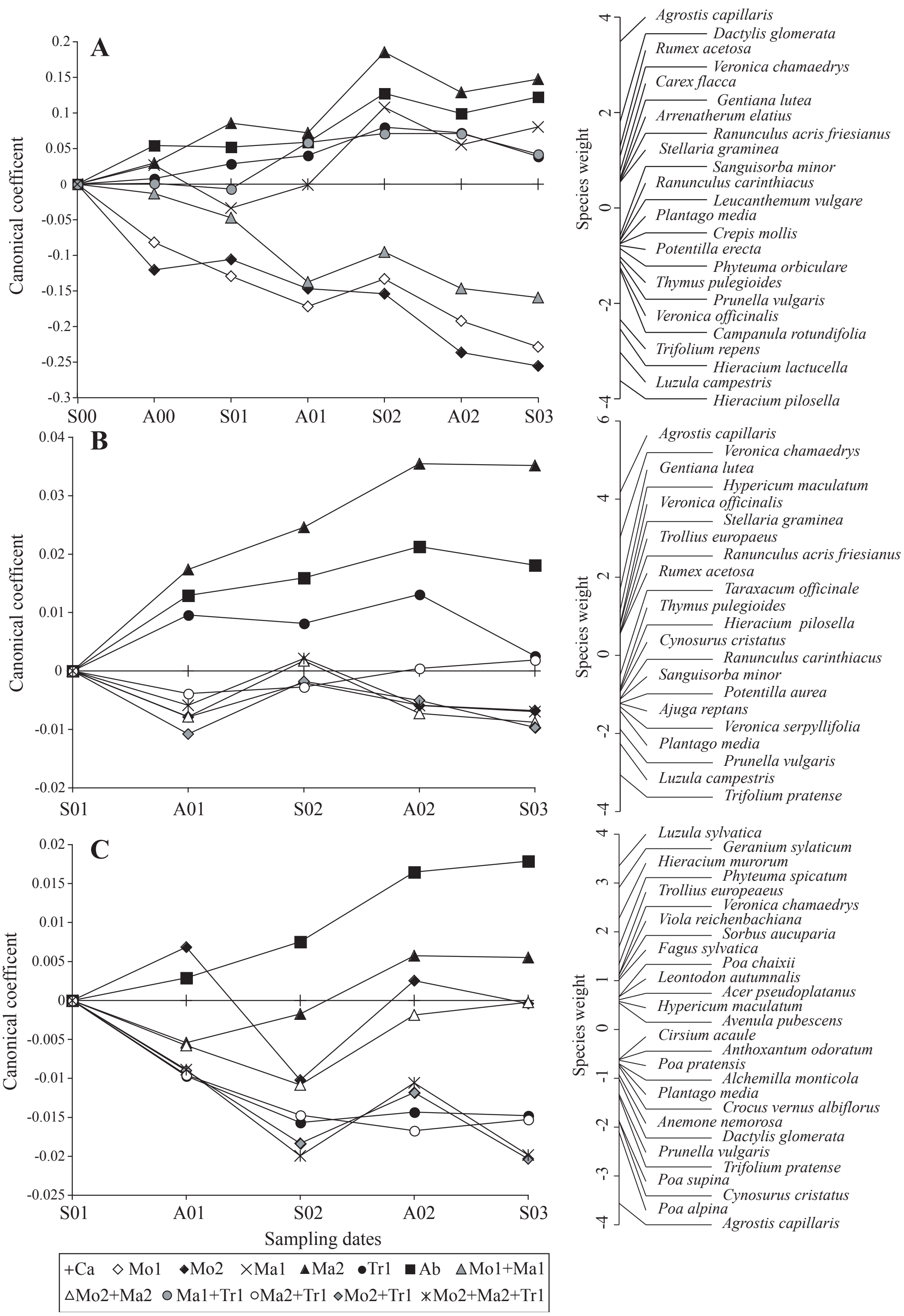

Figure 3.2.1: PRC diagram and species weights on PRC axes 1 for the species matrix in A-GM (A), B-GM (B) and B-FE (C) after Hellinger transformation. Rare species with only one appearance were excluded. Plots with natural cattle activity were used as reference. Only species with weights outside the range -0.5 to +0.5 are presented. Variation explained by treatments while controlling for overall temporal trend (all tests with 999 permutations): A-GM: 44.4 % (*P* = 0.001); B-GM: 38.2 % (*P* = 0.001); B-FE: 28.3 % (*P* = 0.01). Variation explained by axis 1: A-GM: 15.3 % (*P* = 0.001); B-GM: 13.1 % (*P* = 0.001); B-FE: 6.3 % (*P* = 0.19). Treatments: Mo: repeated mowing; Ma: manuring; Tr: trampling; Ab: abandoning; Ca: natural cattle activity; 1 and 2: levels. S: spring; A: autumn; 00-01-02-03: years.

an equivalent amount of explained variation in autumn than in the following spring. At the end, the factors and their interactions explained in both GMs almost 60 % of the total variation. In B-FE (Figure 3.2.2C), the variation increased regularly during the study, was significant from the second spring on and reached almost 45 % at the end of the experiment. The three communities presented at the first records a high amount of non-significant explained variation. This can be due to the high number of explanatory variables (6 in A and 8 in B) compared to the number of samples (24) or species (Legendre and Legendre 1998). The importance of each factor explaining variation in the species matrices varied between communities (Figure 3.2.2D, E and F). Mo was the most important factor in both GMs, while Tr is the most important in B-FE. Furthermore, the decrease of explained variation between the first autumn and the second spring observed in GMs for the complete model, did not appear in each case here. For example in B-GM (Figure 3.2.2E), Mo showed a very important decrease, while Tr did not change. Relation between factors and their interactions at the last record session showed similar pattern for the three

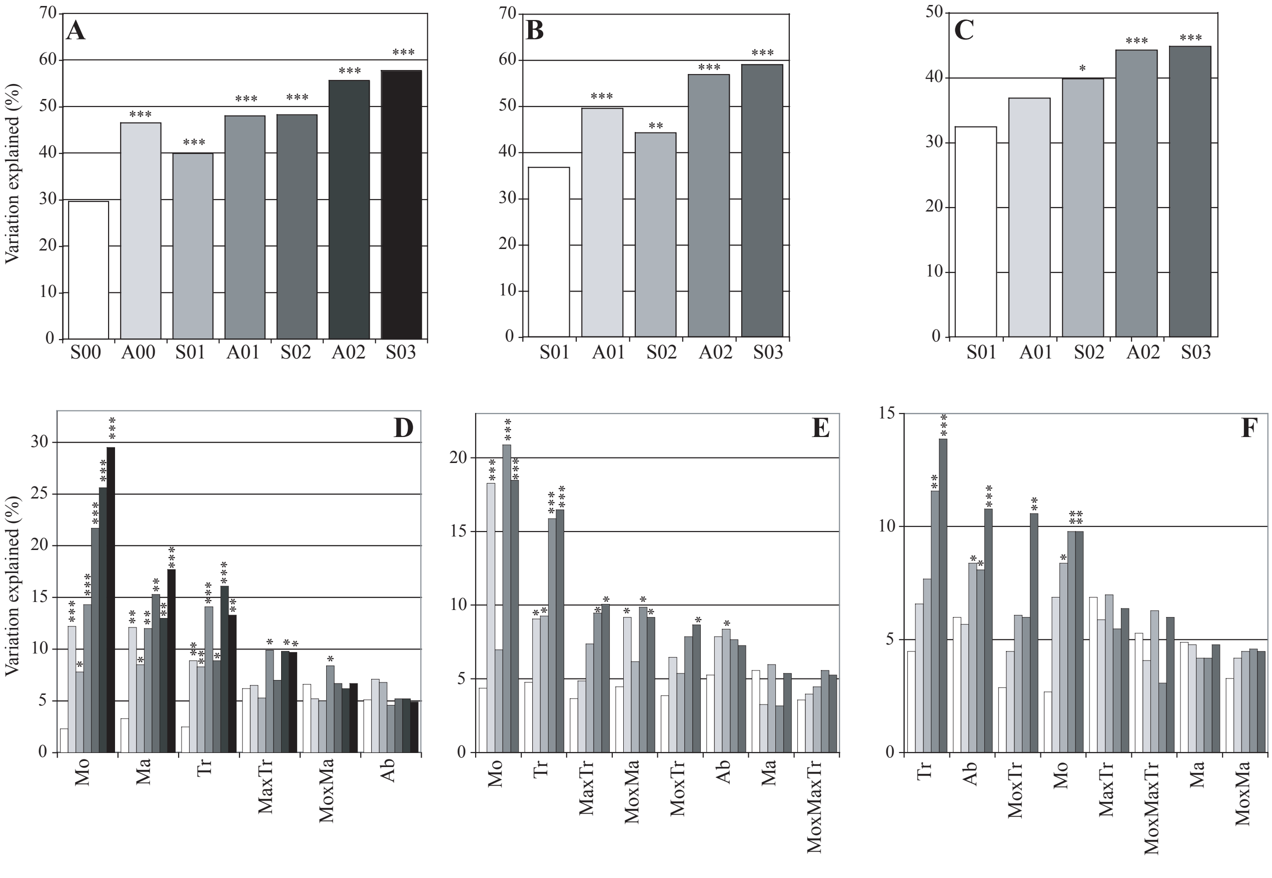

Figure 3.2.2: Evolution of variation explained by the factors and their interactions during the experiment by mean of separated RDAs on species records (without plots with natural cattle activity) at each sampling date after Hellinger transformation. Above: variation explained by the full model (all factors and their interactions) in A-GM (A), B-GM (B) and B-FE (C). S: spring; A: autumn; 00-01-02-03: years. Below: variation explained by each treatment (Mo: repeated mowing; Ma: manuring; Tr: trampling; Ab: abandoning) or interaction separately in A-GM (D), B-GM (E) and B-FE (F). Different greys showed different recording sessions as in A, B or C. Asterisks showed significant result of the Monte Carlo permutation test (999 permutations): ***: $P = 0.001$; **: $P < 0.01$; *: $P < 0.05$.

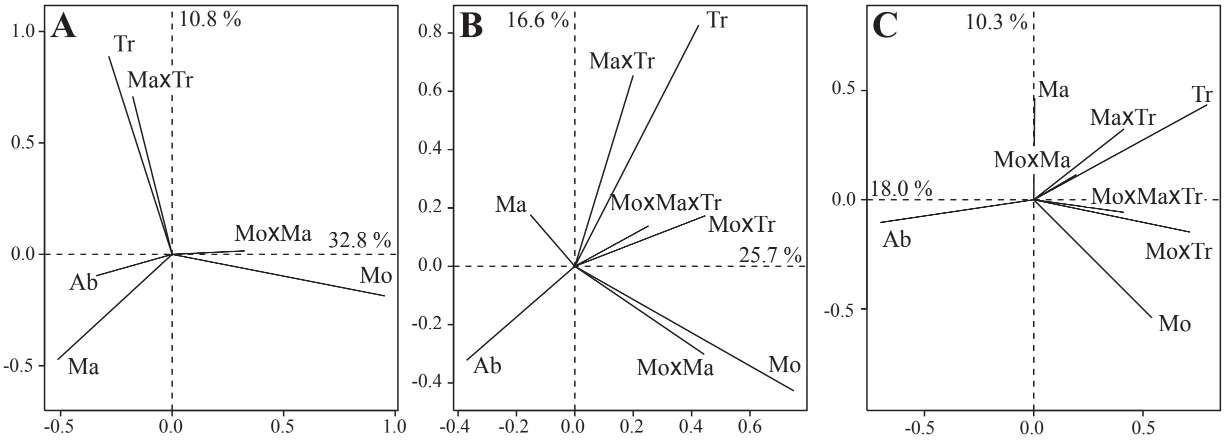

Figure 3.2.3: RDAs on each community type (A: A-GM; B: B-GM; C: B-FE) for species records after Hellinger transformation at the last session (spring 2003), constrained by the treatments (Mo: repeated mowing; Ma: manuring; Tr: trampling; Ab: abandoning) and their interactions (when they were simulated). Block effects were removed for site B. Variation explained by all explanatory variables: A: 57.7 % (*P* = 0.001 with the Monte Carlo permutation test after 999 permutations); B: 59.0 % (*P* = 0.001); C: 44.8 % (*P* = 0.001).

communities (Figure 3.2.3). Tr and MaxTr showed in each case the same behaviour and MoxTr and MoxMaxTr presented similar trends in B-GM and B-FE. In both GMs, the first axis separated Mo and its interactions from Ab and Ma and the second axis Tr and its interactions from the other factors. In B-FE, the first axis separated Ab from the other factors and the second axis Mo from Ma and Tr. In this MoxMa, linked to Mo in both GMs, showed an intermediate behaviour between Mo and Ma.

3.2.3.3. General trend at the fifth records

For the three community types together, light conditions explained about 33 % and treatments about 14 % of the variation at the fifth record session (Figure 3.2.4A). Relation between factors and their interactions without the effect of site and light conditions showed a similar pattern (Figure 3.2.4B) than in Figure 3.2.3, in which communities were analysed separately. Figure 3.2.4C showed the relations between species for the same analysis as in Figure 3.2.4B.

3.2.3.4. Classification tree

Composition of each species response group is presented in Figure 3.2.4C. Five species response groups were defined depending on: 1: Mo and MoxMa (22 species), 2: MoxTr and MoxMaxTr (7 species), 3: Tr and MaxTr (5 species), 4: Ma (9 species) and 5: Ab (16 species). The first split of the classification tree, depending on plant height, separated clearly the groups 1 and 2 from 4 and 5 (Figure 3.2.5). Both following splits depended on life-forms. Grasses characterised group 4 and legumes group 2. Group 1 was principally composed by rosettes or leafy stems species, which are not legumes and which have a maximum height lower than 35 cm. Group 5 was mainly composed by species taller than 55 cm, which were not grasses, presented a duration of flowering shorter than 5 months and a high lateral spread. Group 3 was not clearly defined by this model.

C-S-R strategy

In the C-S-R space the three communities were placed in the middle of the triangle (Figure 3.2.6) with a little deviation in direction of the S-corner. The pattern of the trajectories

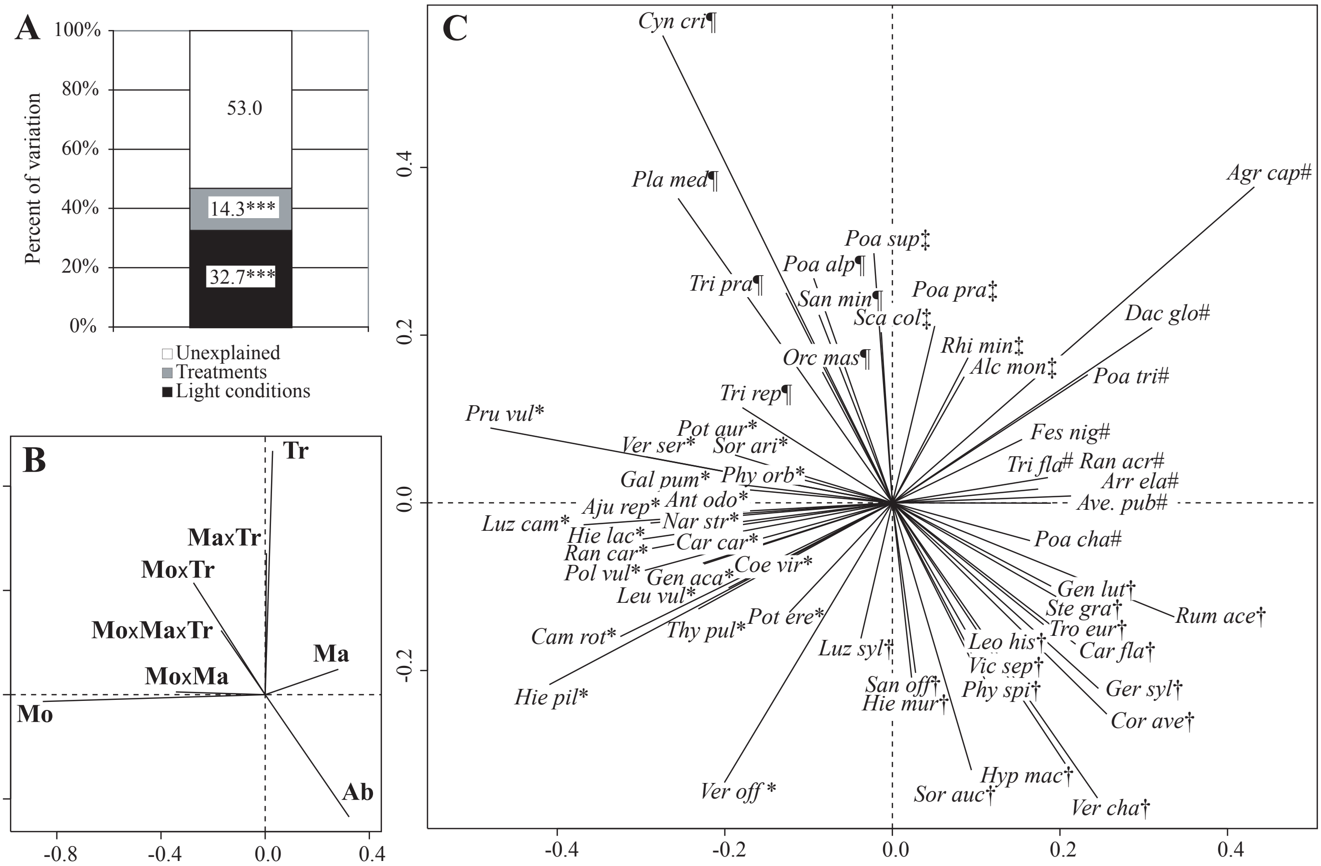

Figure 3.2.4: RDA on species records after Hellinger transformation at the fifth session for the three community types together. Rare species with one record were excluded. Explanatory variables were the treatments (Mo: repeated mowing; Ma: manuring; Tr: trampling; Ab: abandoning) and their interactions, and the light conditions (each level coded as binary variable). Site effects were removed. A. Variation partitioning (there was no shared variation between treatments and the light conditions). Asterisks showed results of Monte-Carlo permutations test (999 permutations) on each part of the variation (***: $P = 0.001$). B and C Plots of explanatory variables (B) and species (C) for the effect of treatments on species matrix without the effect of the hours of sunshine. Explained variation: axis 1: 8.0 %, axis 2: 6.1 %. Variation explained by all explanatory variables: 21.7 %. The Monte Carlo permutation test was significant for the first axis ($P = 0.001$), for the second ($P = 0.001$) and for the overall regression ($P = 0.001$). Species with a arrow length larger than the circle of equilibrium (Legendre and Legendre 2001) are presented with signs indicating the species response groups (1: *, 2: ¶, 3: ‡, 4: #, 5: †, see in the text for details) : *Agr cap = Agrostis capillaris; Aju rep = Ajuga reptans; Alc mon = Alchemilla monticola; Ant odo = Anthoxanthum odoratum; Arr ela = Arrhenatherum elatius; Ave pub = Avenula pubescens; Cam rot = Campanula rotundifolia; Car fla = Carex flacca; Car car = Carex caryophyllea; Coe vir = Coeloglosum viride; Cor ave = Corylus avellana; Cyn cri = Cynosurus cristatus; Dac glo = Dactylis glomerata; Fes nig = Festuca nigrescens; Gal pum = Galium pumilum; Gen aca = Gentiana acaulis; Gen lut = Gentiana lutea; Ger syl = Geranium sylvaticum; Hie lac = Hieracium lactucella; Hie mur = Hieracium murorum; Hie pil = Hieracium pilosella; Hyp mac = Hypericum maculatum; Leo his = Leontodon hispidus; Leu vul = Leucanthemum vulgare; Luz cam = Luzula campestris; Luz syl = Luzula sylvatica; Nar str: Nardus stricta; Orc mas = Orchis mascula; Phy orb = Phyteuma orbiculare; Phy spi = Phyteuma spicatum ssp. spicatum; Pla med = Plantago media; Poa alp = Poa alpina; Poa cha = Poa chaixii; Poa pra = Poa pratensis; Poa sup = Poa supina; Poa tri = Poa trivialis ssp. trivialis; Pol vul = Polygala vulgaris; Pot aur = Potentilla aurea; Pot ere = Potentilla erecta; Pru vul = Prunella vulgaris; Ran acr = Ranunculus acris ssp. friesianus; Ran car = Ranunculus carinthiacus; Rhi min = Rhinanthus minor; Rum ace = Rumex acetosa; San min = Sanguisorba minor; San off = Sanguisorba officinalis; Sca col = Scabiosa columbaria; Sor ari = Sorbus aria; Sor auc = Sorbus aucuparia; Ste gra = Stellaria graminea; Thy pul = Thymus pulegioides; Tri fla = Trisetum flavescens; Tri pra = Trifolium pratense; Tri rep = Trifolium repens; Tro eur = Trollius europaeus; Ver cha = Veronica chamaedrys; Ver off = Veronica officinalis; Ver ser = Veronica serpyllifolia; Vic sep: Vicia sepium.*

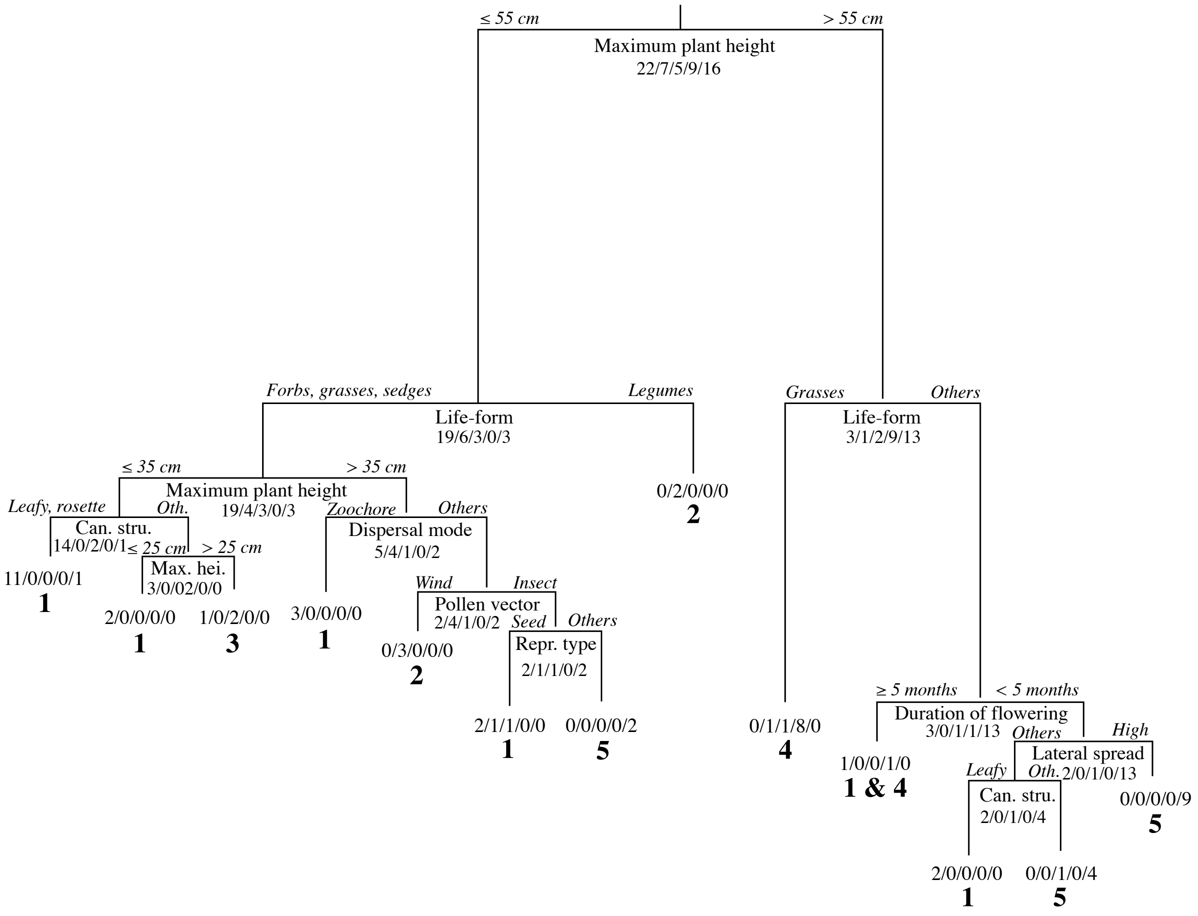

Figure 3.2.5: Classification tree on the five species response groups regarding to treatment reactions (see Fig. 3.2.4). The explanatory variables were all plant traits of the Table 3.2.1. Each leaf is labelled (classified) according to the predominant group (1: Mo and Mo×Ma; 2: Mo×Tr and Mo×Ma×Tr; 3: Tr and Ma×Tr; 4: Ma; 5: Ab). At each node and at each leaf, number of species per group is indicated in the following order: 1/2/3/4/5. The misclassification rate of the model was 13.6 %, compared to 62.7 % for the null model. Abbreviations: Can. stru. = Canopy structure; Max. hei. = Maximum plant height; Oth. = Others; Repr. type = Reproduction type (see Table 3.2.1 for details).

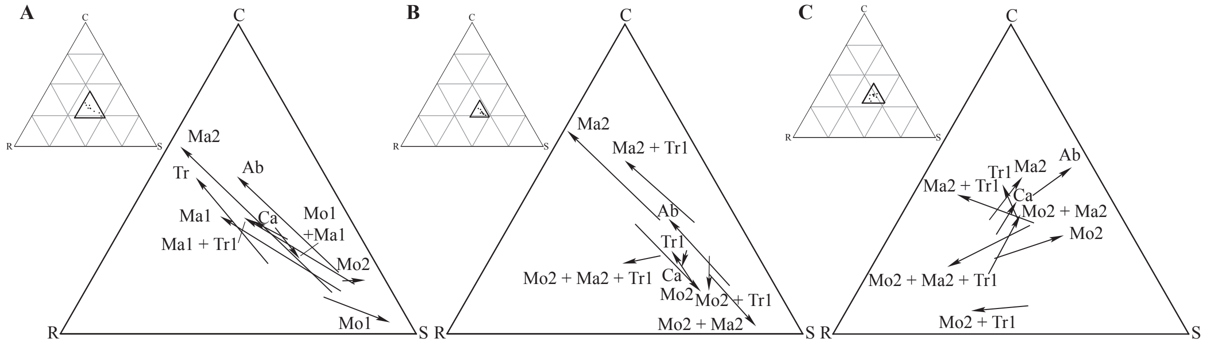

Figure 3.2.6: Mean trajectories in C-S-R space of communities between initial and final stage for A-GM (A), B-GM (B) and B-FE (C). Little triangles at the left show the place of the bigger in the complete C-S-R space. Treatments are indicated at the end of arrows. Mo: repeated mowing; Tr: trampling; Ma: manuring; Ab: abandoning; Ca: natural cattle activity; 1 and 2: levels.

Table 3.2.4: ANOVA tables computed for multiple linear regression models of effects of factors and their interactions on evolution (difference between the first and the last record) of C-S-R signature (N = 24). For A-GM, which is unbalanced, type I sum of squares was chosen and factors were included in the model in the order presented in the table (from left to right). For site B, block effects were removed. F: F-value, *P*: *P*-value. ***: *P* < 0.001, **: *P* < 0.01, *: *P* < 0.05, •: *P* < 0.1, ns: not significant.

		Mo		Ma		Tr		MoxMa		MoxTr		MaxTr		MoxMaxTr		Treatments into mean ascending order
		F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	Italicised: negative values
C	*A-GM*	35.2	***	5.0	*	<0.1	ns	8.5	**	-	-	1.7	ns	-	-	*Mo1+Ma1* < *Mo1* < Mo2 < Ma1 < Ab < Ma1+Tr1 < Tr1 < Ma2
	B-GM	18.8	***	1.0	ns	0.1	ns	2.1	ns	2.1	ns	<0.1	ns	<0.1	ns	*Mo2* < *Mo2+Ma2* < *Mo2+Tr1* < *Mo2+Ma2+Tr1* < Tr1 < Ma2+Tr1 < Ab < Ma2
	B-FE	1.5	ns	<0.1	ns	2.8	ns	<0.1	ns	2.5	ns	1.4	ns	0.4	ns	*Mo2+Ma2+Tr1* < *Mo2+Tr1* < Mo2 < Ab < Ma2+Tr1 < Tr1 < Ma2 < Mo2+Ma2
S	*A-GM*	26.1	***	3.3	•	<0.1	ns	3.0	ns	-	-	<0.1	ns	-	-	*Ma2* < *Ma1+Tr1* < *Tr1* < *Ma1* < *Ab* < Mo2 < Mo1+Ma1 < Mo1
	B-GM	12.4	**	1.4	ns	0.5	ns	<0.1	ns	3.5	•	<0.1	ns	<0.1	ns	*Ma2* < *Ma2+Tr1* < *Ab* < *Tr1* < *Mo2+Ma2+Tr1* < Mo2 +Tr1 < Mo2+Ma2< Mo2
	B-FE	0.3	ns	5.0	*	34.2	***	<0.1	ns	0.1	ns	<0.1	ns	2.6	ns	*Ma2+Tr1* < *Mo2+Ma2+Tr1* < *Mo2+Tr1* < *Tr1* < Mo2+Ma2 < Ma2 < Ab < Mo2
R	*A-GM*	12.0	**	1.3	ns	<0.1	ns	0.2	ns	-	-	0.7	ns	-	-	*Mo1* < *Mo2* < *Mo1+Ma1* < Ab < Tr1 < Ma1 < Ma1+Tr1 < Ma2
	B-GM	1.6	ns	0.9	ns	0.8	ns	<0.1	ns	2.6	ns	0.1	ns	<0.1	ns	*Mo2* < *Mo2+Ma2* < Tr1 < Mo2+Tr1 < Ab < Ma2+Tr1 < Mo2+Ma2+Tr1 < Ma2
	B-FE	0.7	ns	2.9	ns	41.2	***	<0.1	ns	3.5	•	1.4	ns	0.3	ns	*Mo2* < *Mo2+Ma2* < *Ma2* < *Ab* < *Tr1* < Mo2+Tr1 < Ma2+Tr1 < Mo2+Ma2+Tr1

in the C-S-R space was similar in both GMs, but B-FE showed a very different behaviour (Figure 3.2.6). Multiple linear regressions on differences between the first and the last record showed significant differences (Table 3.2.4). In both GMs, repeated mowing promoted S-strategy and had a negative impact on C-strategy. Furthermore, R-strategy decreased in A-GM. Manuring had a positive impact on C-strategy in A-GM and a negative impact on S-strategy in B-FE. Finally, trampling acted negatively on S-strategy and positively on R-strategy in B-FE.

3.2.4. Discussion

3.2.4.1. Vegetation structure and species richnesss

Effects of treatments on vegetation structure, had an important impact and were similar in the three vegetation types. In site B, the combination of Mo2 and Tr1 induced a clearly lower biomass and vegetation height. Gremmen et al. (2003) observed also a reduction of vegetation height induced by trampling and Cole (1995a) a decrease of vegetation cover with increased trampling. According to our hypotheses, manuring induced higher biomass, but not significant in B-FE where a combination of Ma2 with other treatments softened the effect of nutrient addition. Interestingly, trampling affected height but not biomass in site B. In B-FE trampling favoured short or medium grasses (*Agrostis capillaris*, *Poa supina*) and disadvantaged tall forbs like *Geranium sylvaticum* or *Phyteuma spicatum*. This fact induced a smaller but denser vegetation in trampled plots and, consequently for a same biomass a difference in height.

Concerning species richness, all species appearing in the plots after treatments belonged to the original communities and therefore were adapted to regular cattle activity. Most treatments provoked a decrease of the number of species. By applying homogeneously each treatment on each plot, we erased the original heterogeneity, promoting species richness (Schläpfer et al. 1998). Nevertheless, Mo1 in site A and Mo2 and Mo2+Ma2 in site B promoted species richness. The treatments acted differently in the three communities. In both GMs, Mo is the main factor acting positively on species richness, while in B-FE trampling acted negatively on species richness. For trampling, this decrease is in accordance with Liddle and Greig-Smith (1976), who recorded a decrease in species richness with increasing intensity of trampling. The greater difference between both GMs and B-FE lay in the effect of Ma2 and Ab, which had a heavy negative impact on species richness in both GMs, while they increased the number of species in B-FE. This fact can be explained by a different starting position of the community along the "humped-backed" curve, describing the relation between biomass and species richness (Grime 1973a and b; Rapson et al. 1997, but see Oksanen 1996). For Ab and Ma2 biomass was high compared to other treatments, but in B-FE it was about half of the amount of B-GM and two-thirds of the amount in A-GM. Al-Mufti et al. (1977), describing the relation between maximum standing crop plus litter and species richness of herbs, showed that woodlands, having a lower biomass of herbs, were placed before the maximum of species richness, while grassland were at the maximum or already at the decline of the curve. Consequently, the increase of biomass induced by nutrient addition (Ma1 or Ma2) or the absence of disturbance (Ma1 or Ma2 and Ab) could have an inverse impact on species richness. If we then suppose that both GMs were after the maximum along the "humped-backed" curve, the increase of species richness by Mo1 or Mo2 could also be explained by the decrease of biomass.

3.2.4.2. Relation between treatments and plant succession

Succession induced by treatments differed among the three communities. Ma2 plots were the most stable between first and last records in B-FE, while the most stable plots were Mo2+Ma2+Tr1 in B-GM and Mo1 in A-GM (Table 3.2.1, turnover). Ma2 plots showed the more severe deviation from plots with natural cattle activity in B-GM. In B-FE plots on the contrary, Tr alone or in combination with other factors, and abandoned plots showed the heavier deviations (Figure 3.2.1). In A-GM, as in B-GM, Ma2 showed a great deviation, but in this case plots with repeated mowing also showed important differences from reference. The various levels of repeated mowing induce the same pattern, while the higher level of manuring showed clearly a more prominent deviation than at the lower level. Abandoned plots showed in each case the same trend than Ma2. These major changes after the grazing stop have already been observed by Krahulec et al. (2001) or Moog et al. (2002). Differences between communities can be explained by a different equilibrium between communities and cattle activity at the beginning of the experiment. As we showed in another study (Kohler et al. 2004b and § 4.1), underwood communities are less grazed than grazed meadows, particularly in spring. Furthermore, stocking rate was higher in site B compared to site A. Therefore, at the beginning of the experiment were different disturbance regimes and consequently different states of vegetation. Seabloom and Richards (2003) showed foraging preference of herbivores (in this case gophers) creating multiple stable equilibria within plant communities and possibly generating multiple plant communities persisting within a herbivore territory.

