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# Low-intensity grazing with domestic herbivores: A tool for maintaining and restoring plant diversity in temperate Europe

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## Abstract

The continuous decline in biodiversity in some European landscapes has led recently to the (re-) implementation of low-intensity grazing systems as an alternative to more cost-intensive conservation practices. This approach aims at developing habitat complexes comprising various successional stages and increasing plant species diversity on local (α-diversity) and landscape scales (β-, γ-diversity). The primary objectives of this review were to uncover ecological processes in which large domestic herbivores (cattle, equids, sheep, goats, pigs) have a key function in affecting plant diversity and to provide a framework for future research and conservation practices. The reviewed literature covers a wide range of ecosystem types in various temperate regions of Europe with a main focus on recent results from Central Europe. Low-intensity grazing enhances existing environmental gradients and generates manifold disturbance patterns on various spatial scales resulting in high habitat diversity. Livestock trampling has a so far underestimated impact on plant species composition and richness. Additionally, selective herbivore behavior facilitates the coexistence of plant species representing different functional types including a considerable number of threatened and grazing-sensitive species. Co-occurrence of progressive and regressive successional processes on low-intensive pastures results in a high β- and γ-diversity, an effect that has been observed soon after the (re-)implementation of grazing. Persistence of species-poor successional stages of dominant competitive graminoid and herb species can in many cases be inhibited by grazing. Large domestic herbivores serve as effective vectors for the dispersal of diaspores, thus improving the connectivity of isolated plant populations. There is a combined effect of diaspore dispersal and microsite creation which can increase the probability of diaspores to successfully germinate and establish. Overall, low-intensity grazing represents a highly flexible concept to maintain and restore plant diversity in cultivated landscapes; general management implications are given.



## Zusammenfassung: Extensive Beweidung mit domestizierten Großherbivoren zur Erhaltung und Wiederherstellung der Pflanzendiversität im temperaten Europa

Der kontinuierliche Rückgang der Biodiversität in einigen europäischen Landschaften hat in der jüngeren Vergangenheit zu einer Wieder- bzw. Neu-Einführung von extensiven Beweidungssystemen geführt, die eine kostengünstigere Alternative zu anderen Naturschutzmaßnahmen darstellen. Dieser Ansatz hat die Entwicklung von Habitatkomplexen zum Ziel, die verschiedene Sukzessionsstadien umfassen und die Pflanzendiversität auf Habitat- (α) und Landschaftsebene (β-, γ-Diversität) erhöhen. Die Hauptziele unseres Reviews lagen zum einen darin, ökologische Prozesse zu bestimmen, die von Weidetieren (Rindern, Pferdeartigen, Schafen, Ziegen, Schweinen) beeinflusst oder initiiert werden und die eine Schlüsselrolle beim Aufbau der pflanzlichen Diversität spielen, zum anderen darin, einen Rahmen zu schaffen für zukünftige Forschung und Naturschutzpraxis. Die ausgewertete Literatur beinhaltet ein breites Spektrum an Ökosystemtypen in verschiedenen gemäßigten Regionen Europas (Schwerpunkt Mitteleuropa). Extensive Beweidung führt zu einer Verstärkung bestehender Umweltgradienten und erzeugt vielfältige Störungsmuster auf verschiedenen Skalenebenen. Dies führt zu einer hohen Habitatdiversität. Der Einfluss von Tritt auf die Pflanzenartenzusammensetzung und die Artendiversität (Bereitstellung von Keimungsnischen) wurde in seiner Vielfältigkeit und Bedeutung bisher unterschätzt. Auch das selektive Fraßverhalten von Weidetieren fördert die Koexistenz von Pflanzenarten verschiedener funktioneller Typen, einschließlich bedrohten und beweidungsempfindlichen Arten. Das gleichzeitige Vorliegen von progressiven und regressiven Sukzessionsprozessen führt zu einer hohen β- und γ-Diversität. Dieser Effekt kann sich sehr schnell nach der (Wieder-)Einführung von extensiver Beweidung einstellen. Beweidung kann in vielen Fällen die Monodominanz von konkurrenzstarken grasartigen und krautigen Pflanzenarten in persistenten, artenarmen Beständen mindern. Als effektive Diasporenvektoren unterstützen Weidetiere die Vernetzung von isolierten Pflanzenpopulationen. Infolge

einer räumlich-funktionellen Verknüpfung von Diasporenausbreitung und Störstellenschaffung werden Keimungs- und Etablierungsraten von Zielarten in vielen Fällen erhöht.

Insgesamt zeigt sich, dass extensive Beweidung ein sehr flexibles Konzept darstellt, um die Pflanzendiversität in Kulturlandschaften zu erhalten und wiederherzustellen. Es werden allgemeine Handlungsempfehlungen für die Beweidungspraxis gegeben.