Results of the separate RDAs showed very interesting dynamic properties of each community (Figure 3.2.2). In B-GM, treatment effects were already significant the first autumn, but the effect got less important in the following spring, after winter and absence of treatments in early spring. The resilience of the community already observed in A-GM (Kohler et al. 2004a and § 3.1) could be then confirmed in B-GM. Furthermore, the fact that the experiment in B-GM began in another year than in A-GM proved this observation not being induced by a particular climatic situation. In both GMs, when considering all factors and interactions together, the resilience did not appear the following years and the explained variation increased till to the end of the experiment. Beholding each factor separately, it is clear that effect of repeated mowing disappeared between the first autumn and the following spring in B-GM, while trampling showed the same explained variation for both sampling periods. Furthermore, the resilience of the community appeared also the second spring after repeated mowing. These results were only partly confirmed by observations in A-GM. In this case repeated mowing showed also a decrease of the explained variation between the first autumn and the following spring, but this was not the case for the following years. For trampling the explained variation was the same between first autumn and the following spring, but thereafter the community showed resilience for this treatment. This very interesting dynamical behaviour was discovered, because of the two recording times per year. Studies on grassland dynamics have generally a temporal resolution of one year or more (e.g., Zobel et al. 1996; Kahmen et al. 2002; Mariott et al. 2002) or are synchronic (e.g., Mitlacher et al. 2002; Vandvik and Birks 2002), so such a phenomenon is not observed. Successions are generally described as directional changes in species composition (Platt and Connell 2003). This was the case in B-FE, where the resilience did appear neither in the global model nor in each factor separately. Vegetation reaction to the treatments was weaker than in GMs showing higher resistance ability to changes of the community with low light availability. Another important difference with GMs: the first significant results appeared in the first spring after the beginning of the experiment. Contrarily to GMs, the effect of treatments can then be greater in spring compared to the preceding autumn. It seemed that this community continued to change in the direction stimulated by treatments, despite the absence of the treatments during winter and the beginning of spring.

The importance of each treatment for explaining the species variation varied also depending on the community (Figure 3.2.2). In both GMs repeated mowing dominated. In A-GM it was followed by manuring and trampling and in B-GM by trampling and the interaction Ma x Tr. This hierarchy was different in B-FE with trampling as most important factor following by Ab and the interaction Mo x Tr. The relation between treatments showed the same pattern (Figure 3.2.3). Mo and Tr have a stronger influence on short-term vegetation dynamic than Ma. It seems Mo and Tr are limiting factors for species composition while Ma is not. The significant impact of manuring on biomass did not seem to induce any impact on species composition. Mo x Ma in B-FE displayed the only case where Ma induced a different behaviour than the treatment coupled with it.

By contrast, interaction between Mo and Tr induced an intermediate species composition between the compositions induced by each treatment alone.

3.2.4.3. Treatments and vegetation composition

Repeated mowing was characterised by species such as *Campanula rotundifolia*, *Hieracium pilosella* or *Anthoxantum odoratum*. The role of palatability in species response to grazing is well known (Fernandez-Gimenez and Allen-Diaz 1999; Jauffret and Lavorel 2003). It is clear that repeated mowing simulates frequent lost of above-ground biomass, but not the selectivity of cattle. Nevertheless, it seems plant selectivity playing a weak role at fine scale in our system. Firstly, there is only one unpalatable species, *Gentiana lutea*, and it is even grazed when stocking rate is high (personal observation). Secondly, at medium scale, cattle select community types (underwood, lawn, grazed meadow, ...) or patch of preferred herbage (Dumont et al. 2002, Rook et al. 2004). At fine scale (within the community or patch) there is no evidence for selectivity of species in grassland with about eight species per dm^2 (Kohler et al. 2004b and § 4.1). Mouthparts form explain the incapacity of cattle to select species where preferred and non-preferred plant grow together on a fine-scale mixture (Grant et al. 1985). Consequently, except for *Gentiana lutea* in case of low stocking rate, repeated mowing was a realistic simulation of herbage removal by cattle. Trampling was linked to species such as *Trifolium pratense*, *Alchemilla monticola* or *Sanguisorba minor*. *Poa supina*, a typical species of trampled vegetation appeared only in B-FE (Figure 3.2.1C). This species is not linked to shade situations. In another experimental study (§ 3.4) we showed that this species is typical of gap colonisation. We could then suppose that this species is favoured by trampling, but can colonise a new area only if there are gaps in the vegetation. This was the case in B-FE, where vegetation is sparse, but not in both GMs, where our trampled treatment was not enough heavy to create gaps in the dense vegetation. In B-FE (Figure 3.2.1C), species typical of underwood such as *Geranium sylvaticum*, *Phyteuma spicatum* or *Hieracium murorum* were sensible to trampling. The decrease of such species induced a community composition more similar to the community observed in both GMs. Manuring was related to species such as *Dactylis glomerata*, *Ranunculus acris, Agrostis capillaris* or *Festuca nigrescens*. It is interesting that both last cited species are not eutrophic species, but appeared to react positively to manuring at short term. Bakker and Olff (2003) showed cattle dung containing a high number of seeds of various species and cattle playing an important role for the dispersion of plant species. In addition, they showed that cattle dung pats by giving a strong nutrient stimulus induce tall vegetation and therefore limit light conditions and opportunities for seeds to germinate. In our case, plots with Ma1 or Ma2 alone reacted globally like Ab plots (with no addition of the mixture of dung and urine) (Figure 3.2.1), but RDAs showed some differences between Ma and Ab. With our method it was not possible to separate and control species coming from seeds, included in the dung and urine mixture and to know if these differences are induced by this phenomenon or not. Abandoned plot were characterised by *Veronica chamaedrys*, *Hypericum maculatum* or *Geranium sylvaticum*. Furthermore, this treatment without disturbance and with a lower concurrence between species than manuring plots (lower biomass) favoured two seedlings species (*Corylus avellana* and

Sorbus aucuparia). In other cases, seedlings did not appear at all in both GMs, showing the great difficulty for tree species to germinate in the dense vegetation of grazed meadow, independently of the treatments.

3.2.4.4. Impact of treatments on plant traits

Our results confirm the high relevance of plant height to predict vegetation dynamics (Westoby 1998). This trait was retained in the classification tree for the first split, separating species responding positively to trampling and mowing and species linked to manuring and abandoned plots. Furthermore, this trait discriminated two other splits at low level. Reduced height in response to disturbance (in our case trampling or repeated mowing), in particularly, to grazing, is already well documented (Noy-Meir et al. 1989; Diaz et al. 1992; Rodriguez et al. 2003). For mowing, Klimes and Klimesova (2002) explained that with the equal level of cutting for all plants, the larger plants lose a higher proportion of their above-ground biomass and are therefore more affected by this disturbance.

The second split of the tree was determined in both sides by the life-forms. Many studies (Noy-Meir et al. 1989, Lavorel et al. 1997) showed significant effects of disturbances on the major life forms. McIntyre et al. (1999) proposed to separate the major life forms *a priori* and then analyse relation between disturbance and functional traits within each group. Grasses, as tall plants, were clearly advantaged by manuring, whereas others life-forms were linked to abandoned area. Legumes, as small plants, were linked to the interaction between Mo and Tr. These results depend only on two species (*Trifolium repens* and *T. pratense*) and consequently, it is dangerous to generalise. Nevertheless, Lavorel et al. (1999a) showed in a Mediterranean pasture dominated by annuals that legume biomass increased with grazing. Furthermore, Wright et al. (2001) showed at short-term in a mixed perennial ryegrass/white clover sward, cattle grazing increasing biomass of white clover. For mountain riparian vegetation, Popolizio et al. (1994) observed higher percent cover of legumes in long-term grazed areas compared to areas protected from grazing.

The lower splits separated species response groups less clearly and terminal leaves presented generally few species linked to various groups. Furthermore, both groups 2 and 3 did not present a clear pattern. Nevertheless, we can point out three important terminal nodes. On the left of the tree, there is a leaf with a high number of repeated mowing increasers, which are rosette or leafy stem plants, not legume species and smaller than 35 cm. Many authors (McIntyre et al. 1995; Lavorel et al. 1998; Stammel et al. 2003) highlighted the relevance of the rosette attribute in disturbed ecosystems. Rodriguez et al. (2003) showed a decrease of rosette species after the removal of domestic herbivores. At this terminal node only one species, linked to abandoned area was misclassified, i.e. *Veronica chamaedrys,* possessing the same attributes as other species of this terminal node, except for a low lateral spread, while the majority of other species presented a high lateral spread. This is consistent with McIntyre and Lavorel (2001) who showed that wide spread forbs with low growth were grazing-tolerant. Only two criteria (grasses with height superior of 55 cm) permitted to classify 8 of the 9 species linked to manuring. The missclassified species was *Ranunculus acris*, an eutrophic forb. On the right of the tree, we found a majority of species linked to abandoned plots, characterized by not grasses, tall species with a flowering duration shorter than 5 months and a high lateral spread. At this terminal node, there was no misclassification.

Regeneration traits were clearly not of primary importance to separate the species response groups. Burke and Grime (1996) showed smaller-seeded species being more dependent on disturbance for establishment, whereas large seeds permitted seedling establishment in closed cover of vegetation. Many other authors confirmed this result (e.g. Winn 1985, Suding et al. 2003). In our case, traits concerning seed mass and seed length were not selected by the computing process. Only traits concerning seed and pollen dispersion were selected, and at a low level in the tree hierarchy. Stammel et al. (2003) showed that seed dispersal traits did not respond significantly to grazing or mowing. By contrast, McIntyre and Lavorel (2001) found that anemochore grasses were associated with low grazing intensity. In our case zoochory permits to separate mowing increaser, which are taller than 35 cm, from others. The low ability of regeneration traits to separate groups could be explained by the fact that sexual regeneration is probably not the primary strategy to regenerate in the closed canopy of grasslands (Marriott et al. 2002), particularly in GMs. Noble and Slayter (1980) pointed on the importance of considering vegetative regeneration (or resprouting) ability in disturbed vegetation. Unfortunately detailed information concerning resprouting ability is not easily obtainable for species-rich herbaceous communities (Klimesova and Kilmes 2003).

Our method to determine traits characterising species response groups present many advantages: (1) We can directly analyse species response groups with the trait matrix. (2) It permits a hierarchical analysis and allows to use the same criteria at different level and in different part of the tree. Furthermore, two or more leaves can characterise the same response group permitting various combination of traits adapted at the same disturbance. The importance of considering plant functional classification in a hierarchical way was pointed out by Pausas and Lavorel (2003) and Suding et al. (2003). Classification trees permit this without an *a priori* hierarchy, as proposed by McIntyre et al. 1999. (3) Main traits are selected by the computing process and therefore a high number of traits can be included in the analysis without increasing the complexity of the results. (4) Missing values, which are frequent in the framework of functional traits are tolerated. If an explanatory variable used to form a split has missing values, we determine the best agreeing variable (surrogate variable (Breiman et al. 1984)) with the original splitting variable and use it to classify species with missing values. Furthermore and contrarily to other methods concerning functional traits (e.g. McIntyre and Lavorel 2001) quantitative variables can be included into the model. This has the advantage that classes subdividing a quantitative variable are determined by the analysis and are not selected *a priori* on subjective criteria. (5) The tree can directly be used for predictions. In our case, we used the method to explore the relation between species response groups and plant traits. Our model has to be validated with independent data from other experiments or observations, before it may be used to predict behaviour of species not included in the observations.

The principal methodological difficulty concerned the creation of species response groups in the context of constrained multivariate analysis in a continuum of species responses. Nevertheless, the solution seems to give relevant results in the context of our complex experiments with three factors inducing various gradients. Any attempt to classify or delineate types, involves the arbitrary drawing of boundaries and according to the chosen method, species near the boundaries could have various classifications.

3.2.4.5. Relevance of C-S-R strategies

The three community signatures were placed almost in the middle of the C-S-R triangle. This is in accordance with Grime (2001), who predicted a vegetation composed of species with intermediate characteristics between those of competitor, stress-tolerator and ruderal in unfertilized extensive pasture in temperate region. Reactions to treatments induced short trajectories in the C-S-R triangle, which is in accordance to the not severe changes induced by the treatments, as we showed in a previous paragraph. Even so we found significant effects of treatments and various reactions of the three communities. Therefore, with the same treatments and with communities starting almost at the same place in the C-S-R triangle, trajectories induced by treatments can be different with a major deviation between the C and S-corners in both GMs and between the R and S-corners in B-FE. As we showed with other analyses, ranking of importance of treatments varied between communities. In B-FE, trampling induced the major change and, as predicted by the model, plots with this treatment and particularly these in combination with other treatments tended to the R-corner. By contrast in both GMs, repeated mowing was the most important factor and induced a deviation to the S-corner, whereas plots without this treatment (principally Ma1, Ma2 and Ab) tend to the C-corner. Increase of competitor strategy without disturbance is then verified. In B-GM, only the triple treatments showed a short shifting in the direction of the R-corner. Following the definition of Grime (2001), repeated mowing should be considered as a disturbance, because it induce a partial or total destruction of the plant biomass. This definition does not include frequency and intensity of the disturbance (van der Maarel 1993). Oksanen and Ranta (1992) pointed out that specific attributes of grazing tolerance incorporate elements of either S or R strategies. Furthermore, they interpreted S-strategy as an adaptation to high-natural grazing pressure, which culminates in a moderately stressful habitat. However, grazing might better be considered as stress factor when acting permanently or regularly upon adapted plant communities. In fact, these concepts are strongly scale-dependent and the same factor can act as a disturbance (accidentally destroying biomass) at the individual level and at short-term, and as a stress or constraint (permanently limiting biomass production) at the community level and on a longer term. Following the trajectories in the C-S-R triangle, our trampling treatment seemed acting as a disturbance, whereas our repeated mowing treatment as a stress factor. In B-FE, repeated mowing alone showed additionally a higher deviation in direction to the S-corner.

3.2.5. Conclusion

Our experiments showed clearly cattle activities inducing various dynamics in the herbaceous layer of pastures at species level and at functional level. Furthermore, high shade conditions produced different dynamics, compared with the one observed in open or moderately closed areas, where communities presented resilience against disturbances. The results reveal a high complexity with species reacting in a multitude of ways, depending on the type of disturbances and their interactions. Otherwise this complexity is higher in reality where gap creation by heavy trampling, not simulated in this experiment, induces other dynamics (§ 3.4) and where soil conditions can change within a very fine mosaic (Gobat et al. 1989). Our observations support the dynamic keyhole-key model (Gigon and Leutert 1996), which permits to explain the coexistence of high number of species in grasslands. Where species α-diversity (keys) and microsite diversity (keyholes) match, coexistence is likely to occur. By crossing biogenic disturbance, induced by cattle activity (but also by small herbivores like voles), with abiogenic microsite diversity, induced by light conditions and soil types, we can define a great number of potential microsites, which could explain the high species richness of mountain wooded pastures. Therefore, it is possible to define a pasture as a patchwork of microsuccession at various stages, depending on the major constraint, i.e. cattle activity, which may change from year to year depending of spatial distribution of the three activities.

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Note:

- *Maps of the geographical situation of Le Haut des Joux and of La Métairie d'Evilard, diagram of the experimental designs and photos of the field, treatments and vegetation measurements are included in Appendix Ia*

3.3. Soil microbial community changes in mountain wooded pastures due to simulated effects of cattle grazing

F. Kohler, J. Hamelin, F. Gillet, J.-M. Gobat and A. Buttler

3.3.1. Introduction

Much research effort has been directed at understanding how agriculture and land use practice influence the structure and diversity of animal and microbial below-ground communities (Donnison et al. 2000; Grayston et al. 2001; Chabrerie et al. 2003; Clegg et al. 2003; Larkin, 2003, Grayston et al. 2004). The role of soil organisms in regulating ecosystem processes received growing attention over the past several years and there is an increasing number of studies on questions such as how decomposers respond to disturbance regimes especially those related to agriculture (Yeates et al. 1997; Wardle et al. 1999; Guitian and Bardgett 2000).

The agricultural activity in mountain regions around the world is mainly based on grazing by large herbivores, principally cattle and sheep. Grazing is the main biotic factor affecting ecosystem structure and dynamics in pastures (Olff et al. 1999; Bokdam and Gleichman 2000). The effect of cattle or sheep on their environment can be subdivided into three categories of stress factors: herbage removal, dunging and trampling. Many studies have addressed effects of grazing (e.g. Dyer et al. 1993; Milchunas and Lauenroth 1993; Schläpfer et al. 1998; Birch et al. 2000; Cingolani et al. 2003), trampling (Cole 1995a; Guthery and Bingham 1996; Kobayashi et al. 1997), dung deposition (Malo and Suarez 1995; Dai 2000), manuring or fertilizing (Gough et al. 2000) on grassland, heathland or woodland plant communities. Recently Kohler et al. (2004a and § 3.1) showed that herbage removal, manuring and trampling have significant different effects on seasonal dynamics of grassland. Effects of herbage removal by large herbivores on soil microbial communities are well recognized (Bardgett et al. 1998). It changes the arrangement of above-ground parts of plants with consequences onto above- vs. below-ground carbon allocation and nitrogen-cycling (Holland and Detling 1990). Defoliation of grass species induces an increase in soil extractable microbial C and C use efficiency in the rhizosphere (Guitian and Bardgett 2000). Bardgett et al. (2001) showed that microbial biomass of soil estimated by mean of PLFA (phospholipids fatty acids analysis) was maximal at low-to-intermediate levels of sheep grazing. By contrast Tracy and Frank (1998) showed no effect of grazing by large herbivores on microbial biomass but on nitrogen mineralization. Dung deposition and more generally fertilizing or manuring change the local nutrient balance. Like defoliation they accelerate nitrogen cycling by more efficient re-circulation of nutrients through the animal excreta pathway (Ruess and McNaughton 1987). By community level physiological profiles (CLPP), it was shown that addition of synthetic urine to upland grassland resulted in a dramatic and short-lived change in soil microbial community structure and activity (Williams et al. 2000). By contrast, Bardgett et al. (1999) observed no effect of N-addition (NH_3NO_4) on microbial biomass or activity despite the finding that nitrogen addition reduced root biomass in all plant species and increased rhizosphere acidity. The effect of trampling by cattle on microbial community is less studied. In tropical forest Martinez and Zinck (2004) showed evidence of soil compaction through cattle trampling after clearing primary forests. Compaction implies an increase in soil bulk density and in soil strength and consequently a decrease in air permeability and hydraulic conductivity (Whalley et al. 1995). These effects have as a consequence a reduction of N mineralization (Breland and Hansen 1996). Moreover, Jordan et al. (2003) showed that compaction affected also microbial activity by reducing acid phosphatase. Jensen et al. (1996) who studied the effect of soil compaction by a tractor, observed that CO_2-fluxes decreased substantially but microbial biomass was not affected.

Among the cited studies each consider only one of the three disturbances or consider herbivores activities as a single factor called 'grazing'. Surprisingly, none of them considers the relative impacts of herbage removal, dung deposition and trampling or their interactions on the activity or the structure of the microbial communities of pastures. There is evidence that spatial patterns of the three activities are not congruent. Cattle have for example favorite resting and dunging areas, which may be different from their preferred grazing areas (Bokdam and Gleichman, 2000). Furthermore, the field studies were generally synchronic (e.g. Donnison et al. 2000, Bardgett et al. 2001, Grayston et al. 2004) and microcosms were usually used in experiments (e.g. Bardgett et al. 1999, Jordan et al. 2003). Only very few studies used controlled field experiments (Wardle et al. 1999; Williams et al. 2000; Clegg et al. 2003; Harrison and Bardgett 2004).

The objective of this study was to assess, separately or in combination in an exclosure field experiment of three years duration, the relative effects of repeated mowing, fertilizing and trampling on the structure of microbial communities in two various light conditions in a wooded pasture using Biolog Ecoplates™ and to compare these effects with effects of soil contents and plant composition or biomass.

3.3.2. Methods

3.3.2.1. Study site

This study was conducted in the Jura Mountains of north-western Switzerland. 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 mean annual rainfall of about 1600 mm (with more than 400 mm snow precipitation) and mean annual temperature of 7°C. The ground is covered with snow from November to April. The area contains a great diversity of habitats, from open grasslands to forest patches, with flat or sloping ground and a heterogeneous soil mosaic (Leptosols, Cambisols, Luvisols; taxonomy after Deckers et al. (1998)). Climax vegetation is a beech forest. This landscape has resulted from decades of cattle activities and extensive management with a rotational grazing system.

3.3.2.2. Experimental design

The experiment was carried out in an exclosure of 1000 m^2 on a flat pasture with a lateral shade gradient (Figure 3.3.1). Two lines with 24 plots (1.8 m x 1.8 m) were established: one in the shady part, with about 3 hours of sun per day from May to October,

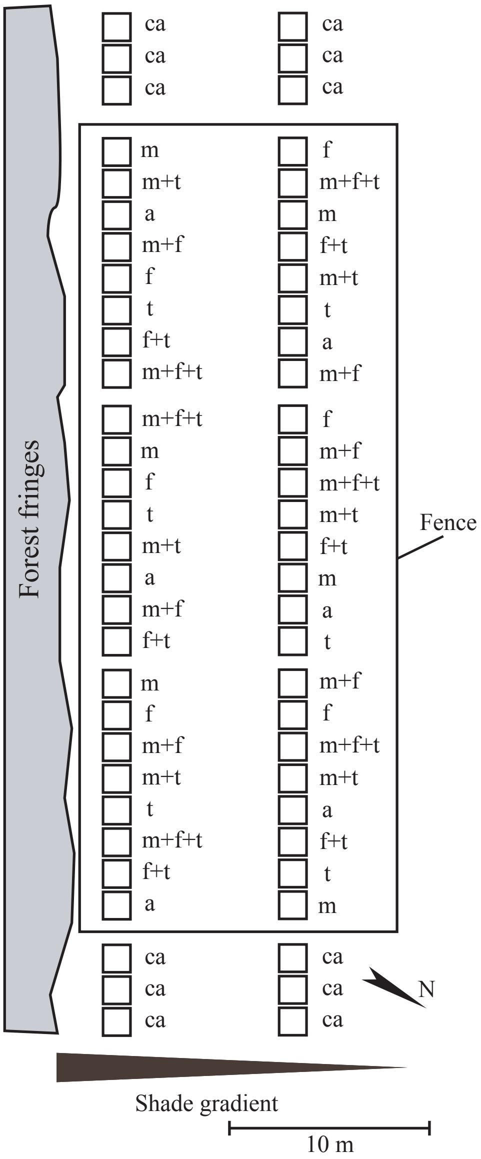

Figure 3.3.1: Experimental design. f: fertilizing, m: repeated mowing, t: trampling, a: adandoned, ca: normal cattle activity.

and another one in the sunny part, with 10 hours of sun per day . In the sunny part the initial plant community was a homogeneous, mesotrophic, unfertilized, extensively grazed *Cynosurion* meadow. Dominant species of this community were *Festuca nigrescens*, *Agrostis capillaris*, *Luzula campestris*, *Trifolium pratense* and *Alchemilla monticola* (Nomenclature follows: Tutin et al. (1964-1980)). In the shady part the initial community was a forest-edge community dominated by *Luzula sylvatica*, *Geranium sylvaticum*, *Festuca nigrescens*, *Anemone nemorosa*, and *Narcissus pseudonarcissus*.

In the exclosure, controlled treatments were applied to simulate herbage removal, trampling and dunging by cattle. The experimental area was fenced in 2001 to prevent large herbivores (heifers and roe deers) from interfering with the treatments. Activities of small herbivores were not controlled but there were only very few ground voles in the area. In the pasture around the exclosure, twelve additional plots were established, six in the shady and six in the sunny part. At the beginning of the experiment, the 30 plots of each line were as similar as possible with respect to floristic composition, canopy structure and biomass. The soil was a homogeneous cambisol in the whole area. Three factors were introduced to be combined into treatments in the exclosure: (1) repeated mowing (m) with a lawn mower twice a month, (2) intensive trampling (t) 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) once a month and (3) fertilizing (f) with a liquid mixture of dung and urine given once a month. The quantity of liquid mixture was equivalent to intensive cattle activity. The liquid mixture came from cattle that lived in the study area. Each factors had two levels: with or without the disturbance. A balanced factorial design with three replicates was established in both communities inducing eight different treatments: three single treatments: m, f, t; three coupled treatments: m+f, m+t, f+t ; one tripled treatment: m+f+t and one treatment without disturbance. The last treatment will be referred to in the paper as “abandoned” (a). The treatments were allocated to plot randomly within each of three blocks in each line (Figure 3.3.1). All treatments were applied homogeneously 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 and snow covered the soil from November to April. The twelve plots outside the fenced area were defined as reference plots with regular, uncontrolled, cattle activity (ca).

3.3.2.3. Vegetation data

Records were made in a 1-m^2 central subplot, leaving a buffer strip of 40 cm around each plot. Absolute and relative cover of vascular plants was assessed using point-intercept frequency measurements (Daget and Poissonet 1969). The number of contacts of green parts with a vertical needle was counted, considering only the first hit for each species. A threshold of 120 points per subplot was retained since it allowed efficient measurements, with a fair estimation of cover. Since rare species are often missed by this method (Buttler, 1992), a complete list of all species observed within each subplot was also recorded. Consequently, in the data set, species found with no contact were allocated the minimum value 1 for their occurrence. The records were made at the beginning of June 2003.

Furthermore above-ground biomass was measured in the middle of June 2003. The 1-m^2 central subplot was cut and the plant material was sorted in three taxonomic groups: forbs, legumes and grasses. The dry weight of each fraction was determined after 48 hours at 60°C.

3.3.2.4. Soil sampling and analysis

To measure the effect of treatments after two complete years of experiment (June 2001 to June 2003), 2 soil cores were extracted at the beginning of June 2003 in each of the 60 plots. Because temporal variation in microbial communities is pronounced at seasonal scale (Griffiths et al., 2003) all cores were taken the same day. The cores had a diameter of 6 cm and a length of 10 cm, corresponding to the thickness of the A horizon of the cambisol. To eliminate the litter we skipped the 2 uppermost centimetres. Both cores from each plot were pooled to get one soil sample per plot, which was then homogenized, sieved (< 2 mm) and further analysed. For each soil sample, 4 variables were measured with standard methods (Anderson and Ingram 1993). On dry ground soil we analysed total organic carbon (C_{tot}), total nitrogen (N_{tot}), total phosphorus (P_{tot}) and water pH.

3.3.2.5. Ecoplates™ inoculation and incubation

The number of viable bacteria in the inocula was first determined as colony forming units (CFU) on ten-fold diluted Tryptone Soy Agar (3 g/l) after incubation at 24 °C for 48 hours. Then, 1 g of each fresh soil sample was diluted in sterile phosphate buffer 10 mM pH 7 (Na_2HPO_4 / Na_2HPO_4) to obtain about 10^3 CFU per ml, according to Zak et al. (1994). One Biolog Ecoplate™ (Biolog Inc., Hayward, CA, USA) was inoculated per sample with 150 µl of suspension per well. One plate contains a triplicate of each substrate type allowing three measurements for each sample. The negative control corresponded to a well without any carbon source. The 31 substrates used are listed in Table 3.3.1, and were classified into the following biochemical categories (according to Insam 1997): Polymers (Po), carbohydrates (CH), carboxylic acids (CA), amino acids (AA), amines/amides (Am). Incubation of the Ecoplates™ was carried out in the dark at 24°C for 120 hours without agitation, and the level of respiratory activity for each well was determined at the end of incubation by measuring the optical densities at 630 nm (OD_{630}) using an automatic microplate reader (Dynatech MR7000).

3.3.2.6. Statistical analyses

For each Ecoplate™, the absorbance value of the control well was subtracted from the well absorption, yielding a single corrected value, according to the manufacturer's instructions. Occasionnaly negative values were set to zero. The average well color development (AWCD) among the three replicates of the 31 substrates was then calculated (Garland and Mills, 1991). The value of each individual well was then divided by the AWCD to eliminate variation in well color development caused by different cell densities of the inocula (Garland 1996). Finally, for each substrate we calculated the average value from the three replicates of each plate. This calculated variable will be referred to "corrected Abs." in the following. Furthermore we calculated a value for each biochemical category (carboxylic acids, polymers, carbohydrates, amino acids and amine/amide) by summing up the average values of all substrates entering into a category (see Table 3.3.1).

In a first step we compared the sunny and the shady situation by calculating the mean and standard error of soil, vegetation and microbial variables. To analyze the multivariate variation of each data set, non-metric multidimensional scaling (NMDS) was used. For soil, pH, Ntot, Ctot, Ptot and the two ratios C/N and N/P were used with the Euclidean distance on standardized data. For microbial data we used the Ecoplate™ matrix (see above) with the Bray-Curtis distance (Legendre and Legendre 1998) and for vegetation data we used the point-intercept records again with the Bray-Curtis distance. Furthermore redundancy analysis (RDA) was used to evaluate and test the amount of variation in each data set explained by the light conditions. Calculations were done with R 1.9.0 (R Development Core Team 2004).

In a second step, partial RDA (Redundancy analysis) was used for partitioning the influence of soil, vegetation and treatments on microbial community. For this analysis, we used three sets of explanatory variables: (1) soil (pH, Ntot, Ctot, Ptot, C/N and N/P), (2) vegetation (total plant biomass, percentage of grass, legumes and forbs) and (3) treatments (fertilizing, mowing and trampling and their interactions coding as binary variables). In this analysis blocks were used as covariables. Plots with natural cattle activity were not taken into account because they were not included in the experimental design. The partial RDA permitted to extract the variation in Ecoplates™ dataset explained by each independent dataset and shared by the three data sets (see Borcard et al. (1992) and Økland and Eilertsen (1994) for details and Kaufmann et al. (2004) for an example with Biolog™ data). The whole process was based on computations made with CANOCO 4.5 (ter Braak and Smilauer 2002). To avoid overfitting in the regression model due to the large number of explanatory variables, we performed forward selection (CANOCO option) retaining for each sets the best significant model with the most variables.

A three-way analysis of variance (fertilizing x mowing x trampling) was carried out on the five biochemical substrate categories, on AWCD, and on the number of culturable bacteria in order to determine statistically differences between the experimental factors. Overall differences among blocks were removed in all ANOVA's and data from plots with natural cattle activity were excluded for the same reason as mentioned above. Calculations were done

Table 3.3.1: Mean (± standard error) of corrected Abs. (see in text) for the 31 substrates in both situations. Biochemical categories: Po: polymers, CH: carbohydrates, CA: carboxylic acids, AA: amino acids, Am: amines/amides.

Substrates	Shady	Sunny
Pyruvic acid methyl ester (CA)	2.56±0.38	2.41±0.36
Tween 40 (Po)	3.24±0.35	2.11±0.24
Tween 80 (Po)	1.57±0.24	1.58±0.19
α-Cyclodextrine (Po)	0.53±0.11	0.43±0.09
Glycogen (Po)	0.55±0.11	0.51±0.10
D-Cellobiose (CH)	0.89±0.19	0.96±0.20
α-D-lactose (CH)	0.25±0.05	0.33±0.10
β-Methyl-D-Glucoside (CH)	0.36±0.15	0.39±0.09
D-Xylose (CH)	1.28±0.27	0.92±0.21
i-Erythritol (CH)	0.36±0.07	0.35±0.07
D-Mannitol (CH)	1.31±0.24	2.83±0.45
N-Acetyl-D-Glucosamine (CH)	2.04±0.39	2.22±0.24
D-Glucosaminic acid (CA)	2.25±0.49	1.34±0.49
Glucose-1-phosphate (CH)	0.18±0.04	0.43±0.11
D,L-α-Glycerol phosphate (CH)	0.10±0.03	0.09±0.02
D-Galacturonic acid γ-Lactone (CA)	1.12±0.39	1.40±0.33
D-Galacturonic acid (CA)	1.41±0.47	2.17±0.51
2-Hydroxy benzoic acid (CA)	0.28±0.06	0.31±0.05
4-Hydroxy benzoic acid (CA)	0.82±0.18	0.84±0.17
γ-Hydroxybutyric acid (CA)	0.93±0.15	0.75±0.14
Itaconic acid (CA)	0.61±0.20	0.47±0.11
α-Ketobutyric acid (CA)	0.99±0.13	0.89±0.18
D-Malic acid (CA)	1.80±0.67	0.90±0.21
L-Arginine (AA)	1.02±0.23	1.31±0.26
L-Asparagine (AA)	0.97±0.20	1.64±0.30
L-Phenylalanine (AA)	0.97±0.19	1.35±0.22
L-Serine (AA)	0.50±0.10	0.36±0.05
L-Threonine (AA)	0.58±0.11	0.61±0.10
Glycyl-L-glutamic acid (AA)	0.45±0.09	0.43±0.08
Phenylethyl-amine (Am)	0.82±0.24	0.35±0.06
Putrescine (Am)	0.24±0.07	0.33±0.09

with R 1.9.0 (R Development Core Team 2004).

3.3.3. Results

3.3.3.1 Differences shady vs. sunny

Table 3.3.1 shows the mean of corrected Abs. in both locations. Only two substrates showed important differences (Tween 40 and D-Mannitol) and there was a high positive correlation between corrected Abs. of both communities (Spearman rank correlation = 0.90, $P < 0.001$) indicating that high-used-substrates and low-used-substrates were about the same in both locations. In the shady situation the five most used substrates were one polymer, three carboxylic acids and one carbohydrate and in the sunny situation one polymer, two carboxylic acids and two carbohydrates. Furthermore standard errors were in most cases high, indicating high variation between plots. For the other variables concerning microbial community (Table 3.3.2), there were again only small differences and high standard errors. Only AWCD was clearly higher for plots in the

Table 3.3.2: Mean (± standard error) of soil, vegetation and microbial community characteristics in the shady (n = 30) and sunny (n = 30) situation.

	Shady	Sunny
Soil		
pH H_2O	4.85 ± 0.04	5.12 ± 0.03
Ctot (%)	5.72 ± 0.19	5.57 ± 0.10
Ntot (%)	0.50 ± 0.02	0.56 ± 0.01
Ptot (%)	0.13 ± 0.01	0.17 ± 0.01
C:N	11.38 ± 0.15	10.01 ± 0.09
N:P	3.83 ± 0.13	3.37 ± 0.10
Vegetation		
Biomass (g/m^2)	98.6 ± 7.4	221.5 ± 16.5
Percentage of grasses	72.8 ± 2.9	47.0 ± 2.3
Percentage of legumes	0.4 ± 0.1	10.4 ± 1.3
Percentage of forbs	26.8 ± 2.9	42.6 ± 2.4
Species richness (species/m^2)	27.0 ± 0.7	29.5 ± 0.7
Microbial community		
Number of CFU (10^7/g)	6.19 ± 0.90	6.03 ± 0.54
AWCD 5 days	0.11 ± 0.01	0.17 ± 0.02
Polymers (Po) (sum of corrected Abs.)	5.89 ± 0.45	4.62 ± 0.33
Carbohydrates (CH) (sum of corrected Abs.)	6.78 ± 0.60	8.53 ± 0.51
Carboxylic Acids (CA) (sum corrected Abs.)	12.78 ± 0.88	11.48 ± 0.62
Amino acids (AA) (sum of corrected Abs.)	4.49 ± 0.40	5.68 ± 0.35
Amines/amides (Am) (sum of corrected Abs.)	1.05 ± 0.25	0.68 ± 0.10

sunny situation. For the soil variables, mean values were also very similar. In the sunny situation pH and Ptot were higher and C/N and N/P lower. Standard errors were low indicating few variations in both situations. Finally, for vegetation, differences were important for the four chosen variables. Biomass was more than two times higher in the sunny situation. Moreover, grasses were dominant in shady plots whereas legumes and forbs were more frequent in the sunny plots. These results were confirmed by NMDS. On the scatter plot, points overlapped for microbial activities, indicating no clear difference between shade and sun (Figure 3.3.2A), whereas a very clear difference appeared for vegetation records (Figure 3.3.2B) and a less clear difference for soil (Figure 3.3.2C). For microbial communities the shady plots were more dispersed indicating more variation between them. For each data set, plots with natural cattle activity were located near those of the experimental design excepted one in the vegetation record. This indicates that treatments mimic well the natural conditions in each of the light condition. Results of separate RDAs on the three datasets confirmed results of NMDSs (Table 3.3.3) with a very high variation explained by light conditions for the vegetation, less for soil properties and only very few for microbial activities.

3.3.3.2. Contribution of treatments, soil and vegetation in microbial variation

Partial RDA analysis was performed separately for the sunny and the shady situations because the analysis with all Ecoplates™ data showed no significant results.

Figure 3.3.3 shows the variation partitioning. For explaining microbial activities in the sunny situation all variables

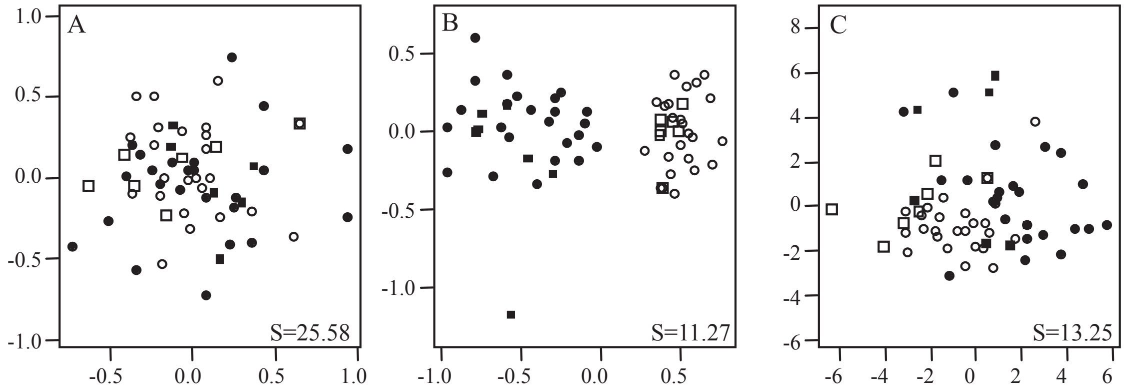

Figure 3.3.2: Non-metric multidimensional scaling for Biolog Ecoplate data (A), vegetation records (B) and soil samples (C). Black: shady; white: sunny; circle: plot in the experimental design; square: plot with natural cattle activity. S: Stress.

of the vegetation data set were selected (rank of explained variance: % legumes > % grasses > % forbs > biomass). They explained together 32.9 % of the variation (Monte Carlo permutation test with 999 permutations: $P = 0.005$). For the treatments the four selected variables were, in the rank of the forward selection: m > m x t > t x f > t. This submodel explained 24.5 % of the variation ($P = 0.02$). For soil variables no significant model was found and consequently soil data were omitted for this analysis. Together the eight selected variables gave a significant model ($P = 0.003$), which explained 55.0 % of the variation. The variation of each set without the effect of the second was also significant (Figure 3.3.3). The shared variation is a consequence of similar structure in the two sets.

For the shady situation (Figure 3.3.3), results were less clear. For the vegetation subset no model were significant and this data set was thus not integrated in the model. For treatments two variables were retained: m > m x f. This submodel explained 13.6 % of the variation and it was significant ($P = 0.04$). For soil variables only pH was retained. This variable explained 9 % of the variation ($P = 0.05$). The full model explained 24.2 % of the variation ($P = 0.02$). The variation of each set without the effect of the second was also significant (Figure 3.3.3). In this case the shared variation was negative. This negative value appeared were there was a strong correlation between the sets (Legendre and Legendre 1998).

Table 3.3.3: Summary of RDAs on Ecoplates™, soil or vegetation datasets constrained by light conditions. Block effects were removed from all analysis and vegetation data transformed with the Hellinger transformation (Legendre and Gallagher 2001). Monte Carlo permutation test was performed by permuting samples freely within each block (999 permutations).

Data set	Explained variance	P-value
Microbial	3.3 %	0.020
Soil	24.9 %	0.001
Vegetation	43.7 %	0.001

3.3.3.3. Treatments effects

ANOVAs were also performed separately for the sunny and shady situation. AWCD and number of culturable bacteria did not show any significant results. By contrast four biochemical categories of substrates, three in the sunny (CA, Po, CH) and one in the shady (AA) situation, showed significant results (Table 3.3.4). The sum of average values of corrected DO for each treatment within these four biochemical categories are presented in Figure 3.3.4. In the sunny situation, carboxylic acids were less used by communities under

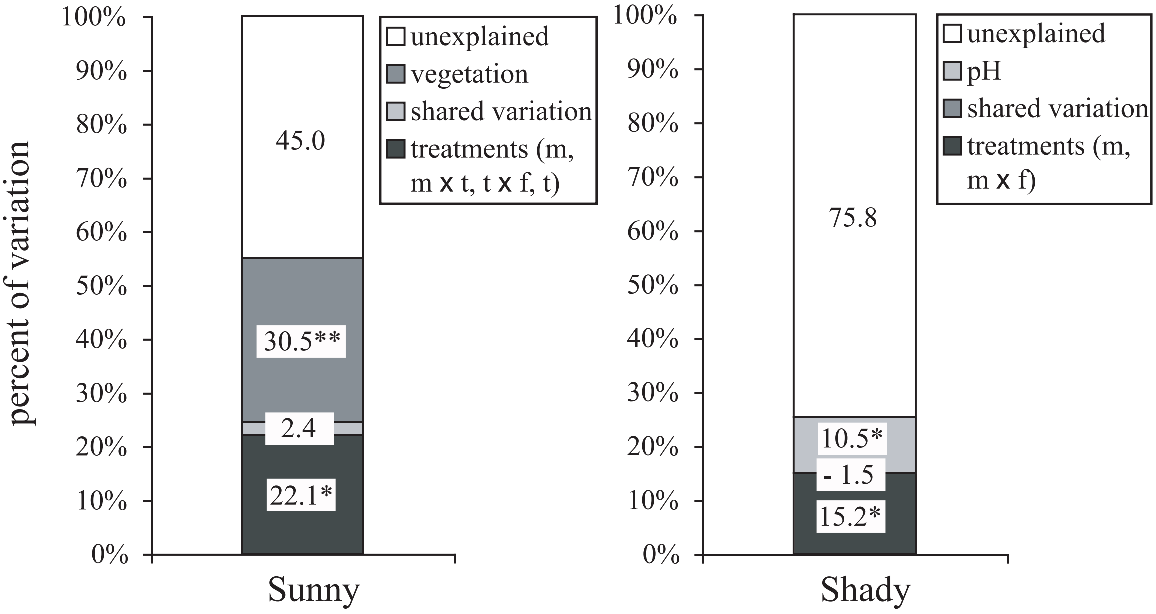

Figure 3.3.3: Variation partitioning with partial RDA of Biolog Ecoplate™ data according to treatments, vegetation and soil data (only significant variables). Monte Carlo permutation test with 999 permutations on each set without the effect of the other (**: $P < 0.05$; *: $P < 0.01$).

repeated mowing and particularly in the mixed treatment m + t. Fertilization and trampling alone induced a greater utilization of carboxylic acids. For polymers, samples from plots with trampling treatment showed less growth. Maximum substrates use was found for repeated mowing treatment alone or in combination with fertilization. For carbohydrates, the triple interaction is significant and the treatments with higher growth was the combination m + t. For these three substrates categories, plots with natural cattle activity showed averages values. In the shade, use of amino acids substrates were significantly affected by repeated mowing. With this treatment growth was clearly

Table 3.3.4: Significant effects of treatments on biochemical categories of substrates (three-way ANOVA m x f x t). Only categories with significant effects are presented. Abbreviation: m: repeated mowing; f: fertilizing; t: trampling; df: degrees of freedom; MS: mean square. **: $P < 0.01$, *: $P < 0.05$, •: $P > 0.1$, ns: not significant.

		Sunny						Shady	
		Carboxylic acids		Polymers		Carbo-hydrates		Amino acids	
	df	F	*P*	F	*P*	F	*P*	F	*P*
block	2	2.04	ns	0.66	ns	1.69	ns	2.52	ns
m	1	6.36	*	1.61	ns	2.41	ns	8.01	*
f	1	0.44	ns	1.83	ns	1.09	ns	0.22	ns
t	1	0.01	ns	4.64	*	2.89	ns	0.19	ns
m x f	1	0.27	ns	0.38	ns	0.13	ns	0.07	ns
m x t	1	0.04	ns	6.29	*	3.13	•	4.55	•
f x t	1	0.66	ns	0.10	ns	1.15	ns	0.25	ns
m x f x t	1	6.22	*	0.08	ns	9.74	**	0.08	ns
Residuals (MS)	14	8.15		2.51		4.72		2.52	

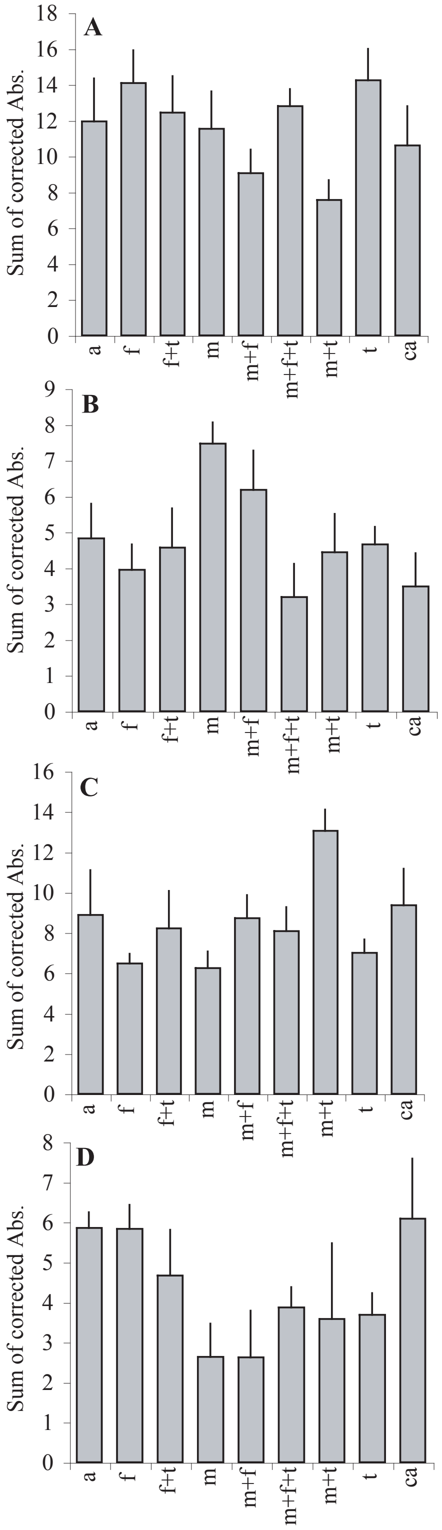

Figure 3.3.4: Effect of treatments on categories of substrates. Only categories with significant effects with ANOVA (Table 3.3.3) are presented. Sunny situation: Carboxylic acids (A), Polymers (B), Carbo-hydrates (C), Shady situation: Amino acids (D). f: fertilizing, m: repeated mowing, t: trampling, a: abandoned, ca: normal cattle activity. Error bars indicate standard error.

reduced. Shady plots with natural cattle activity showed values similar to abandoned and fertilized plots.

3.3.4. Discussion

3.3.4.1. Plant community type and microbial communities

Despite the differences in plant communities and soil properties, the metabolic potential of the microbial communities in the sunny and in the shady situations were very much similar (Table 3.3.3 and Figure 3.3.2). This is consistent with Chabrerie et al. (2003) who showed that microbial communities are independent from successional gradients of vegetation in chalk grassland, in term of functional and genetic structure. Buyer et al. (2002) showed by using PLFA and Biolog™ plates that microbial community structure and function was more influenced by the soil type than by the plant species. By contrast Grayston et al. 2004 showed with Biolog™ GN and MT functional differences between three types of grasslands.

The only important variation between shady and sunny plots was for AWCD, which was lower in the shady situation. For AWCD, difference between both situations was absent and presented very low values after 48 h, but was always present after eight days (data not shown). This means that the lag time was longer than two days for both communities and we can then interprete the difference as a slower reactivity of communities in the shady situation. This difference seems to induce only very little dissimilarity between profiles after correction of the absorbance.

Carbohydrates substrates were generally more used in the sunny situation. In this situation there was more plant biomass and also more roots exudates, which are composed principally by this category of component (Lynch 1990). The least used substrates under both conditions, were phosphate sugars. To use these substrates, bacteria must first excrete phosphatase. We can then suppose that phosphatasic activity was very low. The more amount of activity on polymers in the shady could be explain by a high quantity of beech litter on the ground, this litter being completely absent in the sunny situation.

3.3.4.2. Treatments, soil and vegetation effects on microbial activities

First it is important to note that by taking samples in spring of the third year of the experiment, we did not measure the direct impact of the three disturbances on microbial communities but their long term impact. Therefore, results must be interpreted as a fingerprint of the disturbances at community level (O'Neill et al. 1986) and not as a direct physiological response.

As shown with partial RDAs, microbial communities seem to react differently to the treatment in both situations. The amount of unexplained variation was high in both analyses. In most ecological studies, the amount of unexplained variation is generally fairly high (Borcard et al. 1992; Aude and Lawesson 1998), which is usually interpreted as variation caused by unmeasured environmental variables, complex spatial relationships and stochasticity in biological processes (Borcard et al. 1992; Heikkinnen and Birks 1996).

Treatment effects were more pronounced in the sunny than in the shady situation. In both cases soil microbial activity was most strongly affected by repeated mowing. By contrast fertilising alone was not retained as a significant factor in both situations. For the same experiment, it was recently shown (Kohler et al. 2004a and § 3.1) that repeated mowing was the most important factor explaining plant community differences between plots; followed by trampling and fertilising. Trampling was selected as an important factor in the sunny situation. Malmivaara-Lämsä and Fritze (2003) deduced that human trampling in urban forest had an effect on microbial community structure but they concluded that it was rather indirect due to changes in the vegetation and the litter quality rather than direct through soil compaction. However, in our experimental setup treatments seem to have a direct effect on microbial communities because explained variations were always significant after accounting for vegetation or soil effects (Figure 3.3.3). The principal difference between both situations was that the vegetation showed a high proportion of explained variation under sunny but no significant variation under shady condition. It was the inverse for the soil. The lack of explanation for the soil variables can be explained by the low variability of these or in other words by a high homogeneity of soil conditions. Similarly, Clegg et al. (2003) showed in grasslands no significant relationship between PLFA and soil variables such as organic matter, pH, total C and total N. In our study, only pH explained part of the variation in the shady situation. This variable is recognized to have an important impact on the microbial community in grasslands (Grayston et al. 2004). For vegetation, Grayston et al. (2004) showed that coupled with grazing, plant species composition is an important factor governing microbial community structure in upland grasslands. This is consistent with our results in the sunny situation. The lack of explanation of vegetation variables in the shady situation is probably due to a very low biomass (Table 3.3.2) and also lower influence of rhizosphere exudates.

No effect was found in the number of culturable bacteria and the AWCD for the different treatments. Apparently, trampling did not reduce the number of aerobic bacteria. Jordan et al. (2003) observed a significant effect of soil compaction onto microbial activity by simulating soil compaction by heavy traffic. In an urban forest, Malmivaara-Lämsä and Fritze (2003) measured a decrease of microbial activity due to high human trampling. In our study this treatment was not as extreme and thus probably not sufficient to have a strong effect on aeration, moisture and soil strength. Also, fertilizing did not affect the number of culturable bacteria, which is in agreement with Bardgett et al. (1999) who found no effect of N-addition on microbial biomass.

Only few substrate categories showed significant effects of treatment. Repeated mowing had a negative effect on carboxylic acid metabolism in the sunny situation and on amino acids in the shady situation. A significant negative effect of trampling on polymers consumption was observed in the sunny situation, which could be attributed to the soil compaction that favours anaerobic environments where enzymatic oxidation of polymers by microorganisms is limited (Gobat et al. 2004).

3.3.4.3. Discrimination of microbial communities with Ecoplates™

Community level physiological profiles (CLPP), obtained by Biolog™ microplates, have been used to characterize microbial communities from different plant species and soil types (Garland 1996; Grayston et al., 2001). CLPP is a measurement of community structure and potential activity of culturable, aerobic and fast growing bacteria (Smalla et al. 1998). However it should be kept in mind that similar metabolic fingerprints may be reached by structurally different bacterial communities (Miethling et al., 2003). In most studies Biolog GN™ plates with 95 substrates have been used (e.g. Chabrerie et al. 2003; Larkin 2003; Miethling et al. 2003) with the idea that the combination of these substrates would provide a high discriminating power (Konopka et al. 1998). However, several studies have noted that many of the carbon sources used in the Biolog GN™ method can be highly correlated and contribute little to the discrimination of microbial communities (Campbell et al. 1997; Stevenson et al. 2004). Hitzl et al. (1997) suggested that a reduced set of discriminating carbon sources would be a better approach than the 95 substrates of the Biolog GN™ plates. The 31 Ecoplate™ substrates have been chosen according to the separation power of environmental samples (Insam 1997). Choi and Dobbs (1999) showed that Biolog GN2™ and Ecoplates™ revealed similar differences between the CLPP's of the assessed water samples, but they recommend usage of Ecoplate™ because the substrates in this plate type are ecologically more relevant than those on the Biolog GN2™ plate. Furthermore, the greatest advantage of Ecoplates™ is that they include three replicates of each substrate within a single plate, increasing the likelihood that the CLPP generated is representative for the soil sample assessed (Classen et al. 2003).

In this study, the Ecoplates™ substrate utilization profiles were able to detect differences for treatment effects but only very partly for shade effect. This result is surprising because treatments that have been applied during two summer periods seem to be more important to change microbial activities than the presence of very different ecological conditions acting since decades. However there are two possible explanations for that. Firstly, the microbial communities were indeed physiologically equivalent as suggested results of Charberie et al. (2003) who found that microbial activities were independent from vegetation type in term of functional and genetic structure. Secondly, the Ecoplate™ is not sensitive enough to detect such differences. It is obvious that with this method we obtain only a partial view of the bacterial community (Verschuere et al. 1997, Konopka et al. 1998) and it is thus possible that PLFA would have a better discrimination power (Priha et al. 1999; Grayston et al. 2004). Consequently we deduce from our result that aerobic bacterial species with rapid growth are functionally identical under both ecological conditions but are affected by the treatments.

3.3.5. Conclusion

The results of this study suggest that cattle activities are important factors influencing microbial communities in the soil and that the importance of these factors changes depending on the influence of shade and thus on the precise location in the wooded pasture landscape. By homogeneously applying the treatments to 4 m^2 plots, we created artificially large homogeneous patches of mown, trampled and fertilized surfaces, thus decomposing the successional sequences, which may occur in a cattle grazed pasture, intermingled in a very fine mosaic. In successive years, cattle activities may change spatially at a fine scale and induce changes in the microbial community structure. This process induces, like in the vegetation, a shifting mosaic of the microbial community structure in the pasture.

Acknowledgments

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Note:

- *Map of the geographical situation of La Métairie d'Evilard, diagram of the experimental design and photos of the field and Biolog measurements are included in Appendix Ia*

3.4. Gap colonisation in mountain pastures

F. Kohler, F. Gillet, J.-M. Gobat and A. Buttler

3.4.1. Introduction

Gap creation is a major disturbance participating in the dynamics of a wide range of plant communities like forest (e.g. Hubbel et al. 1999; Wright et al. 2003) or grassland (e.g. Williams 1992; Lavorel et al. 1994; Vandvik 2004). This disturbance, by removing biomass, reduces competition intensity allowing species that are poor competitors to persist in the community if they can colonise the gap first (e.g. Hobbs and Hobbs 1987; Tilman 1994). Moreover, Suding and Goldberg (2001) pointed out that beyond removing biomass, gap creation could 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 competitive reduction. By contrast with forest vegetation where most gap colonisers are of seed origin (Brokaw and Busing 2000), colonists of gaps in perennial grassland can be of seed or clonal origin (Bullock et al. 1995). The high proportion of species with clonal reproduction in grassland (Klimes et al. 1997; Tamm et al. 2002) points to a high possibility of adult plants to colonise gaps. Furthermore, many studies have shown high small-scale turnover and spatial dynamic of plants even in undisturbed vegetation (e.g. van der Maarel and Sykes 1993; Otsus and Zobel 2002; Kohler et al. 2004b and § 4.1). The proportion between seed-derived and clonal varies according to gap size. Increased gap size increased the density and size of seed-derived plants (Bullock et al. 1995; Rogers and Hartnett 2001; Vandvik 2004). It is thus clear that the ability of species to colonise gaps depends on regenerative traits. Traits, which provide advantages in closed canopy are not necessarily an advantage for gap colonisation. Consequently plant species often occur with different relative frequency in recently colonised gaps than they do in the surrounding vegetation (Martinsen et al. 1990; Bullock et al. 1995). This is an evidence that gap colonisation is potentially an important source of vegetation change in grassland. These communities can be seen as patchworks of microsites in different stages of revegetation (Vandvik 2004). At landscape and long time scale 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).

Our study was undertaken in a pasture grazed by cattle from May to September. In this ecosystem, gap creation has various origins such as snow, fossorial mammals and large herbivores (principally cows and wild boars) and various sizes from a few square centimetres to a few square decimetres. Concerning the role of large herbivores for this disturbance, Silvertown and Smith (1988) showed that heavier grazing increased the frequency of canopy gaps. Furthermore, cattle activities such as dung deposition, herbage removal (grazing s. s.) and trampling induce various kinds of disturbance at short term and fine scale. As these three activities have different impacts on vegetation dynamics at fine scale and short term (Kohler et al. 2004a and § 3.1), they probably influence gap revegetation too.

The aim of the present study was to investigate over a three years period at seasonal and square decimetre scale revegetation of artificial gaps under different treatments simulating cattle activity (fertilising, herbage removal and trampling). We compared vegetation dynamics around gaps, at the edge and in the centre of gaps at species and functional traits level. Furthermore we were interested in the similarity between the edge of gaps and the vegetation directly around them and in the role of the gaps for promoting of new species.

Our working hypotheses were: (1) By creating different environmental conditions gaps promote new species. (2) Because a lot of species in pasture have high clonal ability, colonisation of gaps will appear principally from the edge and consequently there is a high similarity between species present in the gap and species present around the gap. (3) Species turnover is higher in the centre of the gap than at its edge and it decreases during the time after gap creation. (4) Plant species occur with different relative frequency in the gaps than they do in the surrounding vegetation but these differences level out during the colonisation. (5) Species that dominate gaps have in common functional traits of the plant regenerative phase. For each hypothesis we supposed that dynamics vary according to the different treatments simulating cattle activity.

3.4.2. Materials and methods

3.4.2.1. Study site

This study was conducted in the Jura Mountains of north-western Switzerland. 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 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. Soil is a Cambisol (Deckers et al. 1998) with a water pH of about 5.

The experiment was carried out in an exclosure on a flat pasture. The initial plant community was a homogeneous, mesotrophic, unfertilised, and extensively grazed *Cynosurion* meadow constituted almost completely by perennial species. Dominant species of this community were *Festuca nigrescens*, *Agrostis capilaris*, *Trifolium pratense* and *Alchemilla monticola* (nomenclature follows Tutin et al. (1964-1980), see Figure 3.4.5 for a more complete list). This stand was an established community in equilibrium with decades of cattle summer activity. Management is a grazing rotation system (the animals pass from one paddock to another according to a variable period of rotation) with heifers; the stock density ranging from 0.6 to 0.9 adult bovine-units/ha.

3.4.2.2. Experimental design

In the exclosure, controlled treatments were applied, simulating herbage removal, trampling and dunging by cattle. The experimental area was fenced to prevent the large herbivores from interfering with the treatments, but activities of small herbivores were not controlled since they were negligible.

Eight plots (2 m x 2 m) separated by a 1-m pathway were arranged along a line. The 8 plots were as similar as possible with respect to floristic composition, 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.

(2) Trampling with wooden shoes once a month (1000 footsteps per m^2 with ca. 70 kg per footstep of 35 cm^2, which represents a mean pressure of 2 kg/cm^2).

(3) Manuring with a liquid mixture of dung and urine of 2 L/m^2 given once a month, which is equivalent 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.

(4) No intervention at all, which corresponded to the treatment abandonment.

All treatments were applied homogeneously 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 60 cm x 60 cm 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). Wild boar or high cattle trampling created similar gaps in this region (personal observation).

3.4.2.3. Vegetation sampling

We chose a spatial resolution of one square decimetre and an extent of one square meter using a square grid with one hundred cells. The grid was positioned at the beginning of the experiment in order to have the 6 x 6 central cells exactly above the gap of 60 cm x 60 cm. It was not possible to lay the grid down onto the soil because of the density of the vegetation. So the grid was kept fifteen centimetres above the ground on four perforated plastic tubes. The eight plots were observed in spring (before gap creation) and autumn 2001, in spring and autumn 2002, and finally in spring 2003. 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. During the whole study, 4000 cell-records were made. We recorded in each cell the exhaustive list of species and we estimated the absolute cover of each species with Braun-Blanquet’s dominance codes. The observations were made vertically above the cells so as to avoid recording twice the margins of contiguous cells. For quantitative analysis, Braun-Blanquet’s dominance codes were transformed in absolute cover as follows: 1 = 3 %; 2 = 14 %; 3 = 32 %; 4 = 57 % and 5 = 90 %. Plants were often only at vegetative state which induced identification problems (Klimes et al. 2001) and indeed, this required training in species recognition. To reduce bias in this respect, all records were made by the same observer. For each sampling date, the plot records were constructed by aggregating the 100 cell records. Species absolute cover at plot scale was the mean of the species absolute cover deduced from Braun-Blanquet’s dominance codes (see above) in the 100 cells. Each record of one square meter required five hours of labour or more, depending on the species richness and on the state of development of the vegetation.

3.4.2.4. Plant functional traits

Plant functional traits were used to detect general trends in trait promotion and inhibition during the gap colonisation. We selected four traits of the plant regenerative phase with two to four attributes each that were supposed to respond to gap colonisation (Table 3.4.1). We focused on traits widely used and easily accessible in database or literature. Attribute classes were large to allow for trait plasticity (Dyer et al. 2001) and 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", "seed bank longevity". See Table 3.4.1 for details and data sources.

3.4.2.5. Statistical analyses

Three area types were defined for data analysis: (1) centre of the gap: square of 4 x 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 (Figure 3.4.1).

To observe the general temporal dynamic of the vegetation in relation to the treatments, the evolution of cover per area type, species number per cell and area type, and species number per plot were calculated. The species turnover between consecutive recorded sessions was also determined at plot scale and at cell scale, according to the area type, by using the Jaccard distance (1 - Jaccard similarity (Güsewell et al. 1998)) on presence-absence data. To test differences between treatments for each area types at each time period, we calculated ANOVAs using the average of the values calculated for each cell and giving blocks as covariable. These analyses were also performed for comparing turnovers between sessions. Moreover the number of new species appearing at least once in the centre of each gap during the study was determined.

To measure the role of surrounding vegetation in gap colonisation, we calculated

Table 3.4.1: Plant functional traits. Trait description, data source, missing values. CLOPLA1 is the database of Klimes et al. (1997) and the numbers refer to types of clonal growth

Trait	Attribute	Number of taxa with attribute	Description	Data source	Missing values (63 species)
Vegetative spread	none	16	CLOPLA1 (1, 2, 4, 12, 16-19, 100)	Klimes et al. 1997	-
	< 0.1 m	21	CLOPLA1 (6, 7, 9, 13, 15)		
	> 0.1 m	26	CLOPLA1 (3, 5, 8, 10, 11, 14)		
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			
Seed agency of dispersal	Wind-dispersed	12		Julve 1998	-
	Zoochore	26			
	Unspecialized	25			
Seed bank longevity	Transient	21	"Transient" in more than 80 % of all records	Thompson et al. 1997	7 (11 %)
	Persistent	35	"Short or long term persistence" in more than 20 % of all records		

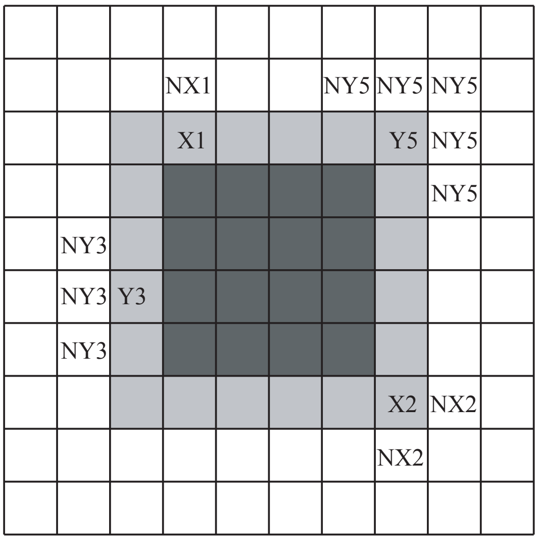

Figure 3.4.1: Scheme of the grid with cells of 10 cm x 10 cm and the 3 distinct areas: white: around the gap; light grey: edge of the gap; dark grey: centre of the gap. Capital letters represent both methods to choose neighbouring cell(s): 1. X: cell from the edge of the gap with 1 (standard) or 2 (corner) vertical or/and horizontal neighbouring cell(s) NX; 2. Y: cell from the edge of the gap with 3 (standard) or 5 (corner) vertical or/and horizontal and diagonal neighbouring cells NY.

the percentage of species in a cell at the edge of the gap, which were also in the neighbouring cells around the gap at the same or at the previous session. Neighbouring cells were chosen in two ways as illustrated in Figure 3.4.1. Computed values were then aggregated per plot and further used to test differences between treatments by means of ANOVAs with blocks as covariable.

To measure the multivariate response of plant community, principal response curves (PRCs) (van den Brink and ter Braak 1999; ter Braak and Smilauer 2002) were used (see Frampton et al. 2000 or Vandvik 2004 for ecological examples). This recent method derivative of partial redundancy analysis made it possible to analyse the effect over the 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. This analysis was done on the species assemblage records with three models: (1) Time x Gap effects, (2) Time x Simulated cattle activity and (3) Time x Gap effects x Simulated cattle activity. For the first model, records around the gap were chosen as references. For the second, records of abandoned plots were chosen as references and for the third, references were records around the gap for abandoned plots. We constructed the species matrix as follows: for each sampling date, cell records from each plot were aggregated per area type by calculating the average absolute cover of each species (deduced from Braun-Blanquet codes). These average absolute covers were used as raw data. Furthermore, because redundancy analysis (RDA) is not appropriate to analyse vegetation matrix with a high number of zeros (Legendre and Legendre 1998), data matrix were transformed with the Hellinger transformation (Legendre and Gallagher 2001), which allows the use of this type of data with RDA. To evaluate the statistical significance of each PRC, permutation tests were done by permuting the whole time series freely within each plot. Overall differences among blocks were removed in all analysis. PRCs were performed using the software package CANOCO 4.5 (ter Braak and Smilauer 2002).

For functional plant traits, relative cover of each attribute was calculated for each area type and treatment by adding the absolute cover of each species belonging to the attribute and by dividing this value by the total absolute cover. As for other analyses, differences between treatments were tested by means of ANOVAs (see above).

Except for PRCs, calculations and graphs were performed with R 1.9.1 (R Development Core Team 2004).

3.4.3. Results

At the first record before gap creation, there was a total number of 53 species in the eight plots. The mean species number by plot was 37.4 (SD: 3.3; max: 43; min: 34; N = 8) and by cells 10.0 (SD: 1.8; max: 17; min: 5; N = 800). The impact of gap creation on species richness was low at plot scale (Figure 3.4.2A) with only a mean loss of 1.9 species per plot. At plot scale, the evolution of the species richness did not show any trend and there were no significant differences between treatments. There were only less species in autumn than in spring. At cell scale (Figure 3.4.2B) the evolution of the species number did not show any trend around the gap. But at the end of the observation there was a significant difference (*P* = 0.01) between treatments with a maximum of species (average = 12.7) in repeated mowing plots and a minimum in trampling plots (average = 10.8). For the edge of the gap, there was an important increase of species richness in the first summer, but the increase was less important between the following sampling dates. One significant difference (*P* = 0.01) between treatments appeared in autumn 2002 with a maximum number of species (average = 8.5) in manuring plots and a minimum (average = 6.6) in repeated mowing plots. In the centre of the gap the increase was lower and more regular than on the edge and there was no differences between treatments. Concerning the evolution of the total absolute cover at cell scale in the three area types (Figure 3.4.2C), cover increased regularly on the edge and in the centre up to the end of the observation

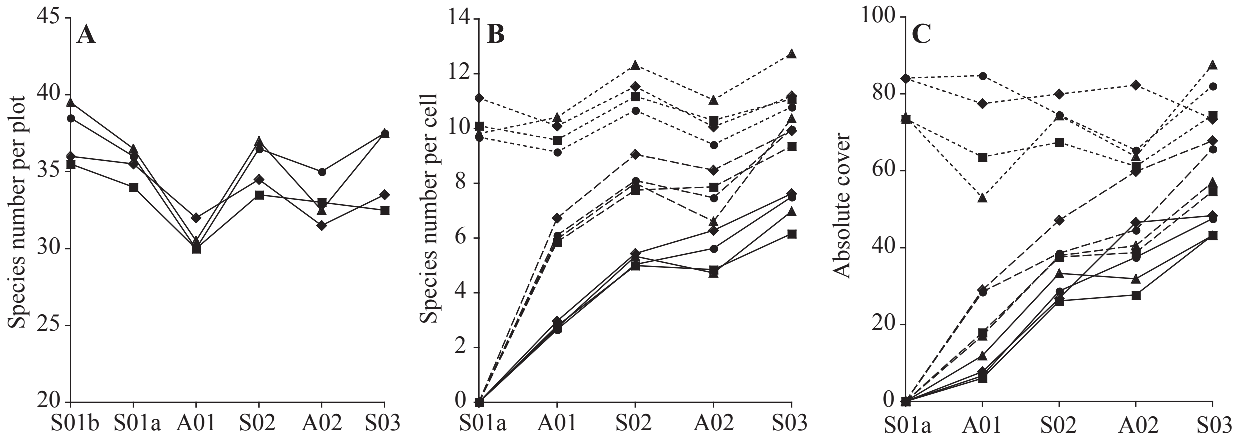

Figure 3.4.2: Mean number (N=2) of species per plot (A), species number per cell (B) and total absolute cover per cell (C) during the time (S: spring; A: autumn; 01-02-03: years; S01b: spring 2001 before the gap creation; S01a: spring 2001 after the gap creation). Average values per area type (continuous line: centre of the gap; large dashed lines: edge of the gap; fine dashed lines: around the gap) and per treatment (●: trampling; ■: abandoned; ▲: repeated mowing; ◆: manuring) are presented.