**Keywords:** biodiversity, conservation, diet selection, disturbance, seed dispersal, succession.

## 1. Introduction

To maintain the biodiversity in European cultural landscapes, efficient nature conservation and restoration measures are urgently required due to the widespread negative impacts of both the intensification of agricultural land use and the abandonment of traditional land management (including grazing) during recent decades (Bakker & Londo 1998, Young et al. 2005). In particular, the biodiversity of semi-natural ecosystems which evolved under human impact, e.g. grasslands and heath lands (Prins 1998, Bakker & Berendse 1999, WallisDeVries et al. 2002, Süss et al. 2011), depends on traditional types of land use. Nature conservation concepts which aim at the maintenance and restoration of these ecosystems include measures such as improving abiotic site conditions (e.g. by re-wetting or the removal of nutrient-rich soil layers), mowing (1–2 cuts/year), grazing with low stock densities and clearing. In contrast to abandonment, which causes a dramatic decline of plant species diversity in semi-natural ecosystems (Jensen & Schrautzer 1999, Marriott et al. 2009, Rosenthal 2010a), these measures in principle are appropriate for promoting species coexistence (Grootjans et al. 2002, Moog et al. 2002, Klimkowska et al. 2007). However, the underlying concept of these management options aims mainly at the small-scale maintenance and restoration of particular successional stages. By contrast, the effect expected to be achieved by large-scale, low-intensity grazing is to realize a mosaic of suitable habitats for target (i.e. habitat-typical) species of early, mid- and late-successional stages which focuses on the enhancement of biodiversity on landscape scale (β- and γ-diversity) (Riecken et al. 2004, Bunzel-Drüke et al. 2008, Irmler et al. 2010, Plachter & Hampicke 2010). This approach could be more effective than a local approach of habitat conservation in buffering local population extinctions because it allows for population exchanges between habitats (Tscharntke et al. 2005).

The main arguments for the implementation of large-scale grazing systems are: (i) grazing of large herbivores (such as cattle, equids, sheep, goats and pigs) on extensive areas represents a type of traditional agricultural management which generated landscapes of a high biodiversity (Vera 2000, Lederbogen et al. 2004, Bunzel-Drüke et al. 2008, Bobiec et al. 2011), (ii) gradients in grazing intensities are expected to allow for the development of succession mosaics and structurally diverse landscapes (Olff et al. 1999), (iii) large herbivores have a keystone function affecting ecological key processes (e.g. diaspore dispersal, colonization, competition), the structure and composition of plant communities and habitat connection (WallisDeVries 1998, Beinlich & Plachter 2010, Auffret 2011, Süss et al. 2011), and (iv) synergy effects between ecological and economic targets promise a certain degree of added agricultural value in contrast to cost-intensive mowing of grasslands (promising only low feed value) or sod cutting (Hampicke 1993, Donath et al. 2004, Süss et al. 2011).

We define 'low-intensity grazing' as a type of land use that occurs on large pastures (at least 10 ha) with a long grazing season and at a stocking density (max. 0.6 livestock units $ha^{-1}$, Bunzel-Drüke et al. 2008) that is (more or less) adjusted to seasonal fodder shortages (i.e. winter or drought shortages) or on spatially separate, smaller pastures with short grazing periods that are functionally connected by livestock routes (typical especially for sheep grazing).

This is in contrast to conventional grazing systems where grazing occurs on small pastures with a high stocking rate, and where demand and availability of fodder resources are closely correlated to the management targets of the farmer. Research on low-intensity

grazing systems has a long tradition for instance in Great Britain, but was only recently intensified in most parts of the European continent (FINCK et al. 2004).

This review especially aims at unlocking and reconciling results of recent studies from Central Europe which have not yet been summarized, and at contextualizing this knowledge with findings from analogous grazing projects in other parts of Europe (excluding the Mediterranean). The investigated projects cover pleistocene river valleys, landscapes of sandy (post-)glacial deposits of the European lowlands, colline and montane regions and pleistocene landscapes of the alpine foothills. We do not consider sub-alpine and alpine pastures and salt marshes because they have been described elsewhere (e.g. BAKKER 1998, DULLINGER et al. 2003, ERSCHBAMER et al. 2003, JEWELL et al. 2005, 2007).

Our approach is to consider low-intensity grazing of large-scale pasture systems as a feedback system of grazing impacts triggering biological processes and the development of biodiversity on different spatial scales which conversely influence grazing behavior and management options (Fig. 1). More specifically, we aim to assess the current stage of knowledge on this topic with respect to (i) the factors controlling grazing behavior on different spatial and temporal scales, (ii) the significance of large domestic herbivores as vectors for diaspore dispersal, (iii) grazing impacts on plants and the role of plant life traits in avoiding and/or tolerating grazing impacts, (iv) grazing-induced microsites and their role for germination, establishment and species diversity, and (v) mechanisms influencing the successional pathways in large-scale pastures. Our review additionally aims to provide a framework for decisions and evaluations in conservational grazing management practice.