Table 3.4.2: New species appearing in the centre of the gap at least once during the study in the two replicates of each treatment. The number presented is the number of different species appearing in both of the two replicates of each treatment and in the bracket is the number of species appearing in each of them.

Treatment	Number of species in the centre of the gap which were not found at this place before the gap creation.	Number of species in the centre of the gap which were not found in the entire plot before the gap creation.	Number of species in the centre of the gap which were not found in all entire plots before the gap creation.
Mowing	9 (4, 7)	2 (1, 2) (*Poa supina*, *Stellaria graminea*)	2 (1, 2) (*Poa supina*, *Stellaria graminea*)
Manuring	9 (3, 7)	2 (1, 1) (*Cynosurus cristatus*, *Veronica serpyllifolia)*	0 (0, 0)
Trampling	13 (7, 9)	6 (3, 4) (*Cerastium fontanum triviale*, *Poa alpina*, *Poa pratensis, Poa supina*, *Rhinantus minor*, *Veronica serpyllifolia*)	3 (1, 3) (*Poa alpina, Poa supina*, *Rhinantus minor*)
Abandoning	9 (4, 7)	3 (0, 3) (*Cerastium fontanum triviale*, *Dactilys glomerata*, *Stellaria graminea*)	1 (0, 1) (*Stellaria graminea*)

with a higher increase on the edge. For the centre, there was a significant difference (P = 0.005) between treatments in autumn 2002 with a maximum cover in manuring plots (average = 47 %) and a minimum in plots without intervention (average = 27 %). Another significant difference (P = 0.01) appeared around the gap in autumn 2001 with a maximum cover in trampling plots (average = 85 %) and a minimum value in repeated mowing plots (average = 53 %). In the centre of the gap an average of 6 species per plot, which were not exactly at this place before the gap, appeared at least once during the observation period (Table 3.4.2), and there was a significant treatment effect (P = 0.04). This corresponded to a total of 26 different species. Most frequent new species were *Veronica serpyllifolia* in six and *Cerastium fontanum* ssp. *triviale* in five of the eight gaps. If we consider the entire community recorded for the eight plots in spring 2001, the number of appearance was much lower with only four new species (*Poa alpina*, *Poa supina*, *Rhinantus minor* and *Stellaria graminea*) (Table 3.4.2). Among these species, *Poa supina*, which appeared in four of the eight gaps (repeated mowing and trampling plots), presented the most important cover. This species appeared in spring 2002, one year after gap creation, and in spring 2003 it was already present in the half of the cells in the gap centre of one trampled plot. Concerning the turnover, there was no trend and no differences appeared between treatments at plot scale with c.a. 20 % of turnover between sessions (Figure 3.4.3A). At cell scale for the three area types, treatments showed generally the same pattern. In the centre of the gap (Figure 3.4.3B), there was a high turnover (c.a. 65 %) between the first and the second session but this value decreased rapidly to c.a. 45 %. On the edge of the gap (Figure 3.4.3C), there was a slight decrease from c.a. 50 % to 45 % during the study. In this case there were significant treatment effects for the first

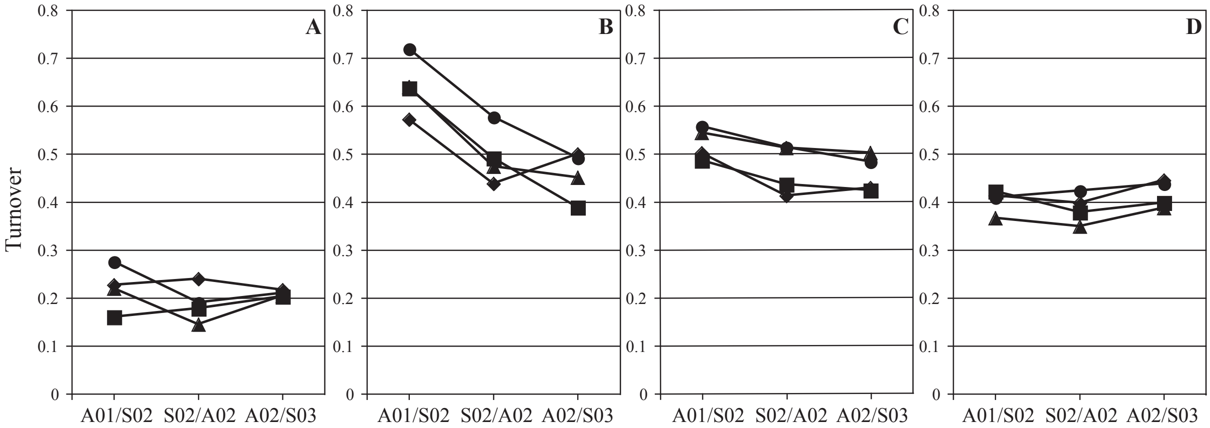

Figure 3.4.3: Average values (N=2) of species turnover at plot scale (A) and at cell scale for the centre (B), the edge (C) and around the gap (D). S: spring; A: autumn; 01-02-03: years; ●: trampling; ■: abandoned; ▲: repeated mowing; ◆: manuring.

(*P* = 0.04) and the last (*P* = 0.03) calculated turnover. Finally, around the gap (Figure 3.4.3D) values showed no trend and almost corresponded to final values of both other area types (c.a. 40 %).

There was a very high species assemblage similarity between cells on the edge of the gap and the neighbouring cells around the gap (Figure 3.4.4). This similarity was always higher than 60 % even if we considered species present around the gap at the previous session. We observed some significant differences between treatments. In autumn 2001 there was a significant treatment effect for the similarity at the same session with 1 (or 2) neighbours (*P* = 0.03) with a maximum for repeated mowing plots (average = 0.82) and a minimum for trampling plots (average = 0.74). With more neighbours, there was always a significant difference (*P* = 0.03) between treatments in autumn 2002 with a maximum for plots without intervention (average = 0.91) and a minimum for trampling plots (average = 0.83). When we considered the previous session for 1 (or 2 in corners) neighbours, there was a significant effect for the first and the second comparison (*P* = 0.03

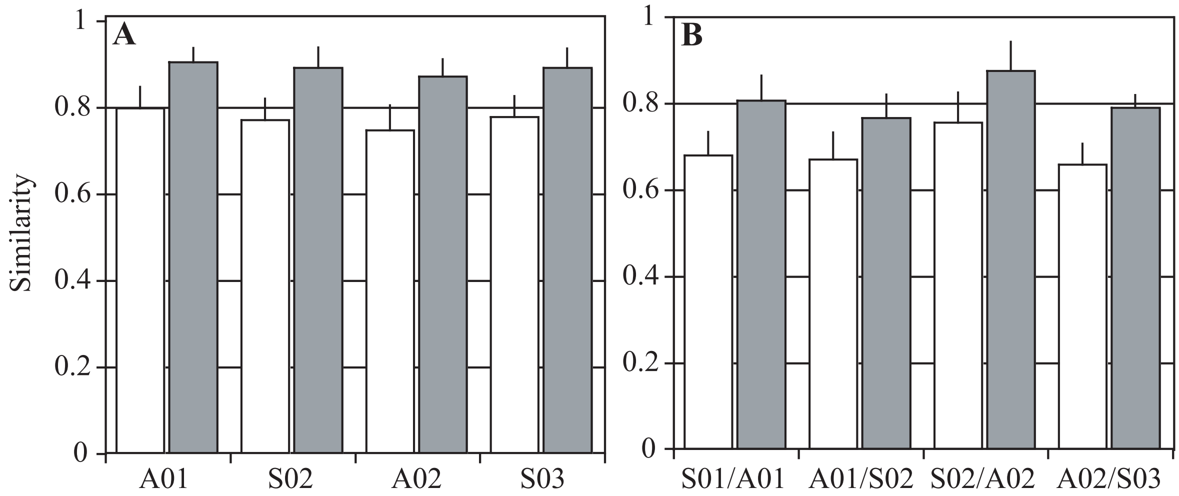

Figure 3.3.4: Mean similarity (N=8) of species assemblages between cells on the edge of gaps and those of the surrounding vegetation at the same session (A) and those of the previous session (B). For 1 (or 2 for corners) neighbours (white) and for 3 (or 5 for corners) neighbours (grey) (see Figure 3.4.1 and in the text for details). Error bars = standard errors. S: spring; A: autumn; 01-02-03: years.

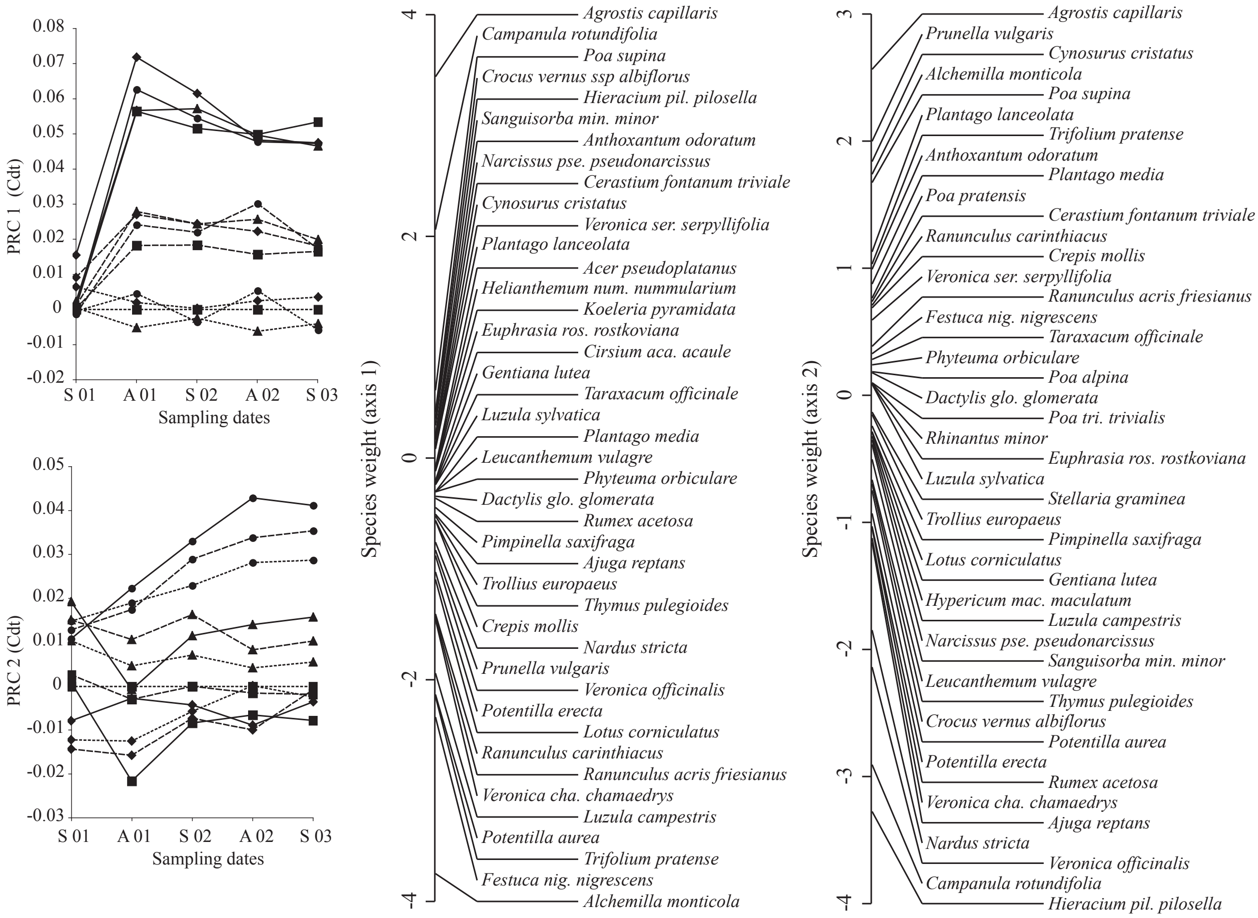

Figure 3.4.5: PRC diagram of vegetation data and species weights on PRC axes 1 and 2 for the species records aggregated by area types and transformed with Hellinger transformation. Area around the gap of abandoned plots was used as reference. Continuous line: centre of the gap; large dashed lines: edge of the gap; fine dashed lines: around the gap. S: spring; A: autumn; 01-02-03: years; ●: trampling; ■: abandoned; ▲: repeated mowing; ◆: manuring. Only species with weight outside the range -0.08 to +0.08 are presented. For percent of explained variation and permutation tests, see Table 3.4.3.

and 0.02). In both cases minimum values were observed for trampling plots (average = 0.62 and 0.62) and maximum values were observed for the first time in manuring plots (average = 0.75) and for the second time in plots without intervention (average = 0.71). Finally with more neighbours accounted, there was a significant effect (*P* = 0.03) for the second observation with also trampling plots with lower values (average = 0.72) and plots with no intervention with higher values (average = 0.81).

For PRCs, differences between the gaps and references (around the gap) during the time accounted for 28.1 % of the variance and were highly significant (Table 3.4.3). For the treatments explained variance was lower but also highly significant (25.8 %). The PRC model for treatments and gap effects during the time explained 67.1 % of the variance. This effect was highly significant and the first axis (Figure 3.4.5) 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 relating to gap colonisation presented positive weights on the first axis (Figure 3.4.5). Spearman rank coefficient between species weight on the PRC

Table 3.4.3: Summary of PRCs of vegetation data to quantify the effect of different factors included in the model. The species matrix contained average absolute cover of each species and cells were aggregated according to area types. For each analysis, time (coded as dummy variable) was considered as covariable and only the interactions times x factors (coded also as dummy variable) were considered as explanatory variables. References were for «Time x Gap effects»: around the gap area type, for «Time x Simulated cattle activity»: abandoned plots and for «Time x Gap effects x Simulated cattle activity»: around the gap area for abandoned plots. Species data set was first transformed with Hellinger transformation. The significance of each variance explained is tested by permuting the whole time series freely within each plot. Variations explained were expressed in percentage relative to the total inertia minus variance explained by the covariables. Overall differences among blocks were removed in all analyses. Axis 1 and 2 of the full model of PRCs (Time x Gap effects x Simulated cattle activity) is presented in Figure 3.4.5.

	Variance explained (%)			
Model	Total	*P* (999)	PRC axis1	*P* (999)
Time x Gap effects	28.1	0.001	23.7	0.001
Time x Simulated cattle activity	25.8	0.002	11.0	0.025
Time x Gap effects x Simulated cattle activity	67.1	0.001	24.4	0.001

axis 1 and species absolute cover (calculated from the eight plots at the first session) was equal to -0.47 ($P < 0.001$). There was then a tendency for species with low cover to increase in relative importance in the gap. There were some exceptions like *Hieracium pil. pilosella* and *Agrostis capillaris*, which were dominant species (principally in autumn for the second one) in 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 (Figure 3.4.5). This axis explained 12 % of the total variation ($P = 0.002$, permutations = 999). Trampling shows the highest deviation from the reference (around the gap area in plots without intervention). Between trampling and without intervention treatment, we found repeated mowing and at the opposite manuring treatment mixed with the reference. *Agrostis capillaris* was a key species for the gap dynamic and for the trampling. By contrast *Alchemilla monticola* was characteristic of the area around the gap and of trampling (Figure 3.4.5).

For most attributes, the three area types showed different patterns (Figure 3.4.6). Attributes that increased in gaps were very light seeds (< 0.2 mg), unspecialised seed dispersal, persistent seed bank and high vegetative spread. Gap decreasers were species with seed mass from 0.2 mg to 0.5 mg and from 0.5 mg to 1 mg, transient seed bank, animal-dispersed seed and low vegetative spread. Only “perennial not clonal”, “wind-dispersed seed” and “seed mass > 1 mg” attributes showed no clear differences between area types. As at species level, differences were maximal at the first record after gap creation. The centre and the edge of the gap tended to become more and more similar from around the gap records during the study, but this process was slow and differences persisted up to the end of the observation period. Seasonal effect was particularly strong for attributes linked to vegetative spread. For each area type at each time, few significant differences between treatments appeared. For records around the gap, there was, in autumn 2001, a significant effect of treatments on species with heavy seed mass (> 1 mg) ($P = 0.007$, maximum in repeated mowing plots (21 %) and minimum in trampling plots (10 %)) and on perennial not clonal species ($P = 0.001$, maximum in repeated mowing plots (8 %) and minimum in manuring plots (2 %)) but these effects disappeared in the following sessions. For the edges of the gap, there was in autumn 2001 and in spring 2003 a significant effect

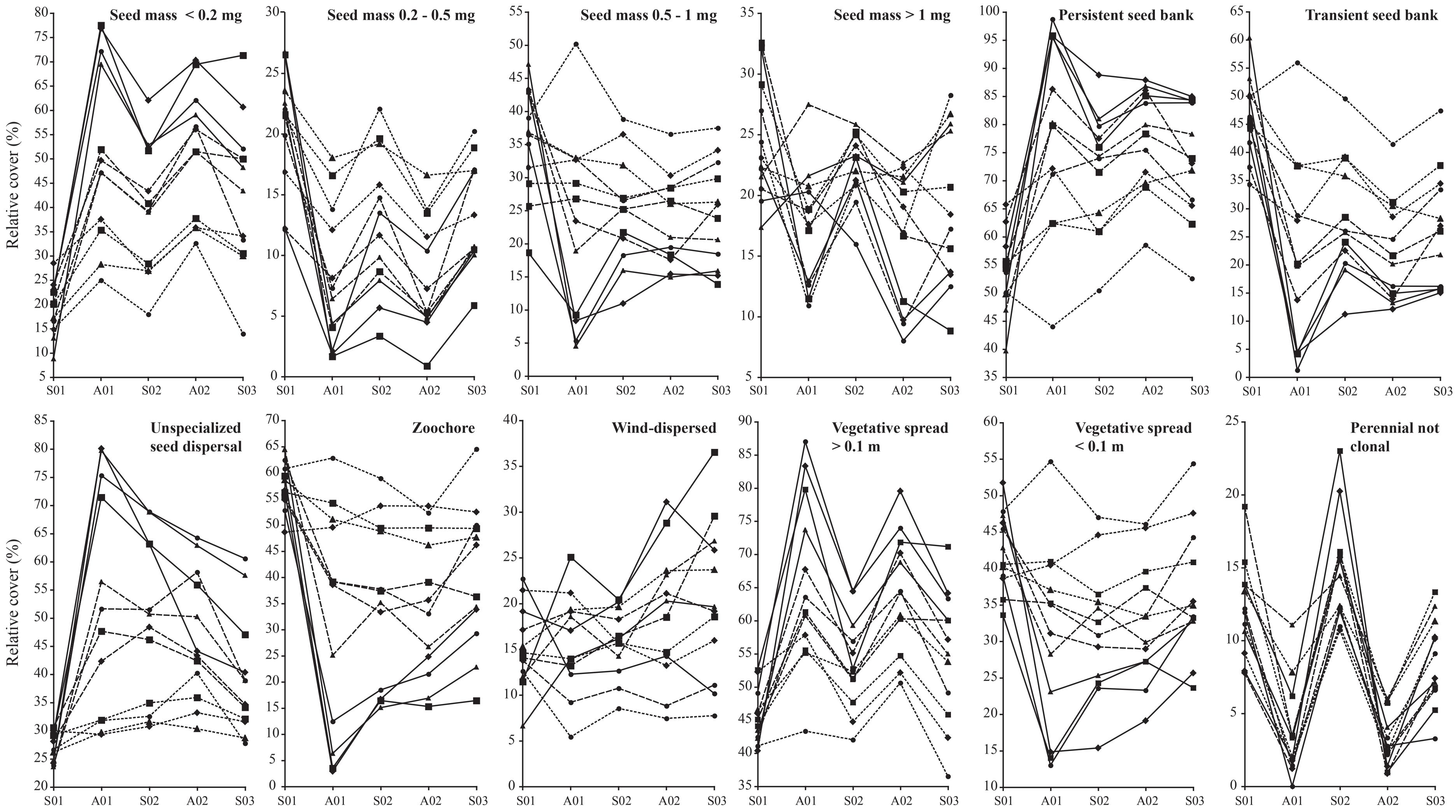

Figure 3.4.6: Evolution of the relative cover of plant attributes (S: spring; A: autumn; 01-02-03: years; S01: before gap creation). Average values (N=2) per area type (continuous line: centre of the gap; large dashed lines: edge of the gap; fine dashed lines: around the gap) and per treatment (●: trampling; ■: abandoned; ▲: repeated mowing; ◆: manuring) are presented.

(*P* = 0.003 and 0.007) on zoochore species with maximum covers for trampling plots (39 % and 50 %) and minimums for repeated mowing plots (25 % and 34 %). In the centre of the gap, in spring 2002, perennial not clonal species showed significant differences (*P* = 0.3). Maximum values were found in abandoned plots (24 %) and minimum values in trampling plots (12 %).

3.4.4. Discussion

3.4.4.1. Impact of gap creation on species richness

At one square meter scale, gap creation had almost no impact on the number of species even if the gap destroyed 36 % of the vegetation cover. The impact of this disturbance on the number of species is perceptible only at the scale of the gap (in this case a few dm^2). The low impact of gap creation at 1 m^2 scale can be explained by a very high number of species per dm^2 and a rather homogenous distribution of plant species. In the same way, Klimes (1995) observed in a subthermophilous meadow an average number of c.a. 3 species in squares of 0.0025 m^2 with a maximum of 8 species. In another study in extensively grazed limestone grassland, van der Maarel and Sykes (1993) observed a maximum of 40 species on 1 m^2 and of 27 on 1 dm^2. This scale dependant response of gap creation means that for the plant community gap creation events do not affect the general texture. As pointed out by Pickett et al. (1989), 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 general plant composition (see below).

3.4.4.2. Impact of gap colonisation on species richness

On the edge of the gap after one season, the number of species had already attained half the number of species observed in the intact vegetation indicating a rapid colonisation of this area type. By contrast, the centre of the gap is colonised more slowly. In the centre of the gap the succession appearing after gap creation promoted new species. The number of new species appearing in the centre area of the gap during the study (between 3 and 9 in 16 dm^2) was equivalent to those observed at this scale in not artificially perturbed vegetation. For the same community type, Kohler et al. (2004b and § 4.1) showed at dm^2 scale an average of about 6 new species appearing during only four months. Van der Maarel and Sykes (1993) observed for example in a square of 25 dm^2 an average of 4.4 new species appearing within two years. So it seems that the rate of appearance of new species was not particularly different in the gap than in the closed surrounding vegetation where the turnover is high at small scale (Herben et al. 1993a; Klimes 1999; Otsus and Zobel 2002). Differences between gaps and intact area will be rather in the species type appearing in the gap than in the quantity of new species (see below). At community scale only four new species appeared. Spackova and Leps (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 rich of species when the regional species pool contained either no or few species that could enrich the actual vegetation. In our case, the studied community had been for decades submitted to gap creation and so gap colonisers were already present. The most important new species was *Poa supina*, which is in this type of pasture, a typical ruderal species of trampled area with sparse vegetation. This species seems to colonise new favourable habitat very quickly, particularly in trampled and mowed plots where plants are frequently partly destructed.

3.4.4.3. Gap colonisation, species composition and functional traits

Colonisation of gaps 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 weaker list of the species around the gap. A part from the four new species cited above all species in the gap were present in the closed community surrounding the gaps. Species favoured by this disturbance were also pointed out in other studies. Vandvik (2004) showed also that *Veronica serpyllifolia* and *Cerastium fontanum* ssp. *triviale* were gap increasers in subalpine grasslands. By contrast *Agrostis capillaris,* which played an important role in our case appeared in species characteristic of areas without gaps. On the other hand, this stoloniferous species was defined by Arnthorsdottir (1994) and Pakeman et al. (1998) as a good coloniser and Lavorel et al. (1998) described it as a representative species of pig disturbance. *Cerastium fontanum* ssp. *triviale* was also recognized as a coloniser by Milberg (1993) who found this species only in gaps. Gigon and 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 the grasses, showed that *Cynosurus cristatus* had a higher colonisation ability and that the proportion of seed-derived colonising tillers was for this species about 95 % of the total colonising tillers. Otherwise, two species with bulbs (*Corcus vernus* ssp. *albiflorus* and *Narcissus pseudonarcissus*) appeared as important species in the gaps. In this case bulbs were probably not destructed by gap creation because they were deeper than the first 3 centimetres of soil removed. So it was impossible, in this case, to say if they were really gap colonisers or if they never disappeared. *Festuca nig. nigrescens*, *Alchemilla monticola* or *Trifolium pratense* were excluded from the gap. Bullock et al. (1995) showed also that *Festuca rubra* (*Festuca nig. nigrescens* is a member of the *Festuca rubra* aggregate) had a low colonisation ability. Furthermore Gigon and Leutert (1996) showed that *Trifolium pratense* had more cover in control vegetation than on vole colonies. Species excluded from the gaps were generally dominant species. This observation reported also by Vandvik (2004) could support the assumption of disturbance theory, which is that gap creation reduces competition intensity, allowing species which are poor competitors to persist in the community (Suding 2001). It is however clear that gap effects are more complex because, like Bullock et al. (1995), we observed that some common species were dominant in the gaps.

There was a clear edge effect supported by the very high similarity between species composition on the edge of the gaps and in the surrounding vegetation and by the faster recolonisation of this area compared to the centre. As already indicated by many authors (e.g. Arnthorsdottir 1994; Bullock et al. 1995; Kotanen 1997), this shows the importance of clonal strategy in gap revegetation in perennial grassland. It is so clear that we cannot predict species composition of gap colonisation without knowing the composition of community directly around this perturbation.

Small seed, unspecialized seed dispersal, persistent seed bank and high vegetative spread characterised species favoured in the gaps. Among the present species, *Agrostis capillaris*, *Veronica serpyllifolia* and *Campanula rotundifolia* showed these four attributes. It is important to note here that these four attributes were related to gap colonisers but with our method it was not possible to say if they played really a role in the gap colonisation. Burke and Grime (1996) showed that smaller-seeded species were more dependent on disturbance for establishment, large seed size permitting seedling establishment in a closed cover of vegetation. Kalamees and Zobel (2002) and Suding et al. (2003) had also showed smaller seed mass for gap species. By contrast Glodberg (1987) and Lavorel et al. (1999b) found no association between small seed and disturbance colonisation. For the seed agency of dispersal results were surprising, due principally to the fact that zoochorous species were related to intact vegetation. We could suppose that like species with wind-dispersed seeds, this type of dispersal permits colonisation at greater distance than non-specialised 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. Zoochorous species present in the study site were principally epizoochorous and myrmecochorous (dispersal by ants) species. For the first type the exclusion of large herbivores of the study area could explain the observation, but of course not for the second type. Otherwise, the relative small size of our artificial gaps could explain this result. Seeds did not need a specialized dispersal mechanism to move the few centimetres up to the centre of the gap. Our results showed that persistent seed bank was clearly an attribute of gap increasers. In a calcareous grassland, Kalamees and Zobel (2002) found that the soil seed bank density was about 3000 seeds/m^2 and they concluded from a field experiment that the soil seed bank has an important role in gap regeneration. In 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 colonisation, which was clearly dominated by vegetative regrowth. In our case and as reported from perennials grasslands elsewhere (Rapp and Rabinowitz 1985; Milberg 1993; Kotanen 1997; Mariott et al. 1997), high 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 grassland (Klimes et al. 1997; Macek and Leps 2003). Concerning the clonal growth mode of the species with large lateral spread characterising gap colonisation, four (*Agrostis capillaris*, *Poa supina*, *Hieracium pil. pilosella* and *Cerastium fontanum triviale*) are classified by Klimes et al. (1997) as species with “short-lived plagiotropic above-ground stems specialised in spreading”. *Agrostis* is also a member of the type characterised by “long-lived below-ground plagiotropic stems formed below-ground” and *Hieracium* is also described as a species with “short-lived below-ground plagiotropic stems formed above-ground”. Only *Campanula rotundifolia* showed other modes with “ long-lived below-ground stems formed above-ground” and “lateral roots with adventitious buds”.

3.4.4.4. Gap colonisation and cattle activity

In chalk grassland, Bonis et al. (1997) demonstrated that some typical gap species cannot grow in gaps without nutrient-enrichment by animals. Our treatments which simulated cattle activity clearly did not play a primary role in the gap revegetation despite the fact that they induce significant various dynamics in a closed community (Kohler et al. 2004a and § 3.1). It seems that constraints imposed by gap environment were more important than disturbance like trampling or mowing. Furthermore manured treatment did not promote species richness despite potential addition of seeds with the liquid mixture. Differences between treatments appeared, but with secondary importance. In PRCs the variance explained by gap area types and treatments was greatly higher than the variance explained by gap area types only. The second axis of PRC on species data clearly showed differences between treatments. It is interesting to note that gap increasers on this axis were dispatched. *Agrostis capillaris* and *Poa supina* were related to trampling and repeated mowing and *Campanula rotundifolia* and *Hieracium pil. pilosella* to manuring treatment and abandoning. This last result was surprising because both species are oligotrophic and are low statured and so should not be favoured by manuring. It seems therefore that species, which were clearly disadvantaged by manuring in a closed canopy (Kohler et al. 2004a and § 3.1) could become key-species in gap revegetation under the same treatment.

The very few significant effects of treatments at functional traits level was probably due to the high selection of attributes permitting the gap revegetation and to our choice of traits, which were voluntarily centred on regenerative phase and not on traits like stature or height.

Despite few significant differences between treatments, other results showed some interesting aspects. Repeated mowing promoted the number of species per dm^2 while trampling had a negative impact on this variable. At the same time, trampling showed the higher number of new species and the lowest edge effect. We can suppose that this treatment reduced clonal revegetation and favoured seed emergency. By contrast manuring and abandoning showed a high edge effect with a lower turnover on the edge of the gap, which can be explained by the lack of destruction of plant individuals in both treatments. Repeated mowing seemed to result in an intermediate behaviour pattern, but generally induced a rather similar dynamic to trampling.

3.4.5. Conclusion

The results of this study demonstrate that fine scale gap creation can have a high impact on relative contribution of species in the community. This disturbance contributes to high species richness of pasture by creating microsites where specialised species can establish for a while (Gigon and Leutert 1996). The continuous creation of gaps of a few decimetres by cattle or other large herbivores and colonisation of these gaps by a partial set of species of the surrounding may be seen as a series of microsuccessions participating in the grassland properties such as species richness and long-term stability (Grime 2001; Vandvik 2004). Cattle may bring about vegetation change by its effects on the rate of gap creation (Bullock et al. 1995). However relation between gap colonisation and cattle activity seem not to be of primary importance but induces, even so, various dynamics. These complex interactions participate in the high species richness and are probably a key to understand plant coexistence in perennial grasslands.

Acknowledgements

We acknowledge support from the Swiss National Science Foundation (grant 31-64116.00 and NCCR Plant Survival). We are also grateful to Estelle Crippa, Amélie Fragnière, Nadège Farhni, Regula Benz, Nicolas Küffer and Daniel Béguin for help in fieldwork and to Brigitte Corboz and Alwyn A. Robinson for editing support.

Note:

- *Maps of the geographical situation of La Métairie d'Evilard*, *photos of the field, treatments, gaps and the grid method are included in Appendix Ia*

3.4.6. Additional results

To compare the results of this subchapter with subchapters 3.2 and 4.2, analyses on gap colonisation and C-S-R strategies (Grime 2001) are presented.

Figure 3.4.7 presented the evolution of the C-S-R signature (see § 3.2.2.4 for details). Around and on the edge of the gap, vegetation showed similar patterns. The centre of the gap presented different values particularly at the first record after gap creation. The pattern was different depending of the treatment with an increase of S-strategy and a decrease of C and R-strategies in repeated mowing and abandoned plots. Manuring did not show any trend and trampling presented up to the end of the experiment an increase of R-strategy. This increase was also observed in the edge of the trampled gaps.

Therefore there was no increase of ruderal strategy after gap creation. This strategy was favoured only by trampling. Prediction of the model (increase of R-strategy on bare soil) was then not verified in this case.

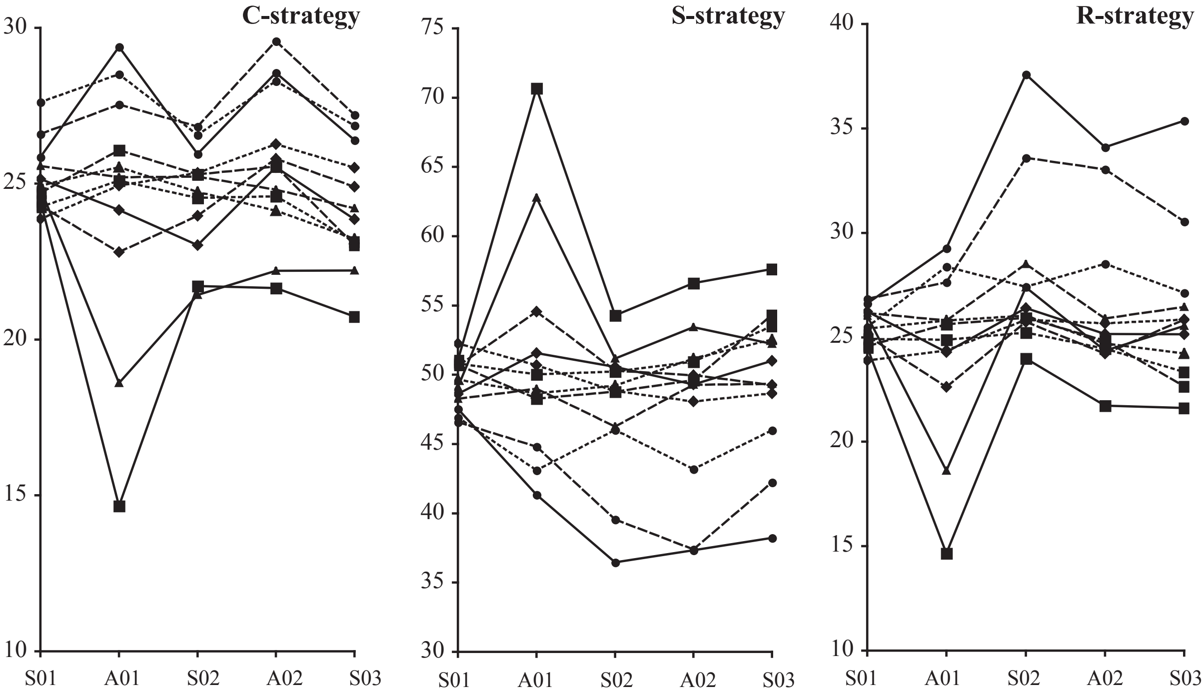

Figure 3.4.7: Evolution C, S and R signature (S: spring; A: autumn; 01-02-03: years; S01: before gap creation). Average values (N=2) per area type (continuous line: centre of the gap; large dashed lines: edge of the gap; fine dashed lines: around the gap) and per treatment (●: trampling; ■: abandoned; ▲: repeated mowing; ◆: manuring) are presented.

CHAPTER 4

Fine scale vegetation dynamics

4.1. Seasonal dynamics of plant species at fine scale in wooded pastures*

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4.1.1. Introduction

Grassland communities are characterized by high small-scale turnover and spatial dynamics of plant species (Herben et al. 1993a; Van der Maarel and Sykes 1993; Otsus and Zobel 2002). This dynamics varies in space and in time within the community according to five different species strategies (Van der Maarel 1996): occasional, local, pulsating, circulating and constant. Palmer and Rusch (2001) have found in recent publications five factors associated with this high species turnover: weather fluctuations that promote establishment by seed, high rates of gap formation, a high proportion of species with short life spans, young age of clonal population and high number of potential colonizers. The role of small-scale dynamics in local species coexistence is still not clear. Otsus and Zobel (2002) made two assumptions: (1) for competitively inferior species, a high mobility could reduce the negative competition of dominant species by escaping in the available gaps; (2) for dominant species, the ability to occupy space efficiently may mean a superior competitive trait.

Van der Maarel and Sykes (1993) proposed the Carousel Model to describe this small-scale dynamics of vegetation. This model suggests that over time any microsite can become a niche for any species participating in the community. Wilson et al. (1995) proposed a variant of this model: the Niche-limited Carousel Model. In this model, there are only a limited number of niches within a microsite. This model predicts a relatively constant richness at fine-scale.

To explore the internal dynamics of an established plant community, the cell-grid method has been used since the middle of the last century (Watt 1962). This method consists in a repeated sampling of vegetation in several small cells. Most studies explored small dynamics with a temporal resolution of one year (e.g. Sykes et al. 1994; Van der Maarel and Sykes 1997; Klimes 1999; Zobel et al. 2000). Only few cases have a recording interval less than one year (Thórhallsdóttir 1990; Lafrage 2001).

Our study was undertaken in a wooded pasture representing a typical landscape of the Swiss Jura Mountains. This ecosystem is characterized by a mosaic of trees, shrubs and grassland grazed by cattle from May to September (Gallandat and Gillet 1999). Cattle activities, such as dung deposition, herbage removal (grazing s. s.) and trampling, induce disturbance at short term and at fine scale. These three activities have different impacts on vegetation at a fine scale (bite and feeding station *sensu* Bailey et al. 1996). Dung pats and urine have two main effects on vegetation dynamics: (1) fertilization involving a stimulation of plant growth, and (2) reduction of the herbage attractiveness for cattle during the first months or years after deposition. Trampling affects the vegetation through detaching plant material with the hoof action and by influencing the water regime in firming the soil (Abdelmagid et al.

1987). Furthermore, trampling creates gaps and thus permits the establishment of new species (Grubb 1977). The effect of herbage removal is principally the loss of biomass and a change in light competition between species (Grime 2001).

The aim of the present work was to investigate at month scale and at two spatial scales (1 dm^2 and 1 m^2) the dynamics of species in the herbaceous layer of four different typical plant communities in wooded pastures. At first, we described community dynamics at two spatial resolutions. Then, we were interested in the behaviour of each species and in its related dominance. After that, we investigated the relationship between the dynamics of species and cattle activity, in particular herbage removal and trampling. Note that dynamics of plant species we consider here, which is sometimes called species mobility, must not be confounded with the mobility of plant individuals. The latter is quite impossible to investigate in mountain pastures, essentially composed by clones of perennial species for which the concept of individual is irrelevant.

We were guided by the following working hypotheses: (1) dynamics is higher at cell scale (1 dm^2) than at plot scale (1 m^2); (2) changes at plot scale are driven by a phenological shift and thus are essentially directional at seasonal scale; (3) dynamics depends on species; (4) herbage removal by grazing depends on qualitative cattle selectivity and thus does not depend on species dominance; (5) selectively grazed species show higher dynamics at cell scale but remain constant at plot scale; (6) trampling increases species dynamics at cell scale.

At the end, we tried to use our results to know which model (Carousel Model or niche-limited Carousel Model) could be relevant to explain dynamics of plant species at seasonal scale in pastures.

4.1.2. Material and Methods

4.1.2.1. Study site

This study was conducted in the Jura Mountains of north-western Switzerland. 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 mean annual rainfall of about 1600 mm (with more than 400 mm snow precipitation) and mean annual temperature of 7°C. The ground is covered with snow from November to April. The area contains a great diversity of habitats, from open grasslands to forest patches, with flat or sloping ground and a heterogeneous soil mosaic (Leptosols, Cambisols, Luvisols; taxonomy after Deckers et al. (1998)). This landscape is the result of decades of cattle activity. Climax vegetation is a beech forest. The management is extensive with a rotational grazing system. During the observation period in summer 2001, 120 heifers (49.2 Adult Bovine Units, 29520 kg live-weight) stayed three times (rotations) during 15 days in the period from May to September in the paddock where plots were placed (see below). Surface of the paddock was about 25 ha. The herd was a mix of Holstein and Swiss brown breeds.

4.1.2.2. Sampling design

We chose four typical community types building the mosaic of the herb layer in wooded pastures, constituted almost completely by perennial species. We placed preferentially one permanent plot in each of them.

The first chosen community was the most widespread in open areas, on soils of about 20-cm depth and with a pH close to 5. This short-grass community was an 'eutrophic grazed meadow' dominated by *Festuca nigrescens*, *Agrostis capillaris, Alchemilla monticola* and *Veronica chamaedrys*. The second community occurred on the same soils, in mosaic in open areas with the first one, but with a higher canopy. This tall-grass community appeared generally where dung pats or urine have been left over by cattle, inducing an excess of nutrients that temporarily inhibits grazing behaviour. It is dominated by *Festuca nigrescens*, *Sanguisorba minor, Taraxacum officinale* and *Cynosurus cristatus,* and will be called 'temporary refused meadow' in this paper. The third community occurred also on the same soils, along the shaded edges of the thickets. This 'underwood herb community' was dominated by *Carex montana*, *Fagus sylvatica* (seedlings), *Festuca nigrescens* and *Narcissus pseudonarcissus*. The last chosen community was an 'oligotrophic lawn' (calcicolous dry grassland) dominated by *Helianthemum nummularium* subsp. *obscurum, Hippocrepis comosa*, *Carex sempervirens* and *Koeleria pyramidata*. It appeared in open areas on soils of about 5-cm depth and with a pH of about 6.5. See Appendix III for complete list of species and mean cover.

4.1.2.3. Vegetation sampling

We chose a spatial resolution of one square decimetre and an extent of one square meter using a square grid with one hundred cells. It was not possible to lay the grid down onto the soil because of the density of the vegetation. Thus, the grid was kept fifteen centimetres above the ground with four perforated plastic tubes. In order to place the grid every time in the same position we fixed in the soil two other perforated plastic tubes at opposite corners. A wooden rod was then placed through the two superposed tubes to adjust the grid. The four plots were observed five times during the vegetation season, between May and September. On the whole study, 2000 cell-records were made. We recorded in each cell the exhaustive list of species and we estimated the absolute cover of each species with Braun-Blanquet's dominance code. Plants were often only at vegetative state and sometimes drastically grazed, inducing identification problems (Klimes et al. 2001) and indeed, this required training in species recognition. To reduce bias with this respect all records were made by the same observer. At each time, the plot records were constructed by aggregating the 100 cell records. Species absolute cover at plot scale was the mean of the species absolute cover in the 100 cells (deduced from dominance Braun-Blanquet's codes). Species frequency at each time was measured by dividing the sum of all occupied cells by 100.

To get information on cattle activities we recorded traces on grazing and trampling. We noted for every species for each cell if it has been grazed or not. Even if rough, this binary index appeared as a good compromise between precision and efficiency. Trampling effect was more difficult to assess. The size of a hoof corresponds to about one square decimetre and trampling disturbance is not selective. Therefore, we planted at the beginning of every rotation a 20 cm long vertical wooden stick into the ground in the middle of each cell and we checked later for broken or bent sticks. We may assume that this measure can be used as a rough binary index of trampling occurrence within the cell even if it could be due to another cattle activity, such as grazing. At plot scale, trampling intensity at each time was calculated by summing all occurrences.

Each record of one square meter required five to eight hours of labour or more, depending of the species richness and on the state of development of the vegetation. Our sampling design did not permit to study dunging and gap creation because these two disturbances were too rare and localised.

4.1.2.4 Statistical analysis

At first, we studied the dynamics from a community point of view. To know if the seasonal dynamics depended on spatial scale, we calculated the richness and the cumulative richness of species (Van der Maarel et al. 1995) per cell (1 dm^2) and per plot (1 m^2). Furthermore, to assess the spatial arrangement of the community through time, we calculated for all vegetation records within each plot and at each session the Mantel correlogram with Pearson's correlation coefficient using the R package (Casgrain and Legendre 2001).

Secondly, we studied the dynamics at a population point of view. To detect different specific behaviours, we defined three exclusive strategies for species according to their dynamics:

- *Casual*: species appearing only once, except in May and September,
- *Pulsating*: species disappearing and appearing newly during the season,
- *Persistent*: species remaining at least through two successive months and which were not pulsating.

Contrary to van der Maarel (1996) who took into account spatial and temporal aspects, this classification uses only time series of one plot or cell. This classification excludes vernal and late species, which appeared only in May or in September, because we do not know what happened before or after that period. Furthermore, because we did not have any control on underground patterns, it is possible that some extinction events represented only disappearance of aboveground shoots, for example after grazing. It is important to remember that our study does not consider individuals but instead species. We calculated at plot and cell scale the percentage of species showing at least one of the three strategies. At cell scale this was done by checking the species behaviour over the five records carried out in the same cell. At plot scale the five 1 m^2 records were used instead. Thus, at cell scale one species may behave according to more than one strategy. So we calculated for each species the relative importance of each strategy using the hundred cells per plot.

Thirdly, we assessed the role of cattle activity in the community dynamics at both scales. We calculated for each cell the grazing intensity as the sum of the relative cover (deduced from Braun-Blanquet codes) of all individual species that were grazed after each rotation. Furthermore, for each plot at each session, we calculated the percentage of broken sticks.

Spearman rank correlations were used to investigate the relationship between the mean annual turnover (mean of turnover in a cell during the study) and the mean annual grazing intensity (mean of grazing intensity in a cell during the study) or the total trampling occurrences (number of sticks broken in a cell during the study). The turnover between consecutive sessions was calculated by using Jaccard's dissimilarity index (1 – Jaccard's binary similarity, Güsewel et al. 1998). Because data in contiguous grid samples are autocorrelated (Jonsson and Moen 1998), we corrected the degree of freedom and the *P*-value, accounting for spatial autocorrelation, by the method of Dutilleul (1993) when testing the Spearman rank correlation. This correction was computed with the Mod_t_test program (Legendre 2001).

From a population point of view, Spearman rank correlation was also used to investigate in each plot for each species the relationship between the relative importance of the three strategies (see above), or the mean annual cover of the species (annual mean species cover of all records) and the mean grazed species cover (annual mean of the proportion of species cover with traces of grazing).

Except the correction of Dutilleul (1993) and the correlograms of Mantel, all calculations were performed with R 1.9.1 (R Development Core Team 2004).

4.1.3. Results

4.1.3.1. Community point of view

The evolution of species richness and cumulative species richness in the different vegetation types at cell scale and at plot scale is shown in Figure 4.1.1. In each plot, the mean number of species per cell did not show any obvious trend whereas the cumulative richness increased. The maximum cumulative number of species per cell was increasing up to about half of the total cumulative number of species per plot. The lawn pattern appeared as the most constant with a small difference between number and cumulative number of species. At this scale, the four vegetation types showed globally the same behaviour. By contrast, at plot scale the richness varied with a maximum in June for the temporary refused meadow, the underwood and the lawn, and in September for the grazed meadow. In the lawn, the underwood and the temporary refused meadow, the cumulative richness increased dramatically in June and more gently after. Correlograms of Mantel (Figure 4.1.2) showed at each period and for all vegetation types significant positive autocorrelation for short distances. This spatial autocorrelation was highest in the underwood and lowest in the lawn. There were significant negative values for longer distances, except in the lawn where only few negative values were significant. The general pattern did not vary over the season in any of the communities except for the grazed meadow in September. At this time, the

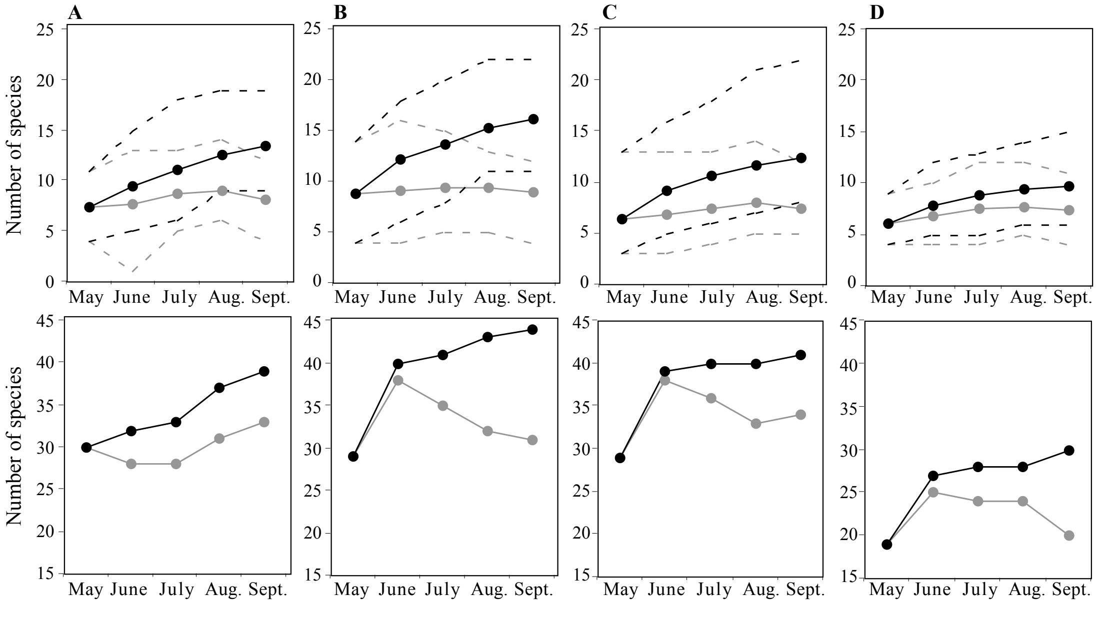

Figure 4.1.1: Species richness (grey lines) and cumulative species richness (black lines) in four vegetation types (A: grazed meadow; B: temporary refused meadow; C: underwood; D: lawn) from May to September. At 1-dm^2 scale (above), mean (solid lines), and maximum and minimum (dashed lines) are represented. At 1-m^2 scale (below), absolute values are given.

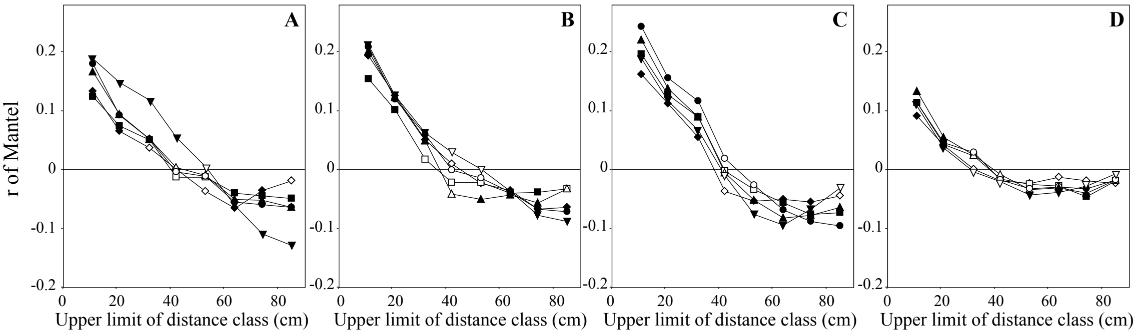

Figure 4.1.2: Mantel correlograms with Pearson's correlation coefficient between vegetation records in 1-dm^2 cells of each plot at each session. Diamonds: May; squares: June; triangles upper: July; dots: August; triangles lower: September. Full: significant *P* value (0.05) with correction of Bonferroni. A: grazed meadow; B: temporary refused meadow; C: underwood; D: lawn.

correlogram was more contrasted with higher positive values at small distances and higher negative values for longer distances.

4.1.3.2. Population point of view

At plot scale, most of the species were persistent and only few were casual or pulsating (Figure 4.1.3). This means that almost all species appeared at one moment, persisted during at least two months and disappeared. On the other hand, at cell scale almost all species could behave as persistent, pulsating or casual. Figure 4.1.4a and b show for each species ordered by annual mean frequency the relative percentage of each strategy. The persistent strategy dominated generally, but in each vegetation type some species presented an important proportion of the two other strategies. By definition species with high frequency are persistent because even if individuals or clones moved there is a high probability that they occupied a cell already occupied at the last session. This explains why the persistent strategy dominated for the most frequent species. Thus it is more interesting to consider species with medium or low frequency. For species with medium frequency the persistent strategy dominated. There were some exceptions. For example in the grazed meadow, the temporary refused meadow and the underwood, *Rumex acetosa* showed a large proportion of pulsating and casual behaviour. *Crepis mollis* in the grazed meadow and in the underwood, *Anthoxantum odoratum* in the temporary refused meadow, *Veronica officinalis* in the underwood or *Potentilla crantzii* in the lawn presented also a high proportion of pulsating and casual strategies. Species with a low frequency showed generally a high proportion of casual behaviour. There were in this case also some exceptions such as *Potentilla erecta* in the grazed meadow or in the temporary refused meadow.

4.1.3.3. Cattle activity

The pattern of herbage removal in June after the first rotation and in September at the end of the season was completely different (Figure 4.1.5). In June the grazed meadow was the most grazed and in September the four communities were almost equally intensively grazed. The variation was very high, indicating that at very fine scale the pattern of herbage removal was very heterogeneous. In the grazed meadow for example, some cells were never grazed despite a high grazing rate in neighbouring cells. The situation was very different for trampling occurrence. In June, an equal high number of broken sticks was recorded in all communities, indicating that every community was visited. In

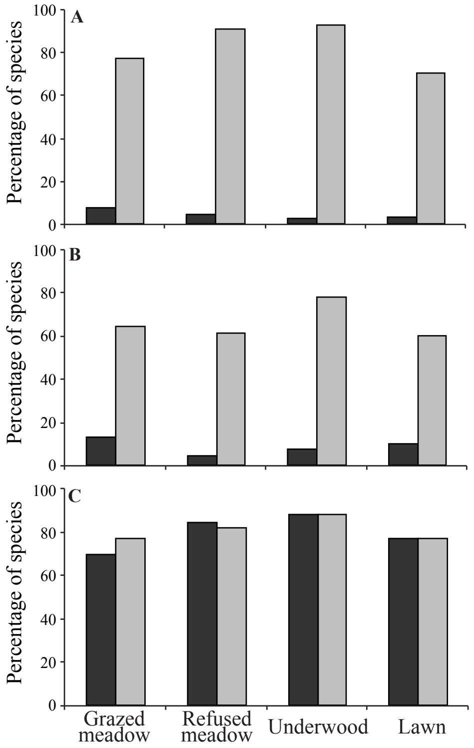

Figure 4.1.3: Percentage of species appearing at least once with the strategy casual (A), pulsating (B) and persistent (C) at plot (black) and cell (grey) scale.

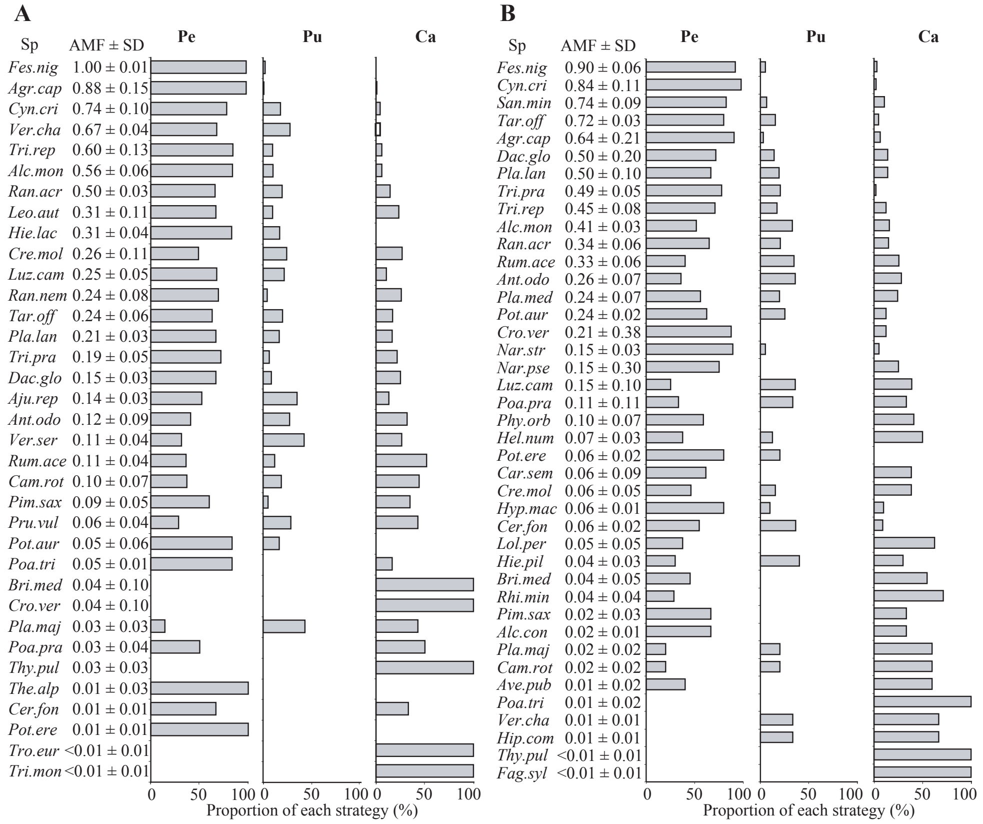

Figure 4.1.4a: Proportion of observed strategies at cell scale for all species. Vernal and late species were excluded (see explanation in the text). AMF ± SD: annual mean frequency ± standard deviation; Pe: persistent; Pu: pulsating; Ca: casual; A: grazed meadow; B: temporary refused meadow. For species abbreviations see Appendix III.

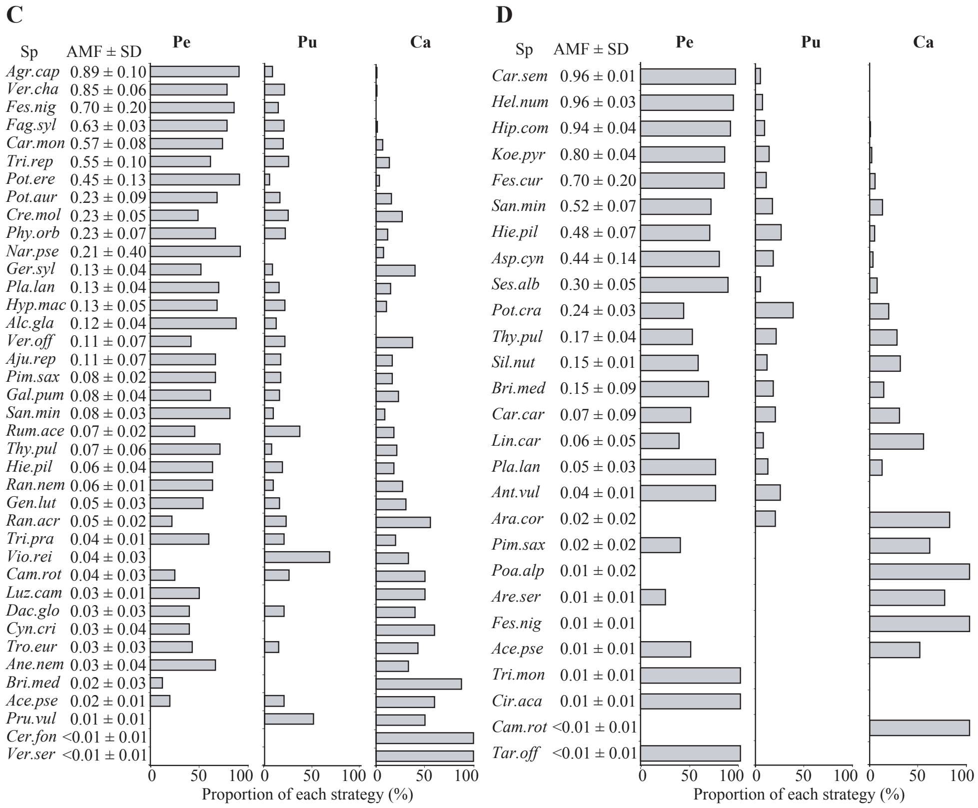

Figure 4.1.4b. Proportion of observed strategies at cell scale for all species. Vernal and late species were excluded (see explanation in the text). AMF ± SD: annual mean frequency ± standard deviation; Pe: persistent; Pu: pulsating; Ca: casual; C: underwood; D: lawn. For species abbreviations see Appendix III.

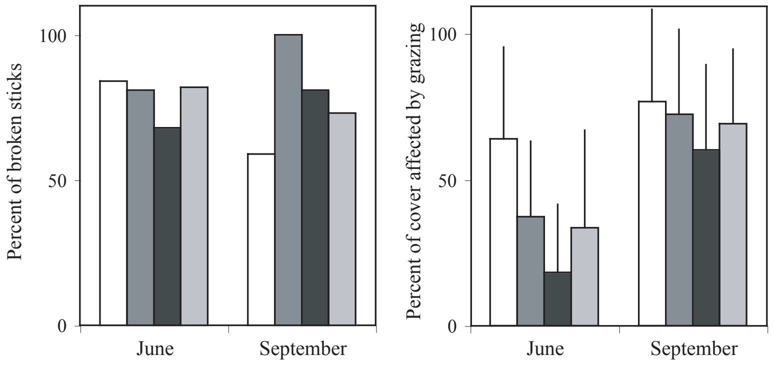

Figure 4.1.5: Proportion of broken sticks for the entire plot (100 cells) and mean with standard deviation of amount of vegetation cover affected by grazing per cell (grazing intensity) in each vegetation type after the first rotation (June) and after the last one (September). White: grazed meadow; dark grey: temporary refused meadow; black: underwood; light grey: lawn.

Table 4.1.1: Spearman rank correlation between for each species the annual mean grazed species cover (G) and the proportion of strategies (Pe: persistent, Pu: pulsating or Ca: casual) in the 100 cells or the mean annual species cover (Co) (see details in the text). •: $P < 0.1$, *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$.

	Pe vs. G	Pu vs. G	Ca vs. G	Co vs G
Grazed meadow	**0.32•**	0.27	**-0.30•**	**0.52*** **
Temporary refused meadow	**0.35***	0.09	**-0.38***	**0.46** **
Underwood	0.24	**0.28•**	**-0.33***	**0.34***
Lawn	**0.51** **	**0.44***	**-0.54** **	**0.86*** **

September, there were more broken sticks in the temporary refused meadow and less in the grazed meadow.

From a community point of view, there was no correlation between the mean turnover and the grazing intensity or the trampling occurrence (results not shown). From a population point of view, there were some significant positive correlations between persistent strategy and the mean grazed species cover (Table 4.1.1). Pulsating strategy was positively correlated as well, whereas casual strategy was negatively correlated with grazing intensity. Additionally, all correlations between cover and grazing intensity were significant, indicating that a species with a high cover had more chance to be grazed than a low-covering species. Thus, there was no clear selection of species at this scale.

4.1.4. Discussion

4.1.4.1. Change in species assemblage and scale effect

Our results showed that seasonal changes in species composition and distribution were very strong and scale-dependent. At plot scale, changes can be explained mainly by a phenological shift, due to life-history traits of species. Indeed, most of the species appeared at one time, persisted in the community at least for two months (persistent type) and disappeared after finishing their life cycle or were waiting for the next favourable season. By contrast, changes at cell scale were only partially due to the phenological shift. Dynamics of species plays an important role at this scale. Almost every species can either appear only once (casual) or disappear and then reappear during the season (pulsating). Herben et al. (1993b) observed the same phenomenon at year scale with high dynamics at 3.3 cm x 3.3 cm and low dynamics at 50 cm x 50 cm. They conclude that at small scale forces act on species composition so as to make dynamics non-directional. Furthermore Pärtel and Zobel (1995) concluded that both relatively stable and successional communities show a similar high small-scale turnover. Also, the spatial autocorrelation pattern was constant over time, indicating that the spatial structure of the community did not change during the season, despite changes in the floristic composition. Therefore, at fine and seasonal scale and despite changes in the vegetation texture, the structure seems to be very persistent in the four communities with different ecological characteristics. The community with the lowest dynamics was the lawn. This vegetation type which grows with low soil nutrient availability and in dry conditions has a low growth rate and consequently probably also less ability to move its species. We can also suppose that this vegetation, with the lowest height and cover, induced less competition between species for space and that there was therefore less strength for a high spatial dynamics. Nevertheless, Chiarucci et al. (2002) suggested recently that physical space is probably never limiting by itself in terrestrial higher-plant communities.

4.1.4.2. Species strategies

Different species showed a contrasting proportion of the three strategies. Otsus and Zobel (2002) observed also high differences among species for vegetative turnover. We can explain the high proportion of casual and pulsating behaviours for medium-frequency species by three different strategies to maintain the population: (1) adult plants are very mobile, (2) adult plants are not mobile at all but there is a flush of seedling establishment which die soon before reaching any significant cover and (3) adult plants have a high regenerative potential after having been completely grazed (pulsating behaviour). On the basis of the present data, we cannot distinguish between these three strategies but there is some indication that all of them are involved. The high proportion of species with clonal reproduction in grasslands (Tamm et al. 2002; Klimes et al. 1997) points to a high possibility to adult plants to move. The importance of the second strategy is less clear. Marriott et al. (2002) concluded that in the closed canopy of the grazed meadow there is little opportunity for seedling development whereas Jakobsson and Eriksson (2000) who sown 50 species in undisturbed grasslands found that 90 % of the species established recruits. About the third strategy, Lardner et al. (2002) showed a high availability of some grass species to regrow rapidly after sheep grazing. Furthermore, Klimes and Klimesova (2002) suggested that higher regrowth ability of less competitive grasses could explain species coexistence in species-rich meadows.

For species with weaker competitive ability, we can interpret the casual behaviour as a mean to escape competition (Huckle et al. 2000). In plots of 10 m^2 Collins and Glenn (1991) have shown that at small spatial scales there is a high degree of stochastic variation over time among satellite species (locally less abundant) within a stable matrix of core species (locally more abundant).

4.1.4.3. Dynamics of species and cattle activity

Concerning the effect of cattle activities on this dynamics, results were less clear. There was no evidence of direct influence of these activities on the turnover of the community, perhaps due partially to the lack of precision of our indices of grazing and trampling. These results could have been explained by supposing a homogeneous pattern of grazing at fine scale but this was clearly not the case (Figure 4.1.5). Furthermore, at plot scale, for the temporary refused meadow or for the lawn there was a clear shift of the importance of grazing during the season and indeed this illustrates the well-known process of broadening of the exploration by cattle, which makes that more vegetation types are eaten when the season goes on. This clear shift in cattle activity did not seem to induce particular dynamics in the plant community. The number or the cumulative number of species at cell scale for the lawn and the temporary refused meadow showed the same trend than the grazed meadow, which was always highly grazed during the season. The absence of links between cattle activities and seasonal turnover at small scale could be explain by the fact that internal dynamics of communities caused by non-linearities in system structure (Herben et al. 1993a) dominate at fine scale, cattle activities acting at larger space and time scales.

There was no evidence in our results for selectivity of species by cattle grazing. The more a species has a high cover, the more it is eaten. Grant et al. (1985) explained this incapacity of cattle to select species at fine scale by its mouthparts form. Positive correlation between persistent strategy and grazing intensity seemed not causal and could be explained by an indirect correlation induced by the amount of cover, which was positively correlated with the removed biomass. On the other hand, this positive correlation could explain the highest mobility of less abundant species. By grazing the more covering species, cattle created free space where other species could immigrate. Positive correlation with the pulsating strategy could be explained by the fact that a high herbage removal may induce a disappearance of aboveground parts, which can reappear later. Like with the persistent strategy, negative correlations with the casual behaviour seemed not causal and could be explained by an indirect correlation induced by the species cover.

4.1.4.4. Carousel model

Many species showed a constant frequency during the season (species with a low SD in Figure 4.1.4a and b) while dynamically active (fairly high proportion of pulsating or casual behaviour), suggesting a carousel at this time scale. This result implies that the 'Carousel times' calculated by Palmer and Rusch (2001) with time resolution of one year could be faster in the reality. *Ranunculus acris* occupied in the grazed meadow at a given time 55 % of the cells but it was observed at least once in 84 % of the cells during the season, which makes a difference of 151 %. This example shows the importance of having an adequacy between time and space scales. Another interesting result is that the mean number of species per cell did not show any trend over time in each cell despite high fluctuations at plot scale (Figure 4.1.1) and high proportion of casual and pulsating strategies (Figures 4.1.3 et 4.1.4). These results seem to be on line with the 'Niche-limited Carousel Model' of Wilson et al. (1995), even if they cannot fully support it. This model supposes that species are mobile in the community but can emigrate in a microsite only if a species disappears.

In conclusion, dynamics and internal species turnover of the community at fine scale and short time seem to be more driven by internal characteristics of the community rather than by disturbances induced by cattle. The latter plays a role at larger scale (more than 1 m^2) by maintaining the composition and the structure of the different communities (Kohler et al. 2004a and § 3.1). Furthermore, at seasonal scale, plant communities may be stable in their structure despite fluctuations in their texture.

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Note:

- *Map of the geographical situation of La Métairie d'Evilard, photos of the field and the grid method are included in Appendix Ia*
- *Pdf file of the printed version in COMMUNITY ECOLOGY is included in Appendix Ib*

4.2. Impact of dung deposition on fine scale and seasonal dynamics of vegetation in mountain pastures

F. Kohler, A. Buttler, S. Reust, J.-M. Gobat and F. Gillet

4.2.1. Introduction

Cattle activity greatly influences the plant species composition, the biomass production and the species richness of grassland ecosystems (Olff and Ritchie 1998; Olff et al. 1999; Bakker et al. 2004), especially through dung deposition (Bakker and Olff 2003). Each cattle produces about 10 to 15 dung patches par day (Marsh and Campling 1970; MacDiarmid and Watkin 1972). Typically, a cattle dung patch covers an area of about 0.05 m^2. Within the patches high nutrient contents, such as 1040 kg N/ha^1, 400 kg K/ha^1, 280 kg P/ha^1 and 100 kg S/ha^1 are deposited (Haynes and Williams 1993). In addition, large quantities of organic matter are deposited with every cattle dung patch (Williams and Haynes 1995). However, these nutrients are not evenly distributed over the pasture, but applied in small areas at high concentrations (MacDiarmid and Watkin 1972). Cattle dung is completely decomposed in a time span from a few weeks to more than one year, depending on water content, climatic conditions, season and activity of the soil fauna (Marsh and Campling 1970; Dickinson and Craig 1990).