The nomenclature is according to WISSKIRCHEN & HAEUPLER (1998) for vascular plant species, DIERSSEN (2001) for bryophytes and ELLENBERG & LEUSCHNER (2010) for plant communities.

| Spatial scales | patch | community | landscape |
|---|---|---|---|
| Herbivore impacts | • trampling (hoof prints, plant damage)<br>• selective feeding of plant species/plant parts<br>• faeces deposition | • trampling (soil compaction, hummock-hollow complexes, gaps, soil erosion)<br>• selective feeding of plant communities | • trampling (livestock trails)<br>• gradients of grazing intensity<br>• selection of preferential sites (e.g. watering points)<br>• (directed) diaspore dispersal |
| Biotic and abiotic processes | • germination<br>• establishment<br>• vegetative regeneration of plant tissue | • competition<br>• dominance<br>• coexistence<br>• succession<br>• nutrient relocation | • colonization<br>• landscape structuring<br>• nutrient relocation |

Fig. 1: Impacts of large domestic herbivores on biotic and abiotic key processes for biodiversity on different spatial scales.

Abb. 1: Wirkung domestizierter Großherbivoren auf einige, die Biodiversität beeinflussende biotische und abiotische Schlüsselprozesse auf verschiedenen räumlichen Maßstabsebenen.

## 2. Factors influencing grazing behaviour on different spatial and temporal scales

As already reviewed by GORDON et al. (2004) the understanding of grazing behavior and the management of large (wild) herbivores must consider appropriate spatial scales in order to match conservation objectives. When herbivores graze on large pastures, decisions concerning distinct spatial scales are necessary in order to optimally utilize fodder resources (FRANK 2006). On the patch scale, animals decide between individual plants and plant parts in direct proximity of the mouth, on the community scale, between patches with varying abundances of species, and on the landscape scale, between structurally distinct plant communities. This Section demonstrates that this approach is also appropriate for domestic herbivores, and discusses additional aspects of herd management such as the grazing period, the choice of animal species and the herd composition. Our basic assumption is that on large, low-intensive pastures, the interaction of animal-based (morpho-physiological) traits and requirements with habitat conditions and spatio-temporal arrangements of food resources determine the grazing behavior of large domestic herbivores, and, hence, their effect on vegetation development and landscape structuring (HOBBS 2006, SEARLE & SHIPLEY 2008).

### 2.1. Selective grazing on patch scale

Selective grazing is defined as the consumption of good forage out of proportion with its abundance where grazing patterns closely track vegetation patterns (GORDON 2003). Regarding the patch scale (see above), it has been highlighted by GORDON & ILLIUS (1988), JANIS & EHRHARDT (1988) and SHIPLEY (1999) that the morphological parameters of the mouth, i.e. the bite dimensions and the size of the incisor arcade, are a direct determinant and a driving variable for intake rate and grazing effects of large herbivores. The hypothesis deduced from these results is that, in nature conservation, the specific implementation of such physiognomic types assists in reaching specific aims. Thus, the narrow and acute incisor arcades of intermediate feeders (e.g. goats), and medium-sized grazers (e.g. sheep)

Photo 1: Horses have a deep bite and are an effective "tool" in eliminating, for instance *Deschampsia cespitosa*: plants are rooted up but not eaten (photo: G. Rosenthal).

Bild 1: Der tiefe Verbiss von Pferden kann bei der Reduzierung zum Beispiel von *Deschampsia cespitosa* wertvolle Dienste leisten: die Pflanzen werden herausgerissen, aber nicht gefressen.

enable a fine-tuned selection of palatable plants or plant parts, whereas large grazers such as cattle and horses select diets based on the characteristics of a larger spatial unit (plant community, landscape) rather than of individual plants (GORDON 2003). Indeed, ARMSTRONG & MILNE (1995) and ARMSTRONG et al. (1997) have shown that sheep are able to more efficiently avoid feeding on unpalatable *Nardus stricta* tussocks than are cattle, which resulted in an increase of *Nardus stricta* in sheep pastures and a decrease in cattle pastures of British heath lands. The effects of precisely targeted feeding of preferred plant parts from shrubs and trees by goats (even the foliage of thorny shrubs) were documented by RAHMANN (2000) in calcareous grasslands in Germany. Grazing with goats, RAHMANN (2000) determined, creates more heterogeneous vegetation structures than does grazing by sheep, which concentrates on ground vegetation. ROOK et al. (2004) documented differing vegetation responses with respect to plant species diversity in cattle grazing versus horse and sheep grazing. The deep bite of the latter resulted in a loss of species diversity as compared with cattle grazed swards.