Many authors studied effects of dung deposition on cattle activity, soil fertility and plant communities. Dung has an impact on the grazing behaviour by creating “refused areas” around deposited dung patches. Edwards and Hollis (1982) observed cattle avoiding grazing in the immediate vicinity of dung patches, in a way that a fringe of 10-20 cm wide of tall herbage surrounded rapidly the fresh dung patches. In this study, the exclusion effect persisted for about 3 months. During this time the dung largely disappeared. Weeda (1967) found herbage at the dung patch being less grazed and usually 3 cm to 5 cm higher than herbage of the surrounding pasture.

Furthermore, dung has an important effect on the chemical status of the soil. Its deposition represents a potential source of N and other nutrients (Shepherd et al. 2000; Aarons et al. 2004). MacDiarmid and Watkin (1972) showed a significant increase of N, P and K around the dung patches. This increase was detected up to 15 cm around the dung patches (MacDiarmid and Watkin 1972; Deenen and Middelkoop 1992). Twelve months after dung application, Williams and Haynes (1995) observed that soil organic C, nitrate and phosphate were still higher in dung patches than in control patches. Some residual effect on organic C was still evident three years after cattle dung application.

Moreover, dung plays an important role in the dynamic of plant communities in pastures. Initially cattle dung is detrimental to herbage growth, because of smothering. Probably the affected plants die from a lack of light, being covered for several weeks by the dung patch (Williams and Haynes 1995). This initial smothering is compensated by an increased plant growth around the dung patches (Borghesio et al. 1999). The effect decreases with distance, but may extend as far as 40 cm from the edge of the patch (MacDiarmid and Watkin 1971). This effect combined with the reject of grazing around dung patches, influences botanical composition (Marsh and Campling 1970). The field layer vertical and horizontal structure influences also the microclimate and, in turn, this has also consequences on the epigeic faunal composition (Gobat et al. 2004). Furthermore, many authors showed the importance of dung for seed dispersal, germination and soil seed bank composition, which induces also changes in vegetation composition (Welch 1985; Akbar et al. 1995; Malo and Suarez 1995; Dai 2000; Bakker and Olff 2003). Dai (1998) showed that patch size of some plant species in alvar limestone grassland were similar to the average size of cattle dung patches, suggesting a correlation between species development and dung patches. However, studies on the effect of dung deposition on vegetation dynamics at a very fine spatial and temporal scale have not been documented so far.

The aim of the present study was firstly, to investigate the evolution of the height of the vegetation and the rate of grazing around the dung patches in two plants community types on a fine spatial and temporal scale (dm and month). Secondly, we were interested in biodiversity, species composition changes and species turnover in the herbaceous layer surrounding this disturbance, and thirdly, in the evolution of the C-S-R strategies (Grime 2001).

We focused on the three hypotheses: (1) Dung patches have an impact on the surrounding vegetation height and on the grazing rate. (2) Dung patch deposition is a disturbance for the vegetation and consequently induces a high dynamic in the herb layer. (3) This dynamic favours competitive species.

4.2.2. Material and Methods

4.2.2.1. Study site

This study was conducted in the Jura Mountains of northwestern Switzerland. The study site is located in La Métairie d'Évilard (Orvin BE, 47°09' N, 7°10' W) at an altitude of about 1200 m a.s.l. The climate is predominantly temperate oceanic, with mean annual rainfall of about 1600 mm (with more than 400 mm snow precipitation) and mean annual temperature of 7°C. The ground is covered with snow from November to April. The area contains a great diversity of habitats, from open grassland to forest patches, with flat or slopping ground on a heterogeneous soil mosaic (Leptosols, Cambisols, Luvisols; taxonomy after Deckers et al. 1998). This landscape is the result of decades of cattle pasturing. Climax vegetation is a beech forest. The management is extensive with a rotational grazing system. During the observation period from May to September 2001, 120 heifers (49.2 Adult Bovine Units, 29520 kg live-weight) stayed three times (rotations) during 15 days in the period from May to September in the paddocks where the study plots were placed (see below). The surface of the paddocks was about 25 ha. The herd was a mix of Holstein and Swiss brown breeds.

4.2.2.2 Sampling design

We chose two typical and well represented plant communities, composed almost completely by perennial species, building the mosaic of the herb layer. The first community was the most widespread in open areas, on soils of about 20 cm depth, with a pH close to 5. This short-grass community was an 'eutrophic grazed meadow' dominated by *Festuca nigrescens*, *Ranunculus acris* and *Trifolium repens* (Nomenclature follows: Tutin et al. (1964-1980)). The second community also occurred in open areas on soils of about 5 cm depth and with a pH around 6.5. This oligotrophic lawn (calcicolous dry grassland) was dominated by *Sanguisorba minor*, *Plantago media* and *Plantago lanceolata*.

In each vegetation type, we selected 20 fresh dung patches, avoiding dung close to each other, six days after cattle came into the paddock for the first time of the year. For the vegetation sampling, we randomly chose 10 dung patches among the 20. Because the two vegetation types were not in the same paddock and cattle not in both paddocks at the same time, the dung patches on the eutrophic grazed meadows were selected at the beginning of June and those of the oligotrophic lawn at the beginning of July.

We chose a spatial resolution of one square decimetre by using a designed frame in the form of a cross, with four arms consisting of 6 quadrates each and a square of 3 x 3 cells in the centre (Figure 4.2.1). Therefore the frame contained 33 cells. The frame was placed so as to include a dung patch in the centre, while arrangement of the arms was random. It was not possible to lay the cross down onto the soil because of the density of the vegetation. Thus, the cross was kept 15 centimetres above the ground with six perforated plastic tubes. In order to place the cross every time in the same position, we fixed two other perforated plastic tubes in the soil at both opposite corners of the central square. A wooden rod was then placed through the two superposed tubes to adjust the cross. The 20 selected dung patches were recorded every 30 days during the vegetation season between June to September, four times for the grazed meadow (June, July, August and September) and three times for the lawn (July, August and September). Unfortunately only five dung patches in the grazed meadow and

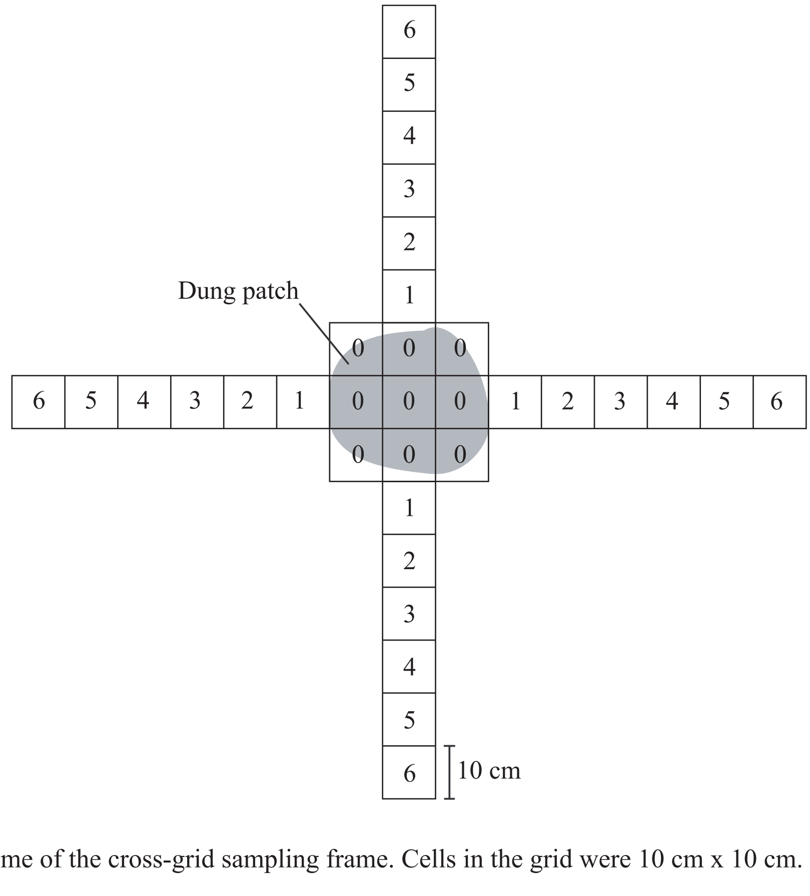

Figure 4.2.1: Scheme of the cross-grid sampling frame. Cells in the grid were 10 cm x 10 cm.

six in the lawn could be monitored throughout the full season. The others were lost due to cattle trampling or because new dung patches were dropped on or very near the selected dung patches. We recorded in each cell the exhaustive list of species and estimated for each one the absolute cover with Braun-Blanquet's dominance code and the maximum height of vegetative parts with a 5 cm class index. Plants were often only in vegetative state and sometimes severely grazed, inducing identification problems (Klimes et al. 2001). To reduce bias with this respect all records were made by the same observer.

To get information on cattle grazing, we noted for every species in every cell if it has been grazed or not. This rough binary index appeared as a good compromise between precision and efficiency.

4.2.2.3. Statistical analyses

For assessing the role of cattle activity on the vegetation, we calculated for each cell at each session the grazing intensity as the sum of the relative percentage cover (median percentage values deduced from Braun-Blanquet's codes) of all the species that showed traces of grazing. For the vegetation height, the index was transformed in quantitative values by taking the median of each class (1 = 2.5 cm; 2 = 7.5 cm; 3 = 12.5 cm; and so on). We calculated for each session an average height per cell, by weighting the height by the relative cover of the corresponding species.

To assess community dynamics, we calculated for each session in each cell the number of species and Pielou's evenness (Pielou 1969; Legendre and Legendre 1998). The species turnover between to successive sessions in each cell was also calculated by using the Jaccard distance (1 - Jaccard similarity (Güsewell et al. 1998)) on presence-absence data. Furthermore, canonical correspondence analysis (CCA) was used to analyse the variation in the species matrix explained by the distance to the dung patches.

To study the relationship between vegetation dynamics and species functional type, we used the C-S-R plant strategy theory (Grime 2001; Colasanti et al. 2001). We calculated the C-S-R signature for each cell at each session following Colasanti (2000): (1) each species is allocated to one of the nineteen C-S-R types following Biostress (2003); (2) within each type present, the sum of the relative cover of all the occurrences of that type is calculated; (3) the sum of each type is allocated to C, S or R depending of the type (example for CSR type: 33 % for C, 33 % for S and 33 % for R or for C/CR type: 75 % for C, 0 % for S and 25 % for R) inducing for each vegetation record three values (C, S and R) which sum equals to 1.

To measure the effects of dung, we grouped the data by distance of the cells to the dung patches inducing seven classes: 0: Dung patch; 1: 0-10 cm; 2: 10-20 cm; 3: 20-30 cm; 4: 30-40 cm; 5: 40-50 cm; 6: 50-60 cm (Figure 4.2.1). For further analysis we used for each dung patch the average value of the 9 middle cells, and for each class of distance the average value on the four arms of the cross. We calculated the Spearman's rank correlation coefficient between the various variables and the distance to the dung patches. For these correlations and also for the CCA, the values calculated for the centre of the cross were omitted, because the dung itself lies not in the gradient. To take into account differences between dung patches, correlations were not directly done on raw data, but on the residuals of a linear regression with crosses as explanatory variable like blocks. For the same reason, variation explained by crosses was conditioned out in the CCA. All calculations and plots were performed with R 1.9.1 (R Development Core Team 2004).

4.2.3. Results

4.2.3.1. Vegetation height and grazing rate

Correlation between vegetation height or proportion of grazed cover and the distance to the dung patches are presented in Table 4.2.1. In the grazed meadow, vegetation was higher near the dung patches already at the first session about six days after dung deposition. The effect became more and more important in the following months. In the lawn, we observed the same pattern except for the first session.

For the grazing intensity, there was a significant positive correlation in all cases, meaning the further we were from the dung patch, the more vegetation cover revealed traces of grazing. Figure 4.2.2 shows the curve for the two variables at the last session in September. The grazing intensity shows a clear increasing gradient up to about 50 cm away from the dung patch. In the lawn, the transition is more abrupt at about 30 cm distance.

The highest vegetation was directly found around the dung patches and its size decreased regularly up to 50 cm distance in the grazed meadow and up to 40 cm in the lawn. Further away vegetation height did not show any trend. The maximum differences between these means within each distance class were about 3.5 cm in the grazed meadow and about 1 cm in the lawn.

4.2.3.2. Biodiversity, turnover and species composition

Correlation between number of species, evenness or species turnover and the distance to the dung patch are presented in Table 4.2.2. There was some tendency in the grazed meadow for the two first sessions to harbour more species near the dung. The correlation was significant in the lawn at the first session. This pattern disappeared during the season.

For the evenness we found a negative correlation at the second and at the fourth session for the grazed meadow. By contrast, the correlation was negatively significant only at the first session in the lawn.

For the turnover a very clear result appeared. There were always significant positive correlations, meaning that vegetation

Table 4.2.1: Spearman rank correlation between mean vegetation height or grazing intensity and the distance to the dung patch. N = 30 for the grazed meadow and N = 36 for the lawn. ***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$.

		Grazed meadow	Lawn
Height			
	Session 1	**-0.474****	-0.027
	Session 2	**-0.432***	**-0.692*****
	Session 3	**-0.441***	**-0.730*****
	Session 4	**-0.829****	-
Grazing intensity			
	Session 1	**0.371***	**0.353***
	Session 2	**0.649****	**0.773*****
	Session 3	-[1]	**0.822*****
	Session 4	**0.824*****	-

[1] There were no cattle in the paddock between session 2 and 3

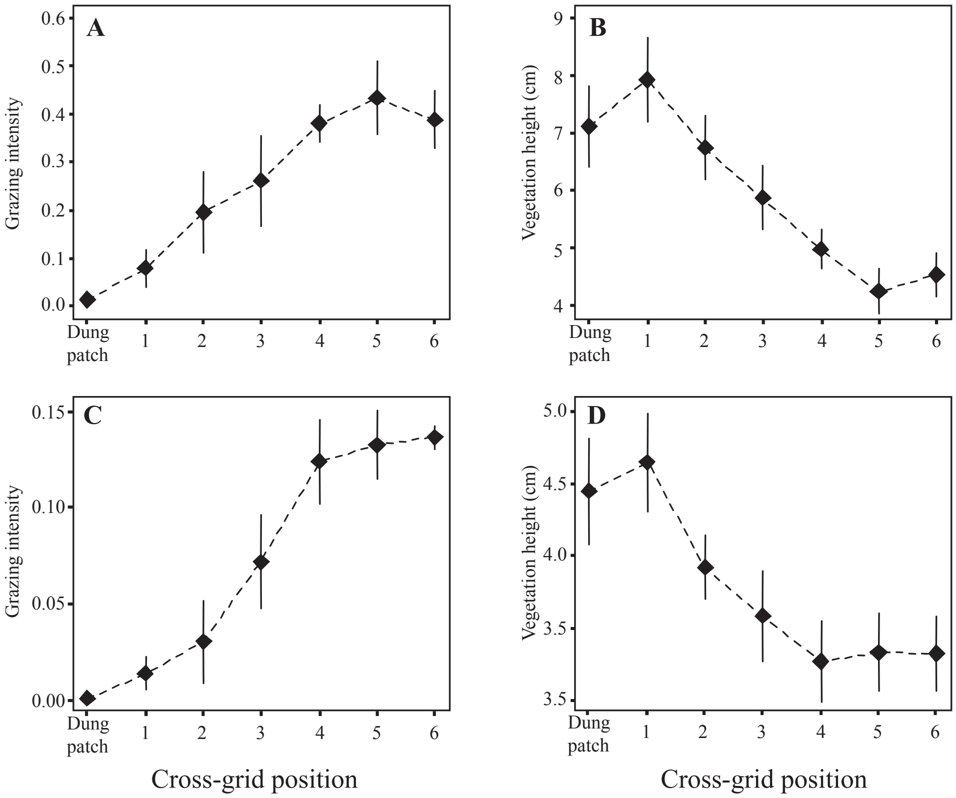

Figure 4.2.2: Grazing intensity (A and C) and mean vegetation height (B and D) by distance to the dung for the last session in September (A and B: Grazed meadow ; C and D : Lawn). Segments represent standard error of the mean.

Table 4.2.2: Spearman rank correlation between species number, evenness or species turnover and the distance to the dung patch. N = 30 for the grazed meadow and N = 36 for the lawn. ***: *P* < 0.001 ; **: *P* < 0.01 ; *: *P* < 0.05 ; •: *P* < 0.1.

	Grazed meadow	Lawn
Number of species		
Session 1	**-0.349•**	**-0.556*** **
Session 2	**-0.320•**	-0.065
Session 3	-0.144	0.073
Session 4	-0.085	-
Evenness		
Session 1	-0.227	**-0.349***
Session 2	**-0.510****	-0.053
Session 3	**-0.330•**	-0.085
Session 4	**-0.590*****	-
Species turnover		
Ses. 1 - Ses. 2	**0.396***	**0.424***
Ses. 2 - Ses. 3	**0.369***	**0.478****
Ses. 3 - Ses. 4	**0.427***	-
First ses. – Last ses.	**0.576****	**0.438****

dynamics was higher afar from the dung patch. The turnover values between the first and the last session along the distance gradient are presented in Figure 4.2.3. The pattern of the curve was almost the same in both plant communities. Turnover was high on the dung patch and lowest in the first 10 cm apart. After this drop, it increased further away in the grazed meadow, but no clear trend appeared in the lawn .

The distance to the dung patch did not explain significant variation of the species assemblage data matrix at the first session (Table 4.2.3), on the contrary to the following sessions. Nevertheless, explained variation was lower and only significant at session 2 in the lawn community.

4.2.3.3. C-S-R signature

Correlation between C-S-R signatures and the distance to the dung patches are presented in Table 4.2.4. Significant results appeared only in the grazed meadow for C and S. C strategy was more abundant near the dung patch at the third and at the fourth session and S strategy was more abundant far away from the dung patch at the fourth session.

4.2.4. Discussion

Concerning cattle disturbance on vegetation, we can define four types of areas around the dung patch: (1) the dung itself, where the vegetation died out, (2) the first decimetre, where the vegetation is not grazed (Figure 4.2.2) but fertilized (MacDiarmid and Watkin 1972), (3) between 2 and 3 dm a zone of intermediate situation with low grazing rates and probably low fertilization (Deenen and Middelkoop 1992) and (4) beyond 4 dm,

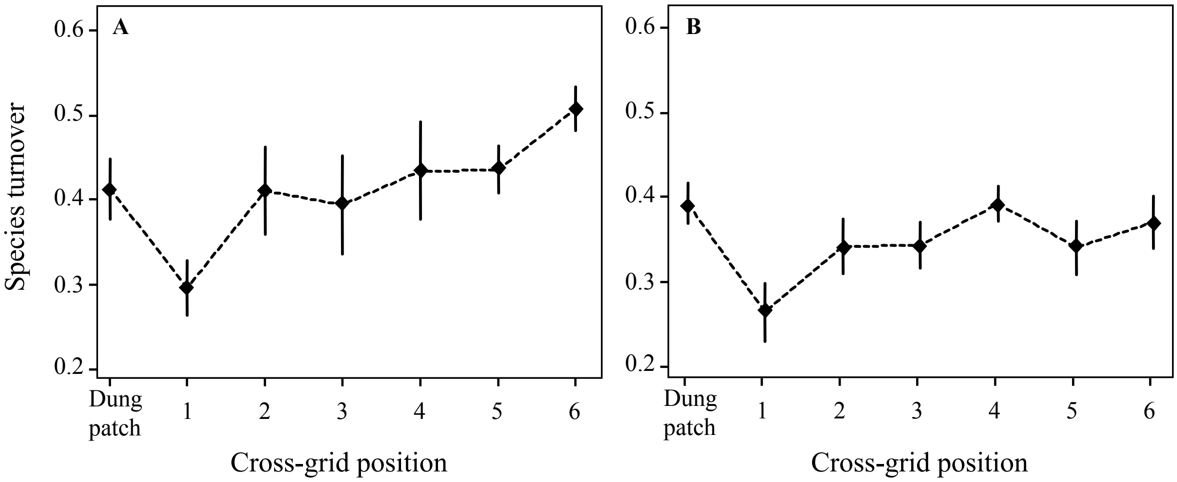

Figure 4.2.3: Species turnover between June and September by distance to the dung patch for the grazed meadow (A) and the lawn (B). Segments represent standard error of the mean.

Table 4.2.3: Variance of vegetation records explained by the distance to the dung patch in the canonical correspondence analysis. In the bracket: *P*-value of Monte Carlo permutation test with 999 permutations.

	Grazed meadow	Lawn
Session 1	4.3 (0.375)	4.3 (0.156)
Session 2	**12.5 (0.001)**	**5.1 (0.049)**
Session 3	**8.8 (0.003)**	5.1 (0.073)
Session 4	**11.9 (0.001)**	-

Table 4.2.4: Spearman rank correlations between C-S-R signature and the distance to the dung patch. N = 30 for the grazed meadow and N = 36 for the lawn. ***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$.

		Grazed meadow	Lawn
C			
	Session 1	0.089	-0.047
	Session 2	0.251	-0.182
	Session 3	**-0.619*** **	-0.163
	Session 4	**-0.576** **	-
S			
	Session 1	0.019	0.072
	Session 2	0.046	-0.038
	Session 3	0.152	0.204
	Session 4	**0.378***	
R			
	Session 1	-0.226	-0.078
	Session 2	-0.030	0.236
	Session 3	0.305	-0.128

high grazing rate and no more effect of the dung patch. This increase of grazing intensity with distance to the dung patch was detected since the first session and increased during the season in both vegetation types (Table 4.2.1). This induced higher vegetation near the dung patch. This phenomenon is well known and has already been observed by many authors (e.g. Weeda 1967; Edwards and Hollis 1982). With our data, we cannot decide, whether the fertilization or the absence of grazing has a stronger influence on vegetation height, but it is clear that both effects were mixed. Interestingly, the pattern of the grazing intensity and vegetation height along the distance gradient were similar in both vegetation types (Figure 4.2.2), indicating that these only depended on the dung patches and not on the vegetation texture and structure. Marsch and Campling (1970) suggested that the smell of the dung may be responsible for the rejection of herbage around the dung patch and so that this rejection is independent of the vegetation type. The difference between both vegetation types was the rapidity of reaction, which was slower in the lawn (Table 4.2.1). For the grazed meadow we detected already higher vegetation near the dung patch a few days after dung deposition. In the lawn we observed this only from the second session, one month after dung deposition. We can explain this difference by a high proportion of oligotrophic species in the lawn, which cannot make an efficient use of higher nutrient supply.

These disturbances around the dung patches induced several changes in the vegetation texture at fine scale and short term. We observed an increase of the number of species near the dung patch at the first session in both vegetation types and for the second session only in the grazed meadow (Table 4.4.2). In a first step, higher nutrient supply may favour every species by stimulating seed germination (Akbar et al. 1995) from the seed bank or from seeds included in the dung (Welch 1985; Dai 2000). This effect disappeared during the season indicating that this increase of biodiversity is only transient. An increased evenness accompanied the increased species richness in the lawn, indicating that at this first session no species dominated the community.

Results were different in the grazed

meadow, where the evenness was higher near the dung patch from the second to the fourth session. This surprising result indicates that higher nutrient supply and grazing abandonment did not, on the seasonal scale, favour exclusively a few dominating species. Another unexpected result was the turnover rates, which were always significantly lower near the dung patch in both vegetation types (Table 4.2.2 and Figure 4.2.3). In the dung patch, we observed a high turnover, which may be explained by recolonisation of the surface after above ground biomass has been suppressed. However, directly beside the dung we observed clearly the lowest turnover (Figure 4.2.3). It seems that dung patches have at short term a stabilising effect on plant composition in the first 10 cm by protecting plants from being grazed. A high turnover at this small-scale is characteristic of grasslands and has been observed elsewhere (Van der Maarel 1993; Otsus and Zobel 2002). As reported by Kohler et al. (2004b and § 4.1) the lawn had a lower turnover than the grazed meadow. Floristic composition varied significantly along the distance gradient from the second session on in both communities (Table 4.2.3). This gradient is represented at functional level in the grazed meadow by higher C-strategy near the dung patch at the third and the fourth sessions and by higher S-strategy far from the dung patch at the fourth session. The same trends were observed in the lawn, but they were not significant. This was probably due to the lower dynamic of this latter community (see above). For C-strategy, this result is consistent with Grime (2001), which defines C-strategy species as species with a high competitive ability, depending on plant characteristics maximising the uptake of resources in productive, relatively undisturbed conditions. Moreover, Grime (2001) distinguished S-strategy species by the capacity of their long-living tissues to resist herbivory (unpalatability) and effects of environmental stress in conditions where growth is severely restricted by low rates of mineral nutrient supply (resistance to stress). R–strategy species include species characterized by a short life-history and adaptation to survive at partial or total destruction of biomass (resistance to disturbance). Following these definitions R-strategy should be favoured by herbage removal (there were almost no unpalatable species in the studied community). In our case, this group showed no reaction and S-strategy had most cover far away from the dung patch. Oksanen and Ranta (1992) pointed out that specific attributes of grazing tolerance incorporate elements of either S or R strategies. Furthermore, they interpreted S-strategy as an adaptation to high-natural grazing pressure, which culminate in moderately stressful habitat. It seems then that this interpretation is confirmed in our study.

We can summarise our results as follows: In a first step at very short-term time scale (a few days) dung patches increase plant biodiversity. At this stage vegetation is still low and there is a high nutrient input. This induces favourable conditions for many species, some of them being not able to survive when height increases, provoking concurrence for light. In a second step the dung patches protect the vegetation around them against grazing activity. This enables species to grow without disturbance and to get higher than the surrounding vegetation. At this stage vegetation near the dung may slowly change with an increase of C-strategy species and a decrease of S-strategy species. However, these changes are not accompanied by an important change in the floristic composition. Only the contribution of species to the overall cover changes. In an experimental study, Kohler et al. (2004a and § 3.1) found similar results. Dai (2000) recognized three types of response in a long-term experiment: negative, positive and neutral depending on the difference in cover along a transect across dung patches. He described changes in relative abundance of species but no establishment of typical vegetation linked to dung patches, which confirms our results.

Dung deposition by cattle plays an important role in grassland ecosystems by changing the equilibrium between plant species and by maintaining favoured species in the community (Malo and Suarez 1995). Every year dungs are dropped in other locations than in the previous years, creating a shifting mosaic. This is a crucial part of the phenomenon, explaining the high biodiversity of pastured grasslands.

Acknowledgements

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Note:

- *Map of the geographical situation of La Métairie d'Evilard, photos of the field and the grid method are included in Appendix Ia*

CHAPTER 5

General discussion and perspectives

5. General discussion and Perspectives

The aim of this chapter is not to repeat conclusions of each subchapter, but to have a general overview on this thesis and to add some interesting information, not included in the articles. In the first part, we will present an overview of species responses to the simulated cattle activities (Chapter 3). We will then explore the effects of the cattle activities on socio-ecological groups of plants. Furthermore, we will compare the results of the experimental approaches (Chapter 3) with the results of our observational studies (Chapter 4). In a second part, we will present an overview of the results on distribution and the factors influencing cattle activity (Chapter 2 and Chapter 4). Thirdly, we will introduce a qualitative model of vegetation dynamics in wooded pastures. Fourthly, we will present some implications of our results for management practices and, finally, we will suggest some perspectives for continuing research.

5.1. Vegetation dynamics and cattle activities

5.1.1. General trends in species and functional responses

Our results highlighted different species favoured by different disturbances. Figure 5.1 represents the various possible combinations of the three cattle activities. This triangular diagram excludes the triple combinations, but as we showed (§ 3.2) the triple combination induced a similar dynamic as the coupled combination of herbage removal and trampling (left corner of the triangle). Following the effects of the three activities and their

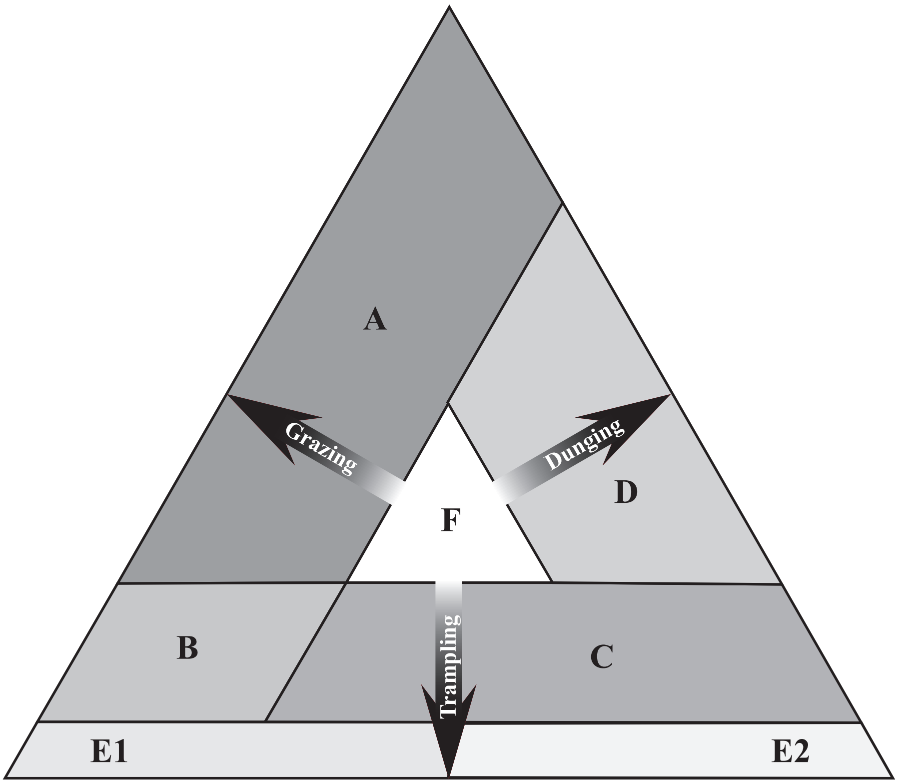

Figure 5.1: Triangle representing the three disturbances acting on vegetation and location of plant functional groups (A-E2), related to the disturbances (see in the text for explanations on each group).

combinations on vegetation dynamics (§ 3.1, § 3.2 and § 3.4), six general species response groups may be defined in this triangle (Figure 5.1):

- Group A: This species group is favoured by herbage removal and the absence of trampling. Except for an increase of the biomass, interaction between herbage removal and addition of nutrients does not induce the appearance of a new species response group. Species such as *Hieracium pilosella*, *Luzla campestris*, *Campanula rotundifolia* or *Thymus pulegioides* characterise this group. It includes a large number of species (Figure 3.2.5) and when it is favoured, there is a positive effect on species number. These species are generally of little height and are adapted to stress (*sensu* Grime 2001).
- Group B: Interactions between herbage removal and trampling favours this species group. As group A, this group is indifferent to the fertilization (this part of disturbance is not represented in the triangle, see above). Species characterising this group are generally the same as group A or C (see below), but some species such as *Trifolium pratense* or *Sanguisorba minor* are more favoured in this case. Small species and legumes also characterise this group. In condition of low light availability the R-strategy is related to this group.
- Group C: This species group is favoured by trampling, but without herbage removal. Nutrient addition did not have any effect on this group too. Species such as *Alchemilla monticola* or *Poa pratensis* characterise it. Number of species in this group is low and when it is favoured species richness decreases, particularly when light availability is low.
- Group D: This group of species is favoured by the fertilisation without grazing and trampling. It is characterised by species such as *Dactylis glomerata*, *Festuca nigrescens*, *Arrhenatherum elatius* or *Ranunculus acris*. Tall grasses with a C-strategy characterise this group. On our short-term scale not only strictly eutrophic species are included (e.g. *Festuca nigrescens* and *Agrostis capillaris* are considered to be tolerant oligotrophic species).
- Group E: This group is favoured when the level of trampling is high enough to create gaps. Species of this group have small seed weight, unspecialized seed dispersal, persistent seed bank and high vegetative spread. Species characterising this group showed some differences depending on the disturbance conditions. When herbage removal is important (E1), species such as *Agrostis capillaris* or *Poa supina* characterise the group and when fertilisation (E2) is important *Hieracium pilosella* or *Campanula rotundifolia* are related to it. Interestingly, species characterising this group are not exclusively found in it, but generally related to a second group as well.
- Group F: This group is favoured by the absence of the three cattle activities. Species characterising this group are in general the same as in group D, but forbs species such as *Veronica chamaedrys*, *Stellaria graminea* or *Hypericum maculatum* find better conditions.

These groups are not mutually exclusive. Traits, important for one disturbance, are not necessarily essential for another. For example, *Agrostis capillaris* is a tall grass favoured by fertilisation, but it is also a species with a high lateral spread and a persistent seed bank, being traits of gap increasers. If we compare the results at the seasonal (§ 3.1) and year scale (§ 3.2), some species will not be included in the same group (e.g. *Campanula rotundifolia* increased in abandoned plots at short term, but was a repeated mowing increaser on the longer run). Furthermore, we observed quantitative changes in the community, meaning that most species were able to survive in all conditions at short term. The resistance of species against the disturbances can be important, grazed meadow showed resilience when disturbances are stopped during winter and beginning of spring. Consequently, in one condition of disturbances the favoured group will dominate, but others can always be present. In grazed meadows, it seems only conditions with fertilisation alone induce a rapid and important decrease of species richness and finally the disappearance of a group. Moreover, our results showed a continuum of species response and a great number of species did not show any reaction to the simulated activities (Figure 3.2.4). This suggests a lot of intermediate adaptations or even an adaptation to all disturbances. Additionally, the hierarchy of the treatments is community-dependent (§ 3.2). Finally we must keep in mind that at fine scale, the communities showed very high internal dynamics (§ 4.1), seemingly not directly linked to cattle disturbances. Therefore, despite general rule pointed out with trait analysis (Figures 3.1.3, 3.2.4 and 3.4.6), it seems difficult to describe these very complex dynamics by classifying species in a few exclusive functional types, depending on a list of easily measurable traits. This may be explained by the fact that we worked on a very short gradient with three disturbances and their interactions and with a high number of species presenting numerous combinations of attributes. Furthermore, it is very probable that not all relevant traits were included in the analysis. In this context, C-R-S strategies, which can be deduced from simple traits (Hodgson et al. 1999), showed relevant results (§ 3.2 and § 4.2). Nevertheless, with this *a priori* functional type classification, the effect of trampling on grazed meadow was not revealed (§ 3.2) and gap colonisation showed no clear pattern (§ 3.4).

There is another interpretation (S. Lavorel, pers. comm.) to the difficulty to describe the complex dynamics with few single traits. As showed recently (Callaway et al. 2003; Garbey et al. 2004; Puijalon and Bornette 2004) the main aspect of adult plant response to disturbances is plasticity. This implies that trait values will change for a same species across disturbance types, and that the same species may be found in different treatments, but with different morphology. In our case, trait values used were standard values per species and not values per «population» with specific measurements in each disturbance type. Such type of measurements, which are highly time consuming would have probably given a clearer picture of the dynamics at functional level.

Interestingly, plant ecologists and soil microbiologists (§ 3.3) followed so far different ways to describe community dynamics by mean of functional groups. Plant ecologists have lists of species from which they have detailed knowledge on ecological and morphological traits. So, they aimed to group the species by selecting relevant combinations of traits, describing the dynamics. Microbiologists know only very few on the thousands of species from which they try to measure the responses, but they have the advantage that function of each species in a bacterial community is essentially related to substrate consumption and to substance excretion. They directly measure “hard” traits (which are almost impossible to measure on plant species). Even so, as plant ecologists have a great number of potential "soft" traits, soil microbiologists have numerous potential substrates. They must found the most relevant substrates with the important technical restriction linked to cultivation methods.

5.1.2. Socio-ecological groups

We will test our results with another *a priori* species classification, deduced from the phytosociological classification. In the floristic catalogue CATMINAT (Julve 1998) each species from France is classified as a characteristic species of a hierarchical unity of the phytosociological classification. By aggregating the hierarchical unities of the phytosociological classification, F. Gillet (unpublished) created seven groups called socio-ecological groups, representing seven general plant community types: lawns; mown meadows; grazed meadows; oligotrophic fallows; eutrophic fallows; underwoods and wetlands. Following CATMINAT, each species is characteristic of one of the seven socio-ecological groups. To improve this classification, fidelity of each species to the phytosociological unities (calculated following Bruehleide (2000)) is determined from about 7000 phytosociological relevés included in the database Phytobase (Gillet 2002). If it is necessary, the affiliation of each species to one socio-ecological group is corrected following the calculated fidelity (F. Gillet unpublished). With this species groups, we can describe a community as a mix of the seven socio-ecological groups in various proportions.

We will use these groups to describe our dynamics observed with the experimental design presented in § 3.2. For each plot, the relative cover of each group was determined by adding the relative cover of each species belonging to the group (as for C-S-R in § 3.2). For each treatment, the difference in relative cover between the first and the last

Table 5.1: Significant effects of the treatments on relative cover of socio-ecological groups (ANOVA table computed from multiple linear regression model). Overall differences among blocks are removed in Site B. Only groups with significant results are presented. See figure 5.2 for mean values of each treatment. F: F-value, *P*: *P*-value. ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$, •: $P < 0.1$, ns: not significant. See §3.2 for details about statistical analysis.

	Mo		Ma		Tr		MoxMa		MoxTr		MaxTr		MoxMaxTr	
Socio-ecological groups	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Site A - Grazed meadow														
Lawn	40.6	***	3.4	•	0.3	ns	0.3	ns	-	-	4.3	*	-	-
Mown meadows	16.9	***	1.4	ns	2.5	ns	1.6	ns	-	-	2.3	ns		
Grazed meadows	9.9	**	0.2	ns	0.5	ns	0.1	ns	-	-	0.9	ns	-	-
Oligotrophic fallows	0.6	ns	6.1	*	0.7	ns	<0.1	ns	-	-	0.2	ns	-	-
Site B - Grazed meadow														
Lawn	23.0	***	6.7	*	5.7	*	0.7	ns	4.5	•	<0.1	ns	<0.1	ns
Mown meadows	21.4	***	24.4	***	3.9	•	0.3	ns	<0.1	ns	1.5	ns	0.9	ns
Grazed meadows	0.5	ns	0.1	ns	7.3	*	<0.1	ns	0.1	ns	0.3	ns	0.1	ns
Site B – Forest-edge														
Lawn	8.6	*	1.8	ns	1.9	ns	0.7	ns	1.2	ns	4.6	*	3.0	ns
Mown meadows	5.6	*	1.4	ns	0.3	ns	0.2	ns	3.1	ns	1.0	ns	2.2	ns
Grazed meadows	2.0	ns	2.2	ns	21.6	***	<0.1	ns	0.5	ns	<0.1	ns	0.6	ns
Eutophic fallows	17.8	***	0.2	ns	14.6	**	0.1	ns	3.4	•	0.2	ns	2.3	ns
Underwoods	6.6	*	8.9	**	9.3	**	0.1	ns	2.3	ns	0.4	ns	<0.1	ns

record are presented in Figure 5.2. Tests on these differences are showed in Table 5.1 (see § 3.2 for details on the statistical analysis). At the beginning of the experiment A-GM and B-GM were dominated by grazed meadow species, but there was a high proportion of lawn species (Figure 5.2). B-FE was also dominated by grazed meadow species, but there was in addition a high proportion of underwood species. Socio-ecological groups showed numerous significant effects of the treatments (Table 5.1). Lawn species increased with repeated mowing and in B-GM decreased with manuring (Figure 5.2). Mown

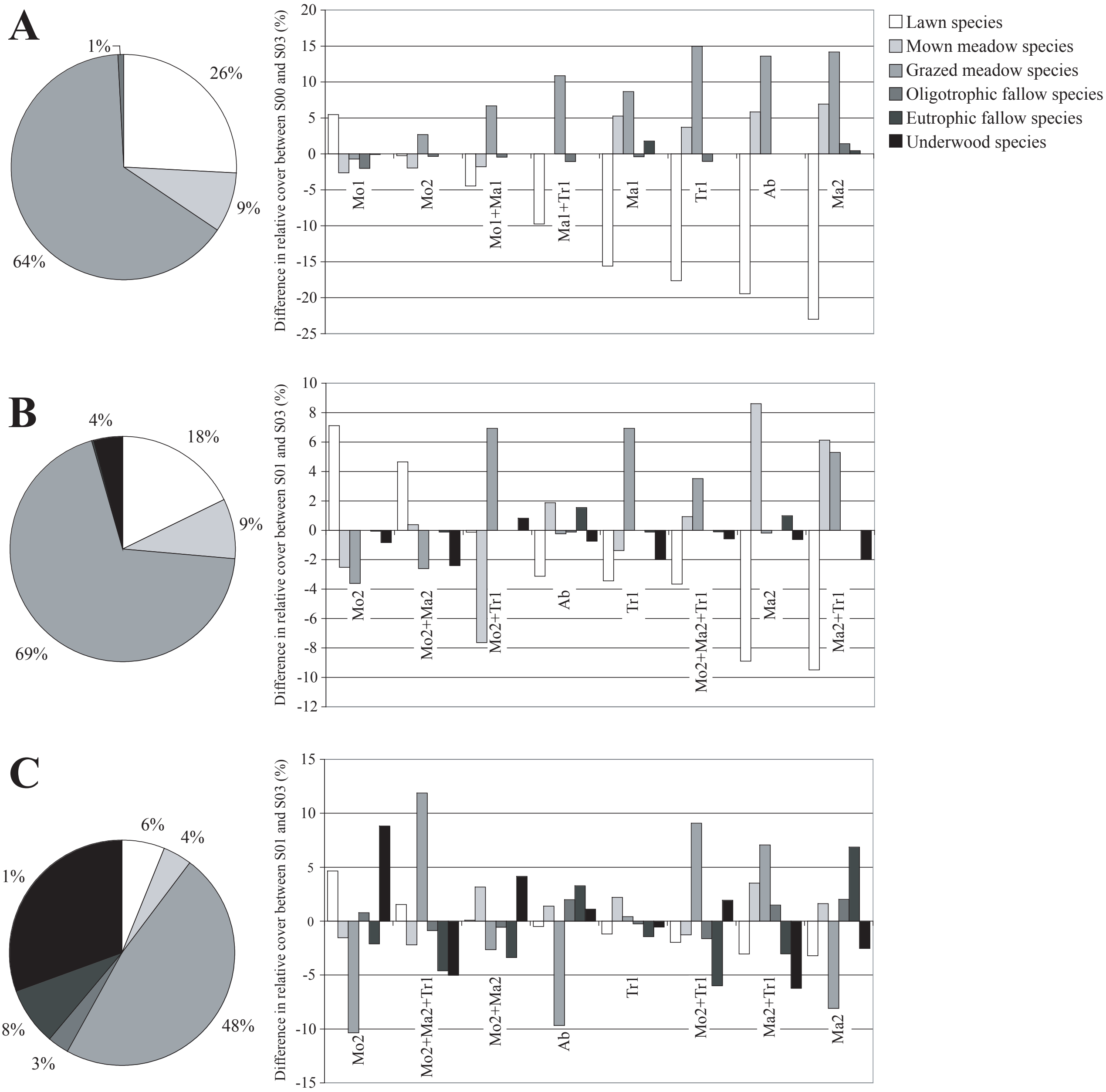

Figure 5.2: Evolution of the socio-ecological groups in the three communities (A: Site A – Grazed meadow; B: Site B - Grazed meadow; C: Site B – Forest-edge (see § 3.2 for details about experimental designs)). Left: proportion of each group at the beginning of the experiment. Right: Mean differences in relative cover between the first and the last records for each treatment, sorted according to the difference for lawns species (for results of multiple linear models see Table 5.1).

meadow species decreased with repeated mowing and increased with manuring in both GMs. Grazed meadow species increased with trampling. In the forest-edge, eutrophic fallow species increased with repeated mowing and trampling and the underwood species increased with repeated mowing and decreased with manuring and trampling.

This classification appeared to be highly relevant with more significant effects than the C-S-R signature (Table 3.2.4). We can separate the effect of trampling from the effect of repeated mowing. Trampling increased the proportion of grazed meadow species. Repeated mowing induced an increase in the proportion of lawn species. The decrease of soil nutrients does not seem essential to increase the proportion of lawn species. Furthermore, the decrease of mown meadow species with repeated mowing showed the importance of the mowing frequency. This species group is favoured by one or two cuts per year, but not with a very high frequency like we simulated the herbage removal. Mown meadow species were at short-term scale favoured in manuring plots. The absence of trampling and herbage removal (Ma1, Ma2 or Ab) induced an increase of eutrophic fallow species, particularly in B-FE and a decrease of lawn species.

The general qualitative model resulting from the research programme PATUBOIS (Gallandat et al. 1995) subdivided the herbaceous layer of wooded pasture in four categories of *synusiae* (Figure 1.4): fallow, underwood, lawn and grazed meadow. This four category types, which are called *homoecies* are defined by their structural and functional characteristics, which determine their role in the networks of interactions. The dynamic model PATUMOD (Gillet et al. 2002) used these entities to model the proportion of each in a *phytocenosis*. In this model each herbaceous *homoecy* is able to change to another depending on livestock, altitude and the percentage cover of shrubs and trees. In our case we worked at a lower organisation level, because we studied the internal dynamics within a *homoecy*. The description of the vegetation dynamics with socio-ecological groups cannot directly be related to the qualitative model of PATUBOIS, because *homoecies* are defined by their structural characteristic and not by their floristic composition. Nevertheless, our results seem to confirm, as supposed by the model, cattle activity may transform a community type into another. Grazed meadows of site B showed, for example, a clear tendency to transform into a lawn with repeated mowing. Furthermore, these changes can be rapid, for example within 4 years a decrease of 23 % of the proportion of lawn species induced in A-GM by manuring. The cause of these changes seems to be slightly different than those supposed in the qualitative model of PATUBOIS, in which trampling and herbage removal are aggregated into one disturbance (grazing).

5.1.3. Simulated vs. natural cattle activities

Experiments (§ 3) showed clearly simulated cattle activities having various impacts on vegetation dynamics and that these impacts are community-dependant. Observations in the field with natural cattle activities (§ 4.1 and § 4.2) only partly confirmed the results of the experiments. At very short-term, we observed, as in § 3.2, an increase of C-competitors around the dung (§ 4.2), but in § 4.1 we found no clear link between cattle activities and vegetation changes, despite high turnover within the plant communities. We can formulate some hypotheses to explain this lack of clear relation in natural conditions: (1) our indices of grazing and trampling were not precise enough, (2) the grain (1 dm^2) was not the adequate scale to observe these links, (3) grid method is not disturbance-centred (excepted for the dung pats or for artificial gaps), so it is probable that the pattern of grazing or trampling do not follow the limit between cells and then the effects of disturbance cannot be revealed in the imposed frame. Consequently, except for the dung, we cannot deduce from our results that at fine scale, in natural conditions, grazing and trampling influenced variously vegetation dynamics. Nevertheless, it would be false to conclude that there is no relation. Grazing and trampling are so intermingled at fine scale that it is very little practicable to measure their separate effects (it was the main reason why we conducted the experiments).

5.2. Pasture as a mosaic of disturbances

At paddock scale, our results showed, the pattern of habitat use differing strongly between herbage removal, dunging and trampling (§ 2). Areas with a lot of dung pats did not correspond with the most or least trampled or grazed areas. Moreover, the distribution of cattle activities was generally similar for the successive rotations, with an increasing use of the paddock, involving a more homogeneous pattern. This was true principally for foraging, less for dunging, but not for trampling. The three attributes of cattle activity depended on different environmental conditions and the relative importance of management-induced or natural structures for explaining patterns was very different between cattle activities. Furthermore, patterns did not seem to be at the same scale for the three effects.

Between community types we observed a strong difference and a clear seasonal effect for herbage removal (Figure 4.1.5). Differences were weaker for trampling. In spring, grazed meadows were more grazed than other community types. Moreover, for the temporary refused meadow or for the lawn, there was a clear shift of the importance of grazing during the season. There was a selection of the community type by cattle. This selection changes during the time. Differences

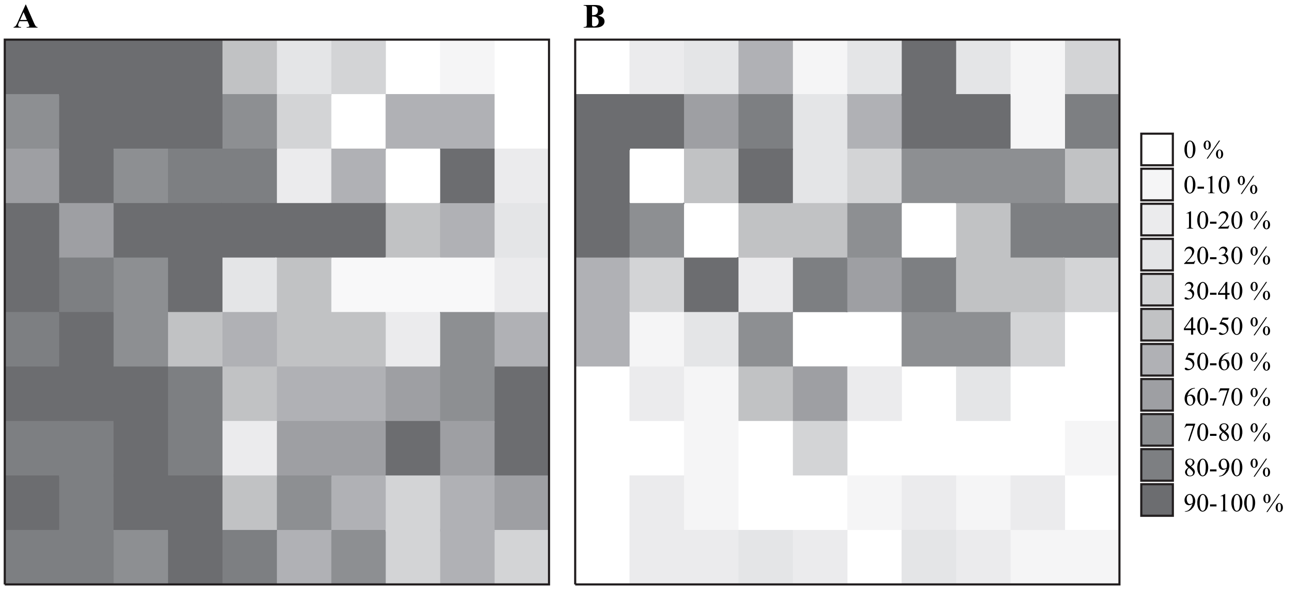

Figure 5.3: Map of the amount of cover affected by grazing in each cell (1 dm^2) (for details see § 4.1). Examples for the grazed meadow (A) and the lawn (B) in June 2001.

between community types for the number of dung pats and gaps were not explored.

Within communities, dung pats and gaps, localised in little areas, induce logically a heterogeneous pattern of their disturbance. Trampling is also much localised depending on the hoof size. We observed in 1 m^2, more than 20 % of the surface not being perturbed (Figure 4.1.5). Nevertheless, this perturbation is very difficult to measure and it is difficult to have hard conclusions about the pattern of trampling at this fine scale. For herbage removal, we observed at 1-dm^2 a very heterogeneous pattern near dung pats (§ 4.2) or in vegetation without dung pats (§ 4.1 and Figure 5.3). In the second case, there was no evidence that this pattern was induced by species selectivity. Species with higher cover were more eaten. This heterogeneous pattern is probably due to the cattle behaviour. 1 dm^2 corresponded approximately at one bite (size of one herbage prehension, *sensu* Bailey et al. 1996) of a cow. A neck movement generally follows a bite and then the following bite will not necessarily be exactly beside the previous, inducing a heterogeneous pattern.

Senft et al. (1987) and Bailey et al. (1996) described large herbivore foraging in an ecological hierarchy. Bailey et al. (1996) defined 6 spatial scales in a foraging hierarchy: bite, feeding station, patch, feeding site, camp and home range. Each scale was functionally defined, based on characteristic behaviour occurring at different rates. At medium (communities) and fine scale (within communities), our methods were principally adapted to measure vegetation dynamics and not to measure factors influencing cattle behaviour. Nevertheless, our measurements seem to be on line, but are not sufficient to support at each spatial scale, because the factors influencing the pattern of the three activities were different. At the larger scale, cattle react to environmental and man-made structures. At community scale, cattle chose communities with the best forage abundance and quality (grazed meadow vs. underwood (Fig 4.1.5)) and within community they avoid

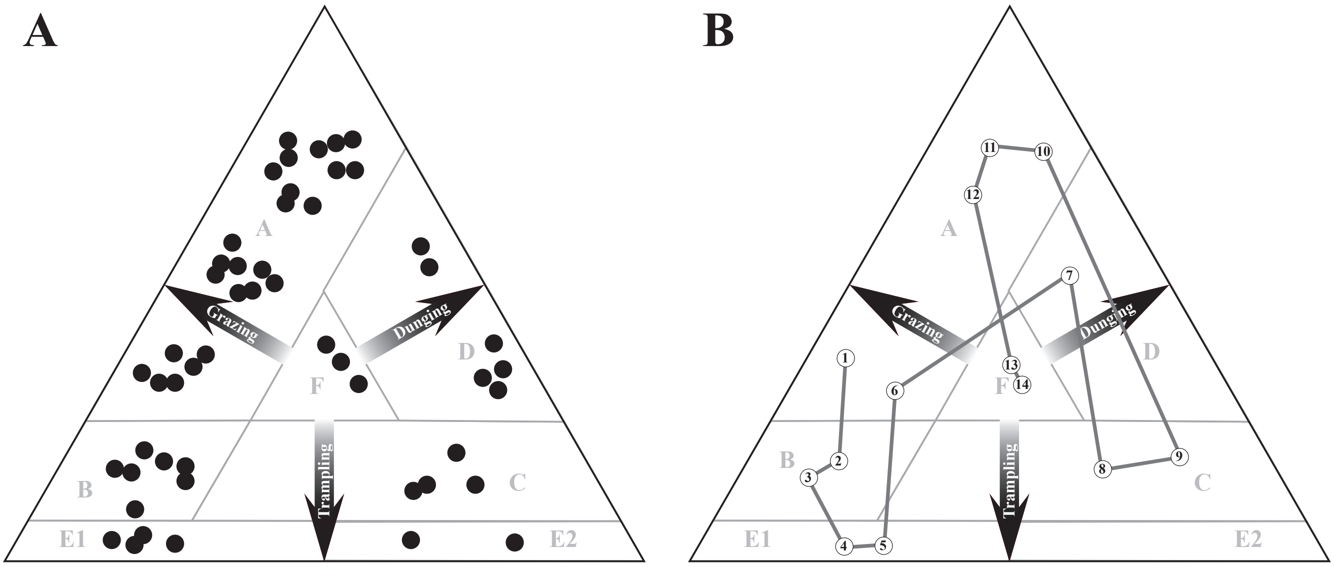

Figure 5.4: Cattle activities in space and in time at dm^2 scale in pastures. A: Hypothetical combination of disturbances acting at a certain point on 50 contiguous squares of one dm^2 (black points). B: Hypothetical succession under 14 years of various combinations of the disturbances, acting on one dm^2 of a pasture. A-E2: plant functional groups (cf. Figure 5.1).

dung pats. It is clear that further observations must be made to define more precisely factors influencing pattern at each spatial scale (see below).

Using the triangular representation of Figure 5.1, we can formulate some hypothesis on cattle activities in space and in time at fine scale. Figure 5.4A shows a hypothetical combination of the disturbances acting on 50 contiguous squares of 1 dm^2. The number of squares in each part of the triangle depends on the factor acting on the cattle activity at the superior spatial scale. For example, in a flat area far the fence, with a high density of dung pats, more squares will place at the right of the triangle, than in the example of Figure 5.4A. If we follow this model, each species response group described above can find in a relative small area of some decimetres with optimal conditions. Furthermore, we can suppose that the combination of disturbance at one place can change during the time (Figure 5.4B). This model suggests that over the time every square of 1 dm^2 can get favourable for each species response group.

5.3. Modelling vegetation dynamics in wooded pastures

By combining our results with conclusion of the PATUBOIS programme and with literature on cattle behaviour (e.g. Senft et al. 1987; Bailey et al. 1996), we will propose a general qualitative model describing relation between cattle and vegetation dynamics in wooded pastures.

The absence of spatial congruence at various scales between the three components of cattle activity and the various dynamics, pointed the necessity to distinguish them when modelling vegetation dynamics, even if we aimed to model vegetation dynamics at hectare scale (§ 2). Furthermore, patterns of cattle activity seem to be related to various scale-depending factors. The best solution to model distribution of cattle activities and deduced vegetation dynamics, seem to be a hierarchical approach (Figure 5.5). Three spatial scales seem to be important. At large

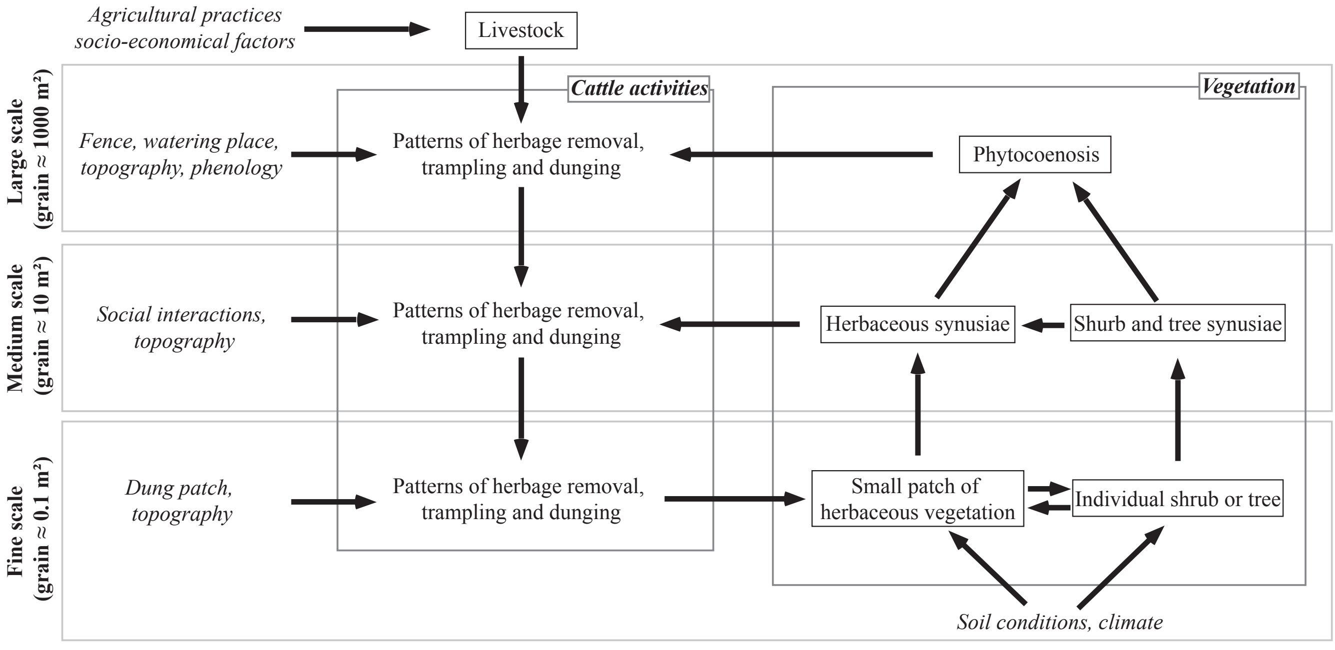

Figure 5.5: Qualitative model of cattle activity and vegetation dynamics in wooded pastures. In italics: examples of potential external factors (see in the text for details).

scale, the human and natural structures of the paddock will induce the first general patterns. At medium scale, plant community structures, but also social interactions, seem to induce heterogeneity within the general pattern (this level must be better explored). At fine scale, dung patch and other phenomena (§ 5.2) induce heterogeneity within a community. Patterns of each cattle activity at medium scale can be deduced by modelling the pattern at the large scale. In the same way, pattern for the fine scale can be deduced in a next step from the medium scale (Figure 5.5). From the more finely modelled patterns and from abiotic conditions, we can calculate herbaceous dynamics (see below for more details). From the pattern of herbaceous vegetation and from abiotic conditions, we can deduce the areas where tree and shrub seedlings are favoured and calculate the pattern of tree and shrub regeneration. Trees and shrubs can be modelled individually and while growing they influence the herbaceous dynamics. By aggregating the fine scale vegetation pattern for herbs, shrubs and trees, we can calculate the pattern of *synusiae* and from this spatial distribution, we can deduce the pattern of *phytocenoses*. Both patterns will influence the spatial distribution of cattle activity at medium and large scale (Figure 5.5).

At this stage, to propose a more detailed model, patterns of cattle activity at various scales still must be further investigated (see below). Besides, dynamics of trees and shrubs are currently explored in a related project. Nevertheless, our results permit to construct a more detailed qualitative submodel concerning dynamics of herbaceous vegetation at small patch scale. We suggest to model herbaceous vegetation with a few numbers of functional types (Figure 5.6), which vary in proportion or in biomass, depending on four general constraints: (1) the three cattle activities, (2) light conditions induced by trees and shrubs, (3) abiotic conditions (e.g. soil nutrients, soil pH, microclimate) and (4) competition

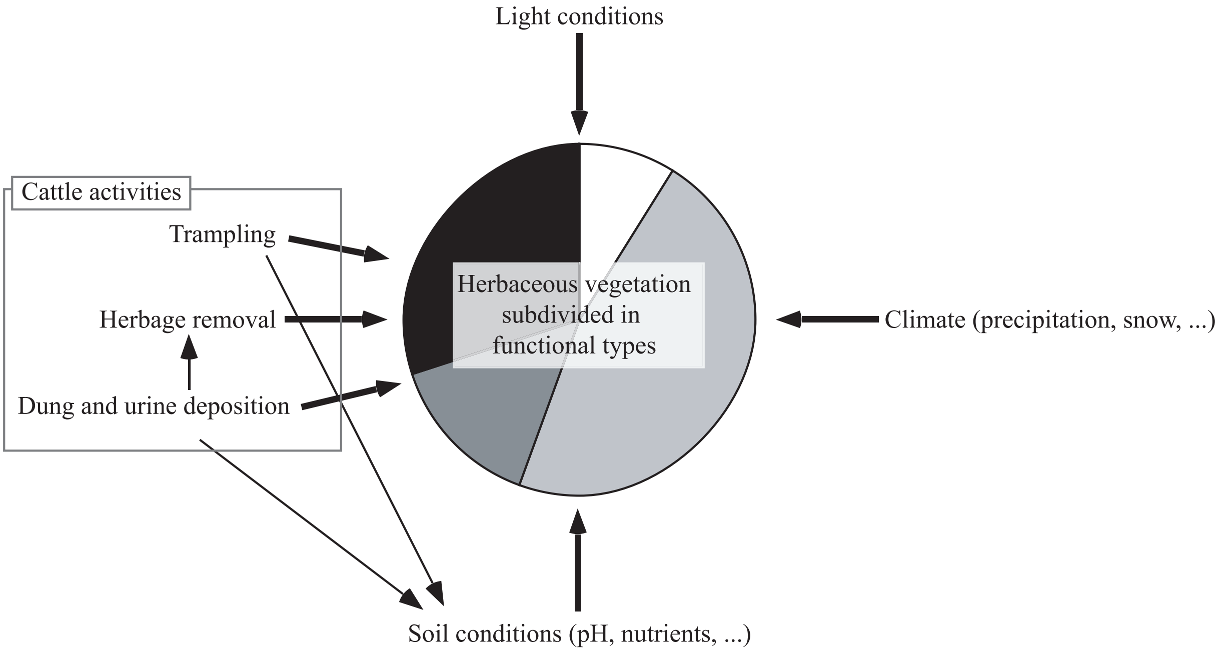

Figure 5.6: Qualitative model including principal factors responsible of the herbaceous dynamics in a small patch (few dm^2) in a wooded pasture (see in the text for details).

between functional types. The importance of each cattle activity depends firstly on superior hierarchical levels (Figure 5.5) and on conditions at small scale (e.g. herbage removal is absent from dung patches). Moreover, these activities may influence soil conditions (nutrient addition and soil compaction) and, indirectly, light conditions by acting on tree regeneration. The plant functional types can be socio-ecological groups, C-S-R strategies or the six species response groups described above (§ 5.1). Each classification has its advantages and disadvantages. Socio-ecological groups showed relevant results and permit to separate trampling effects from effects of the herbage removal. The criteria to classify species in a group are based on phytosociological classifications, which are not universally recognized by vegetation scientist. Nevertheless, recent development of databases containing a large number of phytosociological relevés (e.g. Phytobase (Gillet 2002)) and of computers able to manage high quantity of data will probably soon permit to define these groups with strong statistical criteria. C-S-R strategies are more widely recognised and some models have already used this classification (e.g. Colasanti and Hunt 1997). It has the advantage to be summarised in three variables (the C-S-R signature), useful if we want to construct a spatial quantitative model with a great quantity of small vegetation patches without having to effectuate a very high number of calculations. Furthermore, a detailed description of the behaviour of each strategy is already available in Grime (2001). Nevertheless, the effect of trampling on grazed meadow was not revealed with this classification (§ 3.2) and gap colonisation showed no clear pattern (§ 3.3). The six groups defined in this work are the most relevant for the modelled dynamics, because they are deduced *a posteriori* from our experimental results. Nevertheless, the difficulty to define precise rules for classifying species in groups (§ 5.1), will display a challenge to transpose the model in another situation with different plant species.

5.4. Implication of the results for management

The main topics of this thesis concern fundamental aspects and therefore most results cannot directly be used for management proposals. Nevertheless, some results may be interesting for managers.

Firstly, at large scale the dependency of cattle activity pattern to landscape and human structures, already observed by many authors (e.g. Bailey et al. 1996; Parsons and Dumont 2003), showed this pattern being possible to manipulate. Changing location of the fences and watering the place induce changes in the disturbance pattern and therefore changes in vegetation dynamics. More projects (see below) must be effectuated to better quantify the pattern of disturbance and to predict this pattern for vegetation management proposals. Moreover, if the habitat use patterns are repeated over many years, the spatial segregation of activities at the landscape scale may have important ecosystem implications. In particular the spatial segregation of feeding and excretion activities leads to a transfer of nutrients from the feeding places to the resting places. In this case, management is not sustainable and through manipulation of the disturbance patterns, this may be avoided.

Secondly, herbage quantity and quality vary, depending on the activities. In § 3.2, treatments simulating cattle activities had an important impact on vegetation biomass and on the quantity of potential herbage produced (Figure 5.7ABC and Table 3.2.3). Manuring, alone or in combination with trampling, induced a clear increase of biomass within the three studied communities. The values are almost twice the values observed for repeated mowing plots. Forage quality showed also numerous significant differences between treatments (Table 5.2 and Figure 5.7DEF) (see Table 5.2 for detail on data source and on statistical analysis). In both GMs, trampling favoured species with a high forage value and repeated mowing species with a low forage value. Furthermore, species with an intermediate forage value decrease with repeated mowing. B-FE, containing a higher percentage of species with low foraging values, showed less significant effects of treatments. For this community, species with a high forage value decreased with repeated mowing and species with a low forage value with trampling and/or manuring. These results highlighted the importance of trampling and manuring to maintain high or intermediate forage quality. Areas, without herbage removal, but with trampling and/or manuring are refuges for species with a high or intermediate foraging value. An intensively grazed pasture or a pasture where the none grazed vegetation is mowed, will then lose the most interesting plant species for cattle.

Thirdly, our results highlighted the key-role of cattle activities for the maintenance of high species richness in mountain pastures. The heterogeneous pattern of disturbances induced a wide variety of microsites (§ 3.2) and, as also showed by Schläpfer et al. (1998), the maintenance of open area with mowing cannot replace large herbivores effects. Our results clearly pointed on the relevance of using large herbivores as conservation tools.

5.5. Perspectives

5.5.1. Spatial distributions and disturbance intensities

Our results highlighted the importance of taking into account the various disturbances acting in wooded pastures to understand

Table 5.2: Significant effects of the treatments on relative cover of three levels of forage values[a] (ANOVA table computed from multiple linear regression model). The relative cover of each level was calculated by sum up the relative cover of each species belonging to the levels. Overall differences among blocks are removed in Site B. Only attributes with significant results are presented. See figure 5.7 for mean values of each treatment. F: F-value, *P*: *P*-value. ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$, •: $P < 0.1$, ns: not significant. See § 3.2 for details about statistical analysis.

	Mo		Ma		Tr		MoxMa		MoxTr		MaxTr		MoxMaxTr	
Forage values[a]	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Site A - Grazed meadow														
Low	93.0	***	0.7	ns	22.9	***	0.6	ns	-	-	0.9	ns	-	-
Intermediate	46.5	***	2.5	ns	5.4	*	0.8	ns	-	-	0.9	ns	-	-
High	4.1	•	1.4	ns	6.2	*	0.5	ns	-	-	1.5	ns	-	-
Site B - Grazed meadow														
Low	6.8	*	4.0	•	34.3	***	0.3	ns	0.9	ns	2.1	ns	0.3	ns
Intermediate	19.1	***	0.7	ns	0.1	ns	1.1	ns	5.3	*	0.5	ns	1.2	ns
High	6.1	*	3.1	ns	81.1	***	0.5	ns	22.1	***	10.1	**	0.7	ns
Site B – Forest-edge														
Low	<0.1	ns	4.9	*	5.5	*	2.5	ns	3.4	•	0.1	ns	1.4	ns
High	7.9	*	0.2	ns	4.1	•	<0.1	ns	0.2	ns	0.1	ns	1.9	ns

[a] Forage value: Low: «poisonous for livestock», «no or little forage value» and «little forage value». Intermediate: «little to intermediate forage value», «intermediate forage value» and «intermediate to high forage value». High: «high forage value», «high to best forage value» and «best forage value». Following classification of Klotz et al. 2002.