There are also differences in the digestion physiology and the nutritional requirements of domestic herbivores (e.g. ruminants vs. non-ruminants, and grazers vs. browsers, GORDON 2003, SEARLE & SHIPLEY 2008) which influence the grazing behavior, and, hence, the decision over which species to choose for which aim (e.g. in restoration projects). In general, grazers are relatively non-discriminatory between plant species on patch scale as compared with browsers, except where preference differences between species are high (GORDON 2003). Non-ruminants such as horses and donkeys can meet their nutritional requirements by eating large quantities of low-quality forage, which makes them suitable for large areas with less palatable vegetation, and for the removal of more biomass per body mass than cattle. Equids are well-adapted to feed on fibrous over mature grasses (DUNCAN et al. 1990) such as *Juncus effusus, Deschampsia cespitosa* and *Molinia caerulea* so that they are particularly suitable for counteracting grass encroachment (Photo 1, SÜSS & SCHWABE 2007). In contrast, ruminants would need a sufficient supply of a less fibrous diet of dicotyledons.

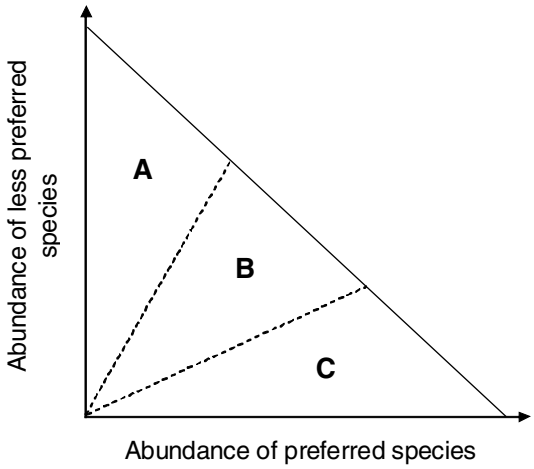


Fig. 2: Degrees of herbivore selectivity on the patch scale as a function of relative abundances of preferred and less preferred plant species in the grazing area. A = non-selective, proportional grazing; B = selective grazing with prolonged searching time for preferred species; C = selective grazing of preferred species. Transitions between segments are fluent.

Abb. 2: Kleinräumige Fraßselektivität von Weidetieren in Abhängigkeit von der relativen Verfügbarkeit bevorzugter und weniger bevorzugter bzw. gemiedener Futterressourcen in einer Weidefläche. A, nicht selektive, proportionale Beweidung/Fraß; B, selektive Beweidung/Fraß mit verlängerter Suche nach bevorzugten Arten; C, selektive Beweidung/Fraß von bevorzugten Arten. Die Übergänge zwischen diesen Typen sind fließend.

But, there exist also common properties of herbivore species beyond such well-established classifications. For instance, both cattle (ruminants) and horses (non-ruminants) select for grasses, whereas donkeys (non-ruminants) select for legumes and sheep (ruminants) select for legumes and other herbs (BUTTENSCHØN & BUTTENSCHØN 1982b, MAYER et al. 2001, BOKDAM 2003, BRENNER et al. 2004, LAMOOT et al. 2005, SÜSS et al. 2009). Furthermore, many species seem to be more flexible in their diet than expected, e.g. goats are extremely flexible in their feeding behavior; they behave as grazers in periods of high resource availability and survive bad seasons by browsing (GORDON & ILLIUS 1988).

A key aspect for understanding feeding choices of large herbivores on the patch and community scale, in addition to animal-based criteria (see above), is the availability of fodder resources, its palatability, and its nutrient concentrations (MENARD et al. 2002, HESTER & BAILLIE 1998, PALMER et al. 2003, FRANK 2006, SÜSS 2006). An important principle domestic herbivores follow during grazing is maximization of energy intake. This leads them to switch between grazing strategies when the proportions of preferred and less preferred plants change. Selective grazing will be applied when preferred fodder plants are more abundant than bad fodder plants (GORDON 2003) (segment C in Fig. 2). At lower abundances of the preferred fodder plants, the grazing strategy changes to prolonged searching times as long as the energy balance is on the positive side (segment B in Fig. 2). When bad fodder plants dominate, search times for good fodder become long enough to tip the energy balance to the negative side, resulting in non-selective, proportional grazing (segment A in Fig. 2). In mixed grass-dwarf shrub vegetation, sheep, for instance, select for grasses as long as grasses represent the dominant fodder resource, but switch to dwarf shrubs when grasses become rare (ARMSTRONG & MILNE 1995, WELCH 1997). Cattle adapted their search times to the abundance of their dietary preference, *Deschampsia flexuosa*, searching longer when *Deschampsia* became less abundant. *Calluna vulgaris* was foraged only when it was dominant, which indicated a change from selective to proportional grazing, i.e. from segment C to segment A in Fig. 2 (WALLISDEVRIES & DALEBOUDT 1994).

However, the degree of selectivity is modified also by landscape grain and patch size, and by contrasts of palatability. Grazing choice experiments with sheep carried out in the British Isles showed that the 'carry-over effects' from preferred into less preferred patches and vice versa were especially pronounced at fine-grained swards (patch sizes of 0.13 $m^2$ of grass and clover, respectively; ILLIUS et al. 1992). Both the failure to respond to local sward heterogeneity in a short time and the continuation of experienced grazing styles from previous swards cause relatively smooth grazing transition boundaries between patches of contrasting vegetational composition (e.g. selectivity reduction in transiting from *Agrostis/Festuca*- to *Calluna*-patches in the British uplands) (ARMSTRONG & MILNE 1995, PALMER et al. 2003).

### 2.2. Selective grazing on community and landscape scale

At the community and landscape scale, additional factors such as spatial arrangement of preferred foraging plants and pasture infrastructure, social constraints, avoidance of parasitism, and microclimatic effects have an important influence on foraging decisions. Low-intensity grazing on large pastures as compared with conventional grazing systems enables manifold interactions between grazing and vegetation patterns with various impacts on landscape heterogeneity. Starting from a homogeneous sward, patch grazing (ADLER et al. 2001) initiates a patchy mosaic of low and tall structures, i.e. an increase in heterogeneity. If low structures are further preferred (cyclic grazing; DRENT & VAN DER WAL 1999) and tall structures are avoided, a positive feed-back loop between grazing and forage quality enhances the structural contrast and may even result in a progressive succession within the avoided tall growing patches. Such a development is particularly common on horse pastures, where avoided tall grass patches may achieve a surface ratio of up to 80 % after some years (SEIFERT et al. 2006). This process causes not only changes in the species composition but also in local nutrient transfers from favored short grass meadows into tall grass patches, which are preferably used as latrines (EDWARDS & HOLLIS 1982, KLEYER 2004).

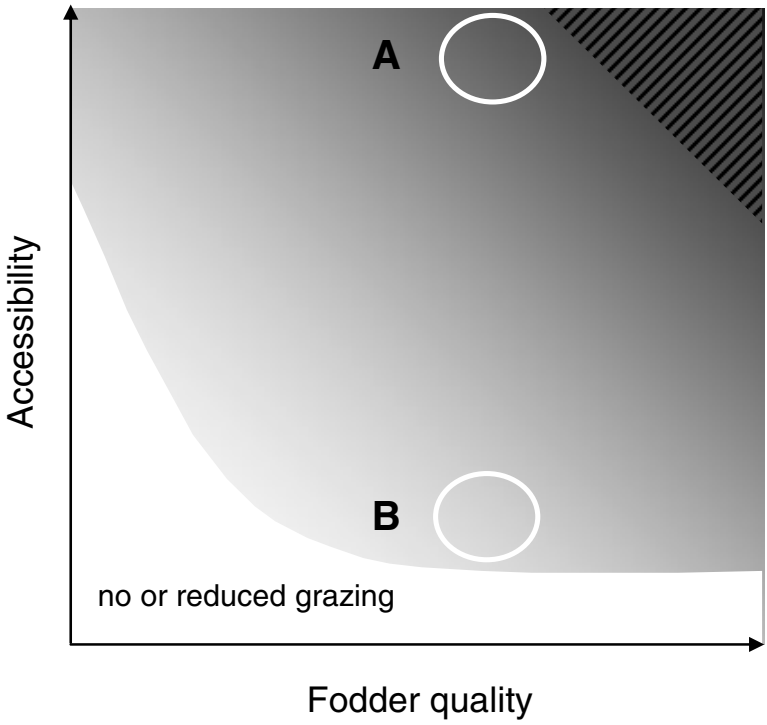


Fig. 3: Grazing intensity relative to fodder quality and accessibility. Grazing intensity (= increasing intensity of the grey hue) on large pastures depends on the fodder quality of the plants and the accessibility of potential grazing sites. Full gradients of grazing intensities occur only when herbivores are allowed to select between different sites (dotted area). Circles A and B show two examples of different accessibility of such sites: Circle A represents easily accessible (preferably grazed) sites, e.g. close to livestock trails, resting or watering areas, circle B represents hardly accessible (less grazed) sites, e.g. shrub thickets. The area below the curve indicates sites that are avoided for grazing, e.g. dense thickets or swamps. Conventional grazing systems with rotational grazing, high herbivore densities and short grazing periods reduce the spectrum of realized grazing intensities and only intensively grazed sites occur (hatched area).

Abb. 3: Beweidungsintensität in Abhängigkeit von der Futter-Qualität und -Erreichbarkeit. Die Beweidungsintensität (ansteigend mit der Intensität der Graufärbung) auf großflächigen Weiden hängt von der Futterqualität der Pflanzen und der Erreichbarkeit potenzieller Weidestandorte ab. Der gesamte Gradient der Beweidungsintensität tritt nur dann auf, wenn die Weidetiere zwischen unterschiedlichen Pflanzenbeständen wählen können (gepunktete Fläche). Die Kreise A und B zeigen zwei Beispiele für die unterschiedliche Erreichbarkeit von derartigen Weiden: A kennzeichnet leicht erreichbare (bevorzugt beweidete) Standorte, d. h. nahe von Trittpfaden, Rastplätzen oder Tränken, B zeigt weniger leicht erreichbare (weniger stark beweidete) Standorte, z. B. Dominanzbestände unterschiedlicher Sträucher. Die Fläche unterhalb der Kurve kennzeichnet Bereiche, die von den Weidetieren gemieden werden, z. B. dichte Gebüsche oder Sümpfe. Herkömmliche Systeme mit Rotationsbeweidung, hohen Weidetierdichten und kurzen Weideperioden reduzieren das Spektrum realisierter Beweidungsintensitäten und es kommen nur intensiv beweidete Bereiche vor (schraffierte Fläche).

Forage selection on the landscape scale results mainly from optimizing the ratio between energy intake and costs of searching for patches with the most digestible fodder. Therefore, in large pastures with a patchy distribution of fodder resources, not only the potentially usable energy yield but also the accessibility of grazing sites and their proximity to pasture infrastructures (e.g. watering places) turned out to represent the most significant factors governing feeding choices and, hence, grazing intensities (Fig. 3) (WallisDeVries & Schippers 1994, Buttenschøn & Buttenschøn 2001, Bailey et al. 2004, Kleyer 2004, Lederbogen et al. 2004, von Oheimb et al. 2006, Searle & Shipley 2008). Easily accessible sites close to livestock trails, resting and watering areas, and grasslands with high fodder quality are grazed most preferably, whereas dense shrub thickets and fens representing sites dominated by unpalatable plants are avoided (Fig. 3). If the grazing pressure increases (e.g. due to a higher stocking rate), selectivity declines, and the correlation between fodder quality and grazing intensity decreases (Hart et al. 1993, Armstrong & Milne 1995, Holsten 2003). In that case, animals are forced to use all available fodder irrespective of its palatability.

There is a set of management parameters such as the stocking rate, the grazing period, fencing, rotation, and the choice of animals which allow the manager to select and adjust them in a way that the grazing intensity supports specific nature conservation aims. For instance, a key problem in achieving conservation targets by means of low-intensity grazing is the balance between creating a heterogeneous landscape with different successional stages (including forest stages) and building up sufficient grazing pressure for supporting non-forest target communities. In cattle pastures of the pre-alpine upland, grazing of species-rich, nutrient-poor fens with *Caricion davallianae* target communities has to be enforced by fodder shortages on the fertilized grassland on mineral soils in late summer. This can be achieved by either a herd size that requires more fodder than is available on such easily accessible sites during that time, and/or by reducing fertilizer input and biomass production on the mineral soils (Lederbogen et al. 2004). Adjusting the herd size to the fodder availability, however, will result in a segregation between intensively grazed grasslands (*Cynosurion*) and almost ungrazed fens and hence in a loss of floristic gradients. In large pastures of north eastern Germany, only winter grazing guaranteed the maintenance of floristic gradients because defoliation by grazers during summer was not sufficient to control vegetation development (Kleyer 2004).

In multi-species grazing systems (simultaneous grazing by a mixed herd or successive grazing by different livestock species), competition between different livestock species and/or complementary diet preferences (see above) are capable of achieving a more complete utilization of the phytomass and significant control of undesired dominant plants (e.g. *Calamagrostis epigejos*) than does single species grazing. This was shown for mixed herds of domestic large herbivores in various ecosystems, including, for instance, calcareous grasslands (sheep and goats; Rahmann 2000), sand grasslands (sheep and donkeys; Süss & Schwabe 2007), and a grassland-heathland complex (sheep and cattle; Menard et al. 2002, Kleyer 2004, Putfarken et al. 2008, DeGabriel et al. 2011).

Besides specific characteristics of a livestock species and spatial settings of a pasture (see above), seasonality and choice of diet offering affect the grazing pattern. This in turn affects the growth of established plants because the timing of defoliation is important in determining plant response (Hester et al. 2006). The compilation of grazing experiments in Table 1 shows that in the course of the year, animals will select for the most palatable fodder at any given time (Photo 2) (high palatability is given by a high nutrient and energy content but low concentrations of defensive substances and/or sclerenchymatic structures). This selection follows gradients in soil fertility and/or the dominance of tall unpalatable grasses or sedges. A continuous search for the most palatable plants will occur only on low-intensive pastures with a rich supply of different fodder resources and a long grazing season (Sonnenburg & Gerken 2004). Pasture weeds such as *Cirsium, Rumex* and *Juncus* species represent mostly winter forage, and their suppression requires 'forced' defoliation by hungry animals. Evergreen *Juncus effusus* plants then even serve as preferred forage, especially during periods of snow cover (Putfarken et al. 2008). A model of seasonal selection from a heath-moorland

Table 1: Seasonal changes in grazing preferences of large herbivores in large, low-intensive pastures. The grazing system is determined by summer and year-round grazing, and the herbivorous animals used. In all cases, variably composed complexes of habitats and plant communities were available as feeding grounds. The lower part of the table presents preferably grazed habitats and plant communities at different seasons, from early summer to autumn (summer grazing system) and from early summer to winter/spring (year-round grazing system). The lowermost row shows plant communities which were avoided and not grazed at all.

Tabelle 1: Saisonalität der Beweidungspräferenzen von Großherbivoren in großflächigen Extensivweiden. Das Beweidungssystem ergibt sich aus der saisonalen Beweidungsdauer und den Weidetierarten. In allen Fällen bestanden die Flächen aus einem Komplex von verschiedenen Habitaten und Pflanzengesellschaften. Der untere Tabellenteil enthält die in verschiedenen Jahreszeiten jeweils als Futterressource bevorzugten Pflanzengesellschaften. In der letzten Zeile sind Pflanzengesellschaften verzeichnet, die gänzlich von den Weidetieren gemieden wurden.

| **Country (reference)** | N-Switzerland (1) | S-Germany (2) | SW-Czech Republic (3) | The Netherlands (4) | NW-Germany (5) | S-Denmark (6) |
|---|---|---|---|---|---|---|
| Grazing system | Summer grazing with cattle | Summer grazing with cattle | Summer grazing with cattle | Year-round grazing with cattle and horses | Year-round grazing with cattle and sheep | Year-round grazing with cattle |
| Available habitats | Complexes of different fen habitats | Complexes of wet and dry habitats | Complexes of wet and dry habitats | Complexes of wet and dry habitats | Complexes of wet and dry habitats | Complexes of mesic and dry habitats |
| **Season** | **Preferably grazed habitats/plant communities in the corresponding season** | | | | | |
| Early summer | Eutrophic *Magnocaricion* (*Phalaridion*) | Eu-, mesotrophic *Cynosurion* | *Deschampsia cespitosa* swards | Eutrophic *Poa trivialis* habitats (cattle and horses) | Eutrophic *Molinietalia* (cattle) | Mesic grassland |
| Midsummer | Eutrophic *Magnocaricion*, *Carex acuta*-group | *Caricion davallianae* | *Nardion* | *Phragmition* (cattle and horses) | Mesotrophic *Cynosurion* (cattle) | Dry grassland |
| Autumn or winter/spring | Mesotrophic *Magnocaricion*, *Carex elata*-group | *Caricion lasiocarpae* | Mesotrophic *Magnocaricion*, *Carex elata*-group | *Calamagrostis epigejos* grassland, shrubs (cattle and horses) | Eutrophic *Magnocaricion* (cattle) | Woodland (field layer) |
| | **Avoided habitats/plant communities (not grazed at all)** | | | | | |
| | Mesotrophic *Magnocaricion* (*Cladietum marisci*) | *Sphagnion magellanici* | | | *Sedo-Scleranthetalia*, young *Betula*- stages | |

References: 1, GANDER et al. (2003); 2, LEDERBOGEN et al. (2004); 3, MATĚJKOVÁ et al. (2003); 4, VULINK & DROST (1991); 5, PUTFARKEN et al. (2008); 6, BUTTENSCHØN & BUTTENSCHØN (2001).

complex in the British uplands supports the afore-mentioned results that the seasonal utilization of forage follows gradients of palatability, in that case from an almost pure *Agrostis/Festuca* diet in early summer to a diet intermixed with *Molinia* in midsummer, and to a diet with significant *Calluna* fractions during winter (ARMSTRONG & MILNE 1995).

Besides this directed sequence of grazing preferences, a positive feedback between repeated (cyclic) grazing of preferred grassland patches and the re-growth of grazing-tolerant palatable plants stabilizes early successional stages (HESTER et al. 2006, SKARPE & HESTER 2008). If grazing is not overly excessive, the loop can enhance for the animals both the offered food quality and the time window of exploitation (DRENT & VAN DER WAL 1999, GANDER et al. 2003).

Furthermore, seasonal grazing behavior is often different for different livestock species. In the year-round pasture 'Höltigbaum' (NW Germany), for instance, cattle changed from

Photo 2: Effects of seasonal grazing in the common pasture "Mühlberger Viehweide" (Upper Bavaria). The grazing season lasts from April to October (the photo demonstrates the situation at the end of the grazing season in October). The *Cynosurion* habitats in the foreground are grazed already in the beginning of the grazing period and are strongly overgrazed due to cyclic grazing. Grazing of calcareous fens (in the middle part of the picture) started much later (June), transitional fens in the lower part close to the lake remained more or less ungrazed until September (photo: G. Rosenthal).

Bild 2: Wirkungen saisonaler Beweidung in der Allmendweide „Mühlberger Viehweide" (Oberbayern). Die Weidesaison dauert von April bis Oktober (Bild aufgenommen am Ende der Weidesaison im Oktober). Die Beweidung der *Cynosurion*-Standorte (im Vordergrund) beginnt bereits mit dem Auftrieb (starke Überweidung während des Sommers). Die Kalkflachmoore (im mittleren Teil der Weidefläche) werden später und weniger intensiv beweidet, die nahe dem See befindlichen Zwischenmoore erst ab September.

*Molinietalia* to *Cynosurion* communities and later to *Magnocaricion* communities whereas sheep stayed on the dryer and less fertile soils during the whole year (Table 1, PUTFARKEN et al. 2008). Species-specific differences are also important with respect to thermoregulation during summer (shade) and winter (wind shelter) (GORDON et al. 2004). These examples demonstrate that understanding the timing of different herbivore grazing activities through the year provides manifold management options: choice of livestock species, grazing period and percentage of fertile and less fertile soils influence grazing behavior and, hence, the possibility to gain a defined nature conservation goal (HESTER et al. 2006).

## 3. Dispersal of diaspores

Livestock species are able to contribute to local plant species diversity by the dispersal of diaspores (seeds and fruits) and in this way counteract negative effects of habitat isolation in fragmented landscapes. The main purpose of this Section is to assess how much evidence we have gained to date in order to confirm this hypothesis. We focus on generative diaspores of vascular plant species; noteworthy, however, is that vegetative diaspores of bryophyte and lichen species are dispersed by livestock as well (sheep-grazed calcareous grasslands; PAULIUK et al. 2011).

In various European open grazed ecosystems large amounts of diaspores and a wide range of species were proven to be dispersed internally (endozoochory) or externally (epizoochory) by livestock species (e.g. FISCHER et al. 1996, STENDER et al. 1997, PAKEMAN et al. 2002, COSYNS & HOFFMANN 2005, EICHBERG et al. 2007, WESSELS et al. 2008, STROH et al.,

in press). The daily number of diaspores transported by a flock of several hundred sheep lies in the range of millions (Fischer et al. 1995, Eichberg & Wessels-de Wit 2011). Zoochory has been studied extensively with regard to cattle, sheep and equids, whereas goats (Mexican thornscrub vegetation, Baraza & Valiente-Banuet 2008) and domestic pigs have only rarely been the focus of dispersal research. With respect to sheep and cattle, it has been shown that half of the pool of plant species generatively reproducing on the paddocks can be dispersed by a single livestock species (Poschlod & Bonn 1998, Wessels et al. 2008). Generally, there is a positive relation between the abundance of a plant species in the established vegetation and its abundance in livestock faeces or fur (Stender et al. 1997, Rasran et al. 2004, Cosyns et al. 2006, Bakker et al. 2008, Wessels et al. 2008).

The production of large numbers of diaspores per area (positively correlated to small diaspore size; Moles et al. 2004) often results in a dominance of small-seeded species in endozoochorous dispersal spectra (Pakeman et al. 2002, Bruun & Poschlod 2006). External diaspore dispersal is supported by elongated diaspore structures (e.g. hooks, hairs, awns) and dense, undulated fur (e.g. sheep and Galloway cattle; Couvreur et al. 2004, Tackenberg et al. 2006, Wessels et al. 2008, Auffret 2011). However, since also diaspores without specialized adhesive appendages are found regularly in livestock fur, the external dispersal of almost every species seems probable in grassland systems (Poschlod et al. 1998, Couvreur et al. 2004); problematic is only the retention of heavy unappendaged diaspores. Diaspore release height and animal behavior (e.g. wallowing) are further important factors influencing dispersal success (Fischer et al. 1996, Stroh et al., in press).

Livestock species provide both modes of zoochory (endo-, epizoochory) to