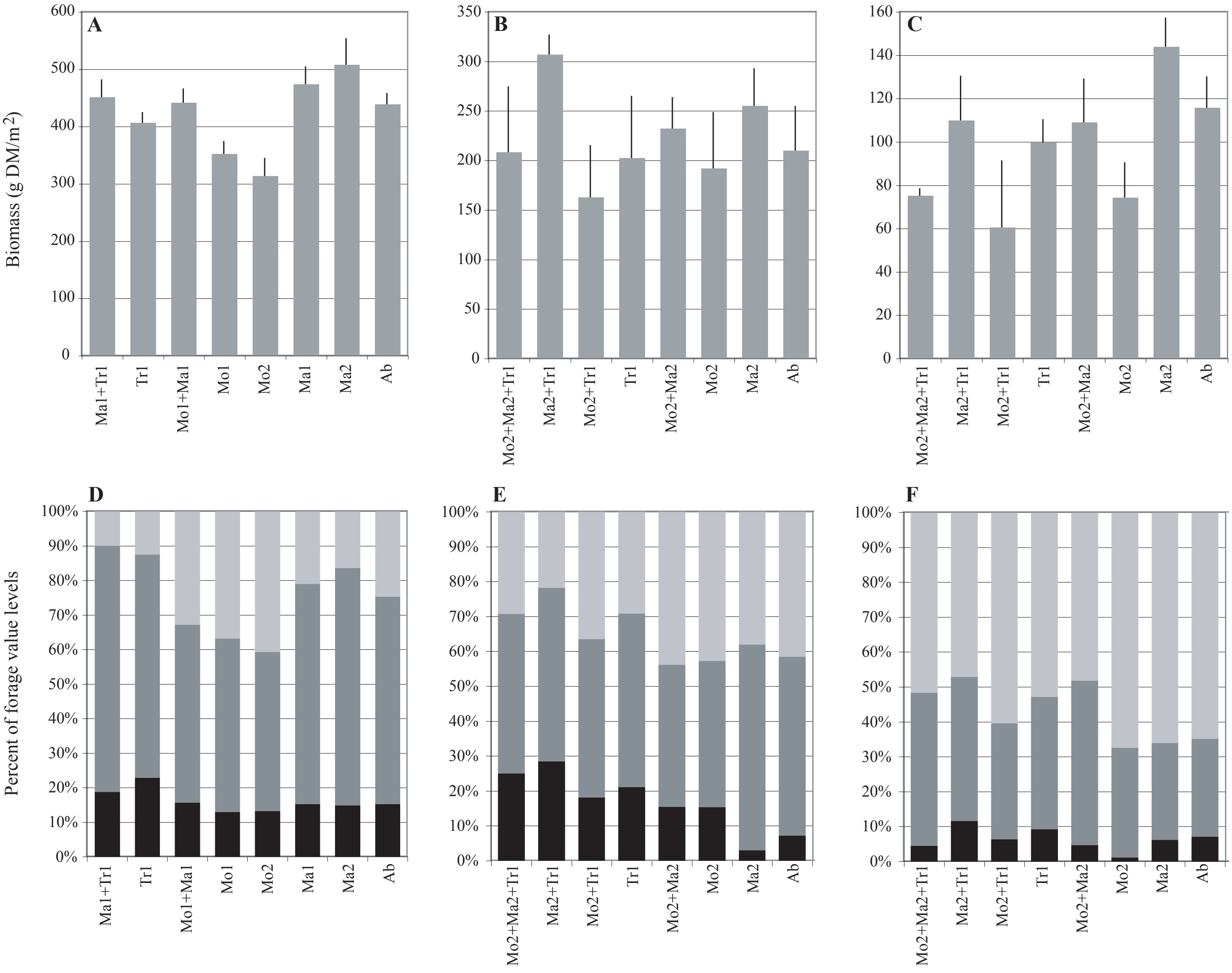

Figure 5.7: Effects of the treatments on biomass and forage quality. Above: for each treatment dry weight of biomass in the grazed meadow of site A (A) and B (B) and in the underwood (C) of site B (Error bar: standard error). For the results of multiple linear models see Table 5.2 for forage values and Table 3.2.3 for biomass. Below: for each treatment, relative percentage cover of the three levels of forage values (see Table 5.2 for details) in the grazed meadow of site A (D) and B (E) and in the underwood (F) of site B (see subchapter 3.2 for details about experimental design). Black: high forage values, dark grey: intermediate forage values, light grey: low forage values.

and model vegetation dynamics. To predict vegetation dynamics, it is essential to define, at various scales, factors inducing the pattern of the different disturbances.

Our measurements on one single paddock are a first step. It would be promising to reproduce the observations on other paddocks or on the same paddock, but in other years to confirm the relations between natural and human structures, especially the negative correlation between dunging and herbage removal, which has important implications for a sustainable management and already observed by Jewell (2002) in alpine pastures.

To evaluate the distribution of the three activities, our approach was centred on the impact of cattle activity on vegetation and not on the cattle movement in the paddock. This had the advantage to describe for an entire paddock the effects induced by cattle activities during few weeks, in one step and with a relatively simple method. The impracticability to evaluate finely the amount of herbage removed was clearly a disadvantage.

Furthermore, the amount of trampling was not easy to evaluate, particularly in dense vegetation where the impact is hardly visible even if it is important. Measurements centred on the cattle by determining the spatial position and activities of animals during time, would be a relevant completion of our studies. It seems necessary to use a multi-scale approach for the analysis of cattle activity patterns. This type of measurement is currently rare in wooded pastures, characterised by a very heterogeneous structure. Actually much of the knowledge about cattle behaviour is derived from simple model system, such as ryegrass-white clover mixture (Rook et al. 2004).

To demonstrate the model described in Figure 5.5, it seems necessary to develop new methods for the fine scale measurement of the disturbances, particularly for trampling. To evaluate spatial grazing intensity, it will be interesting to measure at dm^2 scale with an extent of at least 25 m^2 the height of the vegetation at a month scale during several years.

Another important problematic, not explored in this work, is the quantification of the density, the size and the spatial distribution of gaps and the relative importance of the cattle role for this disturbance against other animals like voles, wild boars or ants.

5.5.2. Vegetation dynamics

Our observational and experimental approaches appeared relevant for the observation of vegetation community dynamics. For a better understanding of the mechanism behind these dynamics, it will be interesting to use a more detailed method.

Firstly, for field observations, we noted that the grid was not disturbance-centred (§ 5.1.3). It is therefore highly probable that the pattern of disturbances do not follow the limits between cells. The effects of disturbance cannot be revealed by the imposed frame. To detect plant dynamics appearing in natural conditions, it will probably be relevant to use a plotless method to provide a "plant-eye view" of the community (Yarranton 1966, Purves and Law 2002). This approach is realised generally by recording presence/absence of plant species on a map of points or with very little square (less than 1 cm^2), including a whole plant or a part of one individual plant. It permits to be at the scale of individual plants and to analyse the spatial pattern without any artefacts due to the size and the spatial position of the plots. These methods are time consuming, but by recording plant positions and the impact of cattle activities in time and in space, more precise indication on the dynamics will certainly appear.

Secondly, from an experimental approach, our results highlighted some key species in the dynamics (e.g. *Hieracium pilosella*, *Agrostis capillaris*, *Veronica chamaedrys*). Our experimental methods permit to measure the difference between species behaviours, but not directly to highlight mechanism responsible for these dynamics. Therefore, it will be interesting to study more detailed, the traits of important species, particularly clonal behaviour and resprouting ability. Furthermore, these species could be selected for mesocosm experiments to create artificial plant communities, more easily controlled and manipulated than the complete community in the field.

Our work started from hypotheses deduced of results of a large study describing vegetation structure in wooded pastures (Gallandat et al. 1995). Based on this description of the vegetation of this ecosystem, we explored some phenomena with experimental methods in the field or with detailed observational methods. Our results induced new questions, which will probably find answers by more detailed methods. This approach from generalities to details seemed the most efficient. By starting from details, we stay in front of a multitude of questions and it is very difficult to select the most important ones. The inverse approach permits to filter questions, which are not of primary importance for the system.

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APPENDICES

Appendix I: Description of files included in the CD-ROM

Appendix Ia. Photos and diagrams

Kohler_2004_Appendix_I/Photos_and_diagrams/
To see photos and diagrams, the file *index.html* must be open in a browser (Explorer, Netscape, Safari, Firefox, …)

Appendix Ib. Pdf files of published papers

Kohler_2004_Appendix_I/Papers/JVS_2004_15_143-150.pdf
Pdf file containing the paper of the Subchapter 3.1 in the published version.

Kohler_2004_Appendix_I/Papers/CE_2004_5_7-17.pdf
Pdf file containing the paper of the Subchapter 4.1 in the published version.

Appendix Ic. Oral presentations and posters directly related to this thesis

Kohler_2004_Appendix_I/Presentations/Birmensdorf03.ppt
PowerPoint file containing the oral presentation: Kohler F., Porgin M.-A., Gobat J.-M., Buttler A. and Gillet F. 2003. A cell-grid method for short-term and fine-scale monitoring of vegetation dynamics in pastures. in Feldmeyer-Christe, E (ed). State of the Art in Vegetation Monitoring Approaches. Abstracts. International Symposium, March 24-26, 2003. Birmensdorf, Swiss Federal Research Institute. p. 25.

Kohler_2004_Appendix_I/Presentations/Luzern04.ppt
PowerPoint file containing the oral presentation: Buttler, A., Kohler, F., Wagner,H. and Gillet, F. 2004. Observed spatial and seasonal patterns of cattle activity versus simulated effects in an exclosure experiment. in Lüscher, A., Jeangros, B., Kessler, W., Huguenin, O., Losbiger, M., Millar, N. and Suter, D. (eds). Land Use Systems in Grassland Dominated Regions. Proceedings of the 20th General Meeting of the European Grassland Federation, Luzern, Switzerland, 21-24 June 2004. p. 578-580.

Kohler_2004_Appendix_I/Presentations/Giessen04.ppt
PowerPoint file containing the oral presentation: Kohler F., Gillet F., Gobat J.-M. & Buttler A. 2004. Vegetation changes in mountain pastures due to simulated effects of cattle activity. in Eco-complexity and dynamics of the cultural landscape, Verhandlung der Gesellschaft für Ökologie, Band 34, September 13-17 2004, Giessen, Germany p. 216

Kohler_2004_Appendix_I/Presentations/Halle03.pdf
Pdf file containing the poster: Kohler F., Porgin M.-A., Gobat J.-M., Buttler A. and Gillet F. 2003. Seasonal fluctuations of species richness at fine scale in wooded pastures. in Biodiversity - from pattern to process, Verhandlung der Gesellschaft für Ökologie, Band 33, September 8-12, 2003. Halle, Deutschland. p. 87.

Kohler_2004_Appendix_I/Presentations/Lugo04.pdf
Pdf file containing the poster: Buttler, A., Kohler, F., Wagner,H. and Gillet, F. 2004. Spatial dependence and seasonal patterns of cattle activity. In Mosquera, M.R., McAdam, J. and Rigueiro-Rodriguez (eds). Silvopastoralism and sustainable management - International congress. Book of abstracts. 19-21 April 2004, Lugo, Spain. p. 123.

Appendix II: Mean absolute cover of species in spring before treatment (S1), in autumn after treatment (A1) and in spring of the following year (S2).

		Cattle activity			Mowing 2			Mowing 1			Mowing 1 + Manuring 1			Trampling + Manuring 1			Trampling			Manuring 2			Manuring 1			Abandoning		
Species	**Abbrev.**	**S1**	**A1**	**S2**	**S1**	**A1**	**S2**	**S1**	**A1**	**S2**	**S1**	**A1**	**S2**	**S1**	**A1**	**S2**	**S1**	**A1**	**S2**	**S1**	**A1**	**S2**	**S1**	**A1**	**S2**	**S1**	**A1**	**S2**
Abies alba	Abi alb	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Achillea mil. millefolium	Ach mil	0.7	1.7	1.3	0.8	1.5	2.0	0.5	2.7	4.2	1.2	2.0	4.5	0.5	1.4	3.2	1.5	2.2	1.7	0.5	1.5	1.7	1.2	1.5	2.7	0.8	1.6	1.0
Agrostis capillaris	Agr cap	-	16.1	14.0	-	8.0	6.5	-	11.7	2.3	-	14.5	8.6	-	14.8	9.8	-	11.1	18.1	-	3.8	23.6	-	14.5	2.0	-	9.5	9.2
Alchemilla monticola	Alc mon	10.1	6.3	4.4	12.7	7.2	6.1	15.0	13.3	4.8	9.5	7.0	5.0	14.7	15.0	10.1	8.2	8.2	5.3	11.2	9.8	8.5	14.3	8.9	6.0	15.2	10.0	7.9
Anthoxanthum odoratum	Ant odo	15.5	9.9	15.6	20.7	10.1	19.0	24.2	10.7	15.7	22.2	9.6	21.5	17.7	7.3	16.0	25.6	2.7	13.7	24.7	19.1	10.3	23.8	21.2	10.6	29.2	10.5	5.9
Anthyllis vul. vulneraria	Ant vul	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	-	-	-	-	-	-	-	-
Arrhenatherum ela. elatius	Arr ela	0.7	-	0.8	1.3	-	-	-	-	-	0.7	-	0.3	0.3	-	0.3	0.3	-	0.3	1.5	1.5	2.2	0.2	-	-	-	-	-
Bellis perennis	Bel per	1.4	1.6	0.7	1.8	2.7	2.3	2.7	1.8	0.9	1.7	3.5	1.1	2.2	1.0	0.9	2.0	0.8	0.6	1.2	1.2	-	1.3	1.4	1.8	1.5	0.8	0.6
Briza med. media	Bri med	1.3	0.1	0.1	1.5	0.7	0.6	1.8	0.7	0.3	1.7	0.5	-	1.0	0.3	0.3	0.8	0.7	-	0.8	1.6	0.3	1.2	1.6	-	0.3	0.7	1.0
Campanula rotundifolia	Cam rot	1.4	0.5	1.8	2.3	0.3	3.6	5.0	1.0	5.1	4.0	0.2	2.5	3.5	0.5	2.3	3.2	0.5	0.3	2.7	0.7	1.4	2.0	0.5	2.9	4.3	1.7	2.9
Carex caryophyllea	Car cay	0.3	-	-	1.7	-	0.3	0.3	-	-	0.3	-	-	0.2	-	-	-	-	-	0.3	0.2	-	-	-	-	3.3	1.0	-
Carex flacca	Car fla	0.4	0.3	0.1	-	-	-	0.2	-	-	-	-	-	0.7	0.2	0.3	0.5	-	-	0.2	-	-	0.2	-	0.6	1.2	2.2	4.5
Carlina aca. simplex	Car aca	2.1	2.3	0.3	2.8	0.7	0.9	2.7	1.3	0.3	3.5	1.3	0.6	1.8	0.5	0.3	3.8	2.2	0.6	3.2	7.6	0.9	2.2	4.1	0.3	2.7	10.7	0.6
Carum carvi	Car car	0.4	0.2	0.1	0.3	-	-	0.3	0.2	-	0.3	0.2	0.8	0.5	0.5	0.3	0.8	1.2	0.3	0.7	0.5	-	0.3	0.2	1.0	0.2	0.2	-
Cerastium fon. triviale	Cer fon	0.1	-	0.6	-	-	0.3	-	-	0.9	-	-	0.6	0.2	-	0.8	-	-	2.2	-	-	-	-	-	1.5	-	-	2.8
Cirsium aca. acaule	Cir aca	0.5	0.5	-	0.2	1.0	-	0.3	1.7	-	-	0.2	-	0.5	0.2	0.3	0.3	1.0	0.6	0.2	-	-	0.8	1.7	-	0.3	0.7	0.4
Coeloglossum viride	Coe vir	0.1	-	-	0.2	-	-	-	-	-	0.2	-	-	0.3	-	-	0.3	-	-	0.2	-	-	0.3	-	-	0.2	-	0.3
Crepis mollis	Cre mol	4.3	2.2	4.1	9.5	6.0	11.2	7.4	4.3	6.0	8.4	5.2	9.8	8.0	5.3	9.7	7.5	6.7	7.5	6.5	0.9	3.1	6.7	1.6	6.3	5.8	1.9	3.3
Crocus ver. albiflorus	Cro ver	12.2	-	15.3	17.8	-	25.3	21.0	-	13.4	13.7	-	12.5	22.0	-	18.6	18.7	-	13.4	12.7	-	11.8	22.0	-	28.2	17.3	-	11.3
Cynosurus cristatus	Cyn cri	1.5	4.0	1.4	2.2	0.9	3.2	2.0	0.8	1.4	1.0	0.7	1.4	2.5	6.6	2.3	1.5	4.5	2.0	1.8	3.9	2.3	1.3	7.4	6.9	1.7	2.2	2.2
Dactylis glo. glomerata	Dac glo	2.7	4.6	6.9	1.0	0.2	0.3	3.0	2.5	0.3	5.3	6.1	4.7	8.8	15.6	10.3	3.2	5.9	8.1	8.7	15.3	2.8	0.2	0.7	-	9.2	6.9	3.4
Dactylorhiza maculata	Dac mac	0.1	-	-	0.2	-	0.6	0.2	-	-	-	-	0.6	0.2	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-
Festuca nigr. nigrescens	Fes nig	76.6	67.5	82.4	66.7	63.9	73.8	75.9	68.0	80.9	78.0	71.9	79.7	71.5	71.5	75.6	69.4	68.9	80.8	77.0	85.9	78.9	75.0	80.0	74.8	66.0	71.1	56.6
Galium alb. album	Gal alb	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-
Galium anisophyllon	Gal ani	0.1	-	-	-	-	0.3	1.5	0.2	0.3	0.8	-	0.8	-	-	-	0.3	0.2	0.3	0.5	0.3	-	1.0	0.5	0.6	1.7	1.9	0.6
Gentiana acaulis	Gen aca	0.2	-	0.1	0.2	-	0.6	0.2	-	0.3	0.2	-	-	-	-	-	0.2	-	-	0.2	-	-	0.2	-	-	0.3	-	0.3
Gentiana lutea	Gen lut	4.3	2.3	0.4	3.8	0.2	0.6	0.7	-	0.3	7.0	0.3	1.4	1.7	-	0.9	2.3	0.2	-	1.8	2.2	0.6	3.8	1.6	0.6	2.7	3.6	1.2
Gentianella cam. campestris	Gen cam	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	-	-	-	-
Hieracium lactucella	Hie lac	1.8	4.1	3.0	4.5	9.3	5.4	3.3	4.2	3.2	1.8	4.0	7.3	4.0	1.9	0.9	4.0	3.2	3.6	4.8	1.4	0.8	3.8	0.7	1.5	4.0	0.7	1.2
Hieracium pil. pilosella	Hie pil	2.1	1.8	1.1	7.3	7.1	4.6	4.7	5.3	4.8	3.7	5.0	3.1	5.0	1.9	1.1	3.5	1.7	0.8	4.7	1.6	-	3.8	0.8	0.9	2.0	1.5	0.3
Hypericum mac. maculatum	Hyp mac	-	-	0.1	-	-	-	0.2	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	0.2	-	-	-	-
Koeleria pyramidata	Koe pyr	0.3	0.1	0.1	0.2	-	-	0.3	-	-	0.2	-	-	0.3	0.2	0.3	0.3	0.2	0.3	-	-	0.6	0.3	-	0.3	-	-	1.0
Lathyrus pratensis	Lat pra	0.5	0.7	1.0	2.2	1.4	2.9	2.8	1.2	0.8	4.7	3.7	2.2	-	0.5	0.3	3.2	1.3	1.4	2.7	3.7	3.6	3.5	6.9	2.4	-	-	-
Leontodon his. hispidus	Leo his	0.3	0.6	0.1	0.2	0.2	0.3	-	0.2	0.3	0.2	0.2	-	0.2	1.0	-	0.2	0.2	-	0.2	0.2	0.3	-	0.3	0.3	-	-	0.3
Leucanthemum vulgare	Leu vul	0.7	-	0.6	0.8	-	2.4	0.3	-	0.6	1.5	0.5	0.8	0.7	-	1.7	0.7	0.8	2.5	0.5	0.2	0.3	0.7	-	0.3	0.7	0.5	1.2
Lotus corniculatus	Lot cor	2.7	2.4	2.2	3.5	4.6	1.8	4.0	3.0	2.3	2.5	2.7	1.1	4.8	3.6	2.8	1.3	1.7	0.6	3.2	6.2	1.4	2.7	1.4	0.6	3.8	2.7	1.7
Luzula campestris	Luz cam	9.3	1.8	11.4	16.0	4.8	19.8	15.2	3.8	19.1	8.0	1.3	13.4	14.0	3.4	8.2	9.4	1.0	8.9	8.5	1.1	7.6	15.7	0.8	15.1	7.7	0.9	9.1
Nardus stricta	Nar str	4.6	2.1	1.3	3.5	0.2	0.6	2.3	-	0.8	0.5	-	-	2.3	-	0.6	4.3	2.8	1.1	2.0	2.6	-	8.8	7.7	3.1	5.5	10.3	2.9
Orchis mascula	Orc mas	0.2	-	0.1	-	-	-	-	-	-	0.3	-	-	0.2	-	-	-	-	-	0.2	-	-	-	-	-	-	-	-
Parnassia palustris	Par pal	-	-	-	-	-	-	-	-	-	-	0.2	-	-	-	-	-	-	-	-	-	-	-	0.2	-	-	0.2	-
Phyteuma orbiculare	Phy orb	0.1	-	-	-	-	0.3	0.7	-	3.4	0.2	-	1.4	-	-	1.4	0.3	-	0.3	0.2	-	0.6	0.2	-	0.6	-	-	0.9
Pimpinella saxifraga	Pim sax	-	0.6	-	-	-	-	-	0.5	-	-	-	-	-	0.2	-	-	-	-	-	0.4	-	-	0.5	-	-	0.3	-
Plantago lanceolata	Pla lan	8.4	12.6	4.8	7.7	11.8	2.9	7.7	11.0	4.0	9.3	11.6	3.6	14.3	20.7	8.1	10.4	17.9	3.6	9.2	13.4	1.4	10.8	16.4	3.5	10.7	14.3	2.7
Plantago media	Pla med	1.8	2.6	1.5	2.7	5.4	1.4	3.3	5.2	0.6	2.3	3.8	1.9	3.8	3.7	1.4	2.5	1.7	1.4	2.3	2.5	0.3	2.0	1.3	-	2.5	1.2	-
Poa pratensis	Poa pra	0.1	-	1.0	0.2	-	-	0.2	-	-	0.2	-	-	-	-	-	0.7	0.2	-	0.2	-	-	0.3	-	0.3	-	-	0.3
Poa tri. trivialis	Poa tri	0.7	0.2	0.3	0.5	-	0.6	1.2	-	-	0.8	-	0.6	0.3	-	0.6	1.3	0.3	0.6	0.3	0.2	0.6	0.8	-	1.6	1.0	-	0.9
Polygala vulgaris	Pol vul	0.5	-	-	0.3	0.2	-	0.3	-	0.3	0.2	-	-	0.3	-	-	0.2	-	-	0.5	-	-	0.3	-	-	-	-	-
Potentilla erecta	Pot ere	7.0	5.5	3.1	8.7	4.1	3.5	5.0	5.0	2.3	7.0	3.7	2.2	9.0	1.0	1.1	3.3	1.5	0.6	5.3	3.1	0.8	7.7	3.3	2.4	5.7	6.9	4.3
Primula ver. veris	Pri ver	0.1	-	-	0.2	-	0.3	-	-	-	-	-	-	-	-	-	0.3	0.2	-	-	-	-	-	-	-	0.2	0.2	0.6
Prunella vulgaris	Pru vul	-	0.4	0.3	-	-	0.3	-	-	0.3	-	-	-	-	-	0.3	-	-	0.6	-	0.2	-	-	-	-	-	0.2	-
Ranunculus acr. friesianus	Ran acr	1.9	1.8	1.6	2.2	1.7	1.2	3.3	1.3	0.9	4.8	2.4	1.1	3.8	1.4	1.4	3.2	1.3	2.2	2.5	1.3	2.8	4.8	1.0	1.6	3.3	0.5	1.6
Ranunculus bul. bulbosus	Ran bul	0.2	0.1	0.3	-	-	-	0.3	0.2	-	0.5	-	-	-	0.2	-	0.3	0.3	-	0.2	-	1.1	0.3	0.2	0.3	0.2	-	-
Ranunculus carinthiacus	Ran car	3.9	3.2	6.2	5.2	2.7	6.7	5.7	2.3	3.8	4.2	1.3	4.2	4.8	1.2	5.4	3.3	2.5	3.6	3.3	1.9	2.3	3.7	1.4	5.4	5.2	1.9	5.7
Rhinanthus minor	Rhi min	0.2	-	-	-	-	-	0.2	-	-	0.2	-	-	2.0	-	-	0.2	-	0.8	-	-	-	-	-	-	-	0.2	0.3
Rumex acetosa	Rum ace	1.4	0.9	0.7	0.3	-	0.3	2.9	0.7	0.8	1.7	0.5	0.8	2.2	0.9	0.3	1.2	0.8	2.2	3.8	1.3	4.2	0.3	0.3	0.3	1.8	2.1	0.4
Sanguisorba min. minor	San min	5.8	5.1	4.1	12.5	7.7	8.1	8.5	9.9	4.8	6.0	7.9	4.2	11.2	9.7	8.9	4.8	5.2	1.9	8.3	9.6	6.0	5.8	8.5	4.2	5.0	8.4	1.2
Taraxacum officinale	Tar off	1.2	0.8	0.7	1.3	0.3	0.3	0.5	0.5	-	1.0	1.2	0.3	1.2	1.7	0.6	1.3	1.2	-	1.2	0.7	-	1.2	0.8	-	0.5	-	-
Thymus pulegioides	Thy pul	2.3	1.9	2.1	0.5	0.7	1.5	2.8	2.2	2.5	2.2	1.0	1.4	1.5	0.2	1.1	2.0	0.5	0.3	4.3	0.7	-	1.0	0.5	4.5	4.0	3.7	2.7
Trifolium pratense	Tri pra	-	1.1	-	-	0.2	-	-	0.8	-	-	0.8	-	1.0	0.5	-	0.2	4.8	0.6	-	7.6	-	0.3	1.8	-	-	2.6	-
Trifolium repens	Tri rep	24.8	26.3	12.7	27.7	19.7	18.2	28.7	20.5	22.6	20.7	16.8	13.6	27.0	20.4	17.9	28.6	24.4	19.5	19.8	5.3	2.9	25.0	4.3	1.2	18.8	4.3	0.9
Trisetum flavescens	Tri fla	0.2	0.7	-	0.8	0.3	0.3	-	0.7	-	2.5	1.3	-	-	0.2	-	0.5	0.3	-	0.3	0.7	-	-	-	-	-	0.2	-
Urtica dioica	Urt dio	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-
Veronica cha. chamaedrys	Ver cha	2.6	1.2	3.4	0.8	1.2	0.9	3.0	3.2	6.3	4.3	3.0	10.6	0.7	1.0	0.6	6.7	4.3	12.8	0.7	0.2	2.0	8.8	9.6	10.1	17.2	16.2	22.6
Veronica officinalis	Ver off	2.3	2.0	3.3	1.0	-	1.2	1.5	1.5	2.9	1.0	1.0	1.1	0.2	-	0.3	4.8	1.3	3.6	0.7	0.5	1.1	2.5	1.6	4.7	1.3	1.0	2.5
Vicia cracca	Vic cra	0.1	-	-	0.2	-	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-
Viola hirta	Vio hir	0.3	0.1	0.3	0.8	0.7	0.3	5.4	0.7	-	1.2	1.0	0.8	3.2	0.2	-	3.0	0.3	-	0.3	0.4	-	1.0	-	2.5	-	-	0.3

Appendix III: Mean absolute cover in percent (deduced from dominance Braun-Blanquet's codes) of species for the five consecutive plot records in the four communities (A: grazed meadow, B: temporary refused meadow, C: underwood, D: lawn).

Species	**Abbrev.**	**A**	**B**	**C**	**D**
Acer pseudoplatanus	*Ace pse*	-	-	0.05	0.07
Agrostis capillaris	*Agr cap*	16.87	4.52	8.03	-
Ajuga reptans	*Aju rep*	1.66	-	1.65	-
Alchemilla conjuncta	*Alc con*	-	0.17	-	-
Alchemilla glabra	*Alc gla*	0.03	-	1.83	-
Alchemilla monticola	*Alc mon*	10.50	5.25	-	-
Anemone nemorosa	*Ane nem*	-	-	1.33	-
Anthoxanthum odoratum	*Ant odo*	0.80	1.43	-	-
Anthyllis vulneraria subsp. vulneraria	*Ant vul*	-	-	-	0.54
Arabis corymbiflora	*Ara cor*	-	-	-	0.14
Arenaria serpyllifolia	*Are ser*	-	-	-	0.01
Asperula cynanchica	*Asp cyn*	-	-	-	3.24
Avenula pubescens subsp. pubescens	*Ave pub*	-	0.11	-	-
Briza media subsp. media	*Bri med*	1.97	0.33	0.20	0.44
Campanula rotundifolia	*Cam rot*	0.38	0.05	0.14	0.03
Carex caryophyllea	*Car cay*	-	0.49	-	0.41
Carex montana	*Car mon*	-	-	11.23	-
Carex sempervirens	*Car sem*	-	0.28	-	13.43
Cerastium fontanum subsp. triviale	*Cer fon*	0.05	0.25	0.03	0.03
Cirsium acaule subsp. acaule	*Cir aca*	-	-	-	0.01
Crepis mollis	*Cre mol*	2.04	0.56	2.21	-
Crocus vernus subsp. albiflorus	*Cro ver*	0.47	5.56	0.83	-
Cynosurus cristatus	*Cyn cri*	6.47	10.54	0.29	-
Dactylis glomerata subsp. glomerata	*Dac glo*	1.84	6.82	0.26	-
Fagus sylvatica	*Fag syl*	-	<0.01	10.34	-
Festuca curvula subsp. curvula	*Fes cur*	-	-	-	3.88
Festuca nigrescens subsp. nigrescens	*Fes nig*	36.63	24.19	10.06	0.02
Galium pumilum	*Gal pum*	-	-	0.50	-
Gentiana lutea	*Gen lut*	-	-	0.94	-
Geranium sylvaticum subsp. sylvaticum	*Ger syl*	-	-	1.98	-
Helianthemum nummularium subsp. obscurum	*Hel num*	-	0.54	-	18.32
Hieracium lactucella	*Hie lac*	4.44	-	-	-
Hieracium pilosella subsp. pilosella	*Hie pil*	0.03	0.46	0.95	4.39
Hippocrepis comosa	*Hip com*	-	0.30	-	18.20
Hypericum maculatum subsp. maculatum	*Hyp mac*	-	0.32	1.33	-
Koeleria pyramidata	*Koe pyr*	-	-	-	8.30
Leontodon autumnalis subsp. autumnalis	*Leo aut*	4.66	-	-	-
Linum catharticum	*Lin car*	-	-	-	0.20
Lolium perenne	*Lol per*	-	0.67	-	-
Lotus corniculatus	*Lot cor*	-	0.17	-	-
Luzula campestris	*Luz cam*	1.58	0.65	0.15	-
Narcissus pseudonarcissus subsp. pseudonarcissus	*Nar pse*	0.30	5.53	9.51	-
Nardus stricta	*Nar str*	-	7.21	-	-
Phyteuma orbiculare	*Phy orb*	-	1.50	2.39	-
Pimpinella saxifraga	*Pim sax*	0.78	0.52	1.35	0.07
Plantago lanceolata	*Pla lan*	1.88	5.70	1.83	0.28
Plantago major subsp. major	*Pla maj*	0.27	0.56	-	-
Plantago media	*Pla med*	-	4.87	-	-
Poa alpina	*Poa alp*	-	-	-	0.13
Poa pratensis	*Poa pra*	0.11	0.60	-	-
Poa trivialis subsp. trivialis	*Poa tri*	0.47	0.31	-	-
Potentilla aurea	*Pot aur*	0.77	4.22	4.06	-
Potentilla crantzii	*Pot cra*	-	-	-	1.48
Potentilla erecta	*Pot ere*	0.20	0.85	8.22	0.03
Prunella vulgaris	*Pru vul*	0.72	-	0.14	-
Ranunculus acris subsp. friesianus	*Ran acr*	6.16	3.43	0.41	-
Ranunculus nemorosus subsp. nemorosus	*Ran nem*	3.41	0.09	0.70	-
Rhinanthus minor	*Rhi min*	-	0.35	-	-
Rumex acetosa	*Rum ace*	0.79	2.92	0.61	0.03
Sanguisorba minor subsp. minor	*San min*	0.06	16.57	1.89	6.88
Sesleria albicans subsp. albicans	*Ses alb*	-	-	-	6.96
Silene nutans subsp. nutans	*Sil nut*	-	-	-	1.65
Taraxacum officinale	*Tar off*	2.35	18.62	0.03	0.02
Thesium alpinum	*The alp*	0.09	-	-	-
Thymus pulegioides	*Thy pul*	0.38	0.03	0.43	1.19
Trifolium montanum	*Tri mon*	0.03	-	-	0.03
Trifolium pratense	*Tri pra*	1.83	6.53	0.39	-
Trifolium repens	*Tri rep*	6.16	4.70	2.73	-
Trollius europaeus	*Tro eur*	0.14	-	0.82	-
Veronica chamaedrys subsp. chamaedrys	*Ver cha*	6.67	0.05	9.92	-
Veronica officinalis	*Ver off*	-	-	1.51	-
Veronica serpyllifolia subsp. serpyllifolia	*Ver ser*	0.63	-	0.14	-
Viola reichenbachiana	*Vio rei*	-	-	0.58	-

Appendix IV: List of tables

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Appendix VI: Curriculum vitae

FLORIAN KOHLER

Date of Birth: 18 September 1975

Nationality: Swiss

Mother tongue: French

Education

2000-2004	University of Neuchâtel, Switzerland, Ph.D. Biology
1994-1999	University of Neuchâtel, Switzerland, M.Sc. Biology
1991-1994	Secondary School of La Chaux-de-Fonds, Switzerland, Baccalauréat

Research Experience

2000-2004	Ph.D. Graduate researcher. University of Neuchâtel and Swiss Federal Research Institute WSL, Antenne romande, Switzerland. Swiss NSF project: ‘Influence of biotic factors in relation to cattle activity onto short-term dynamics of grasslands’. Project leader Prof. A. Buttler
2000-2003	Researcher. Service conseil Zones alluviales, Yverdon, Switzerland. Swiss Agency for the Environment, Forest and Landscape project: ‘Monitoring of vegetation dynamics in floodplains’.
1998-1999	M.Sc. thesis. University of Neuchâtel, Switzerland. Vegetation dynamics in wooded pasture.

Teaching Experience

2000-2004	Graduate Teaching Assistant in Vegetation Science and Numerical Ecology at the Laboratory of Plant Ecology, Neuchâtel University, Switzerland.
2002-2004	Supervisor of three Master Students at the Laboratory of Plant Ecology, Neuchâtel University, Switzerland.
1999-2001	Biology teacher at the Secondary School of Bienne, Switzerland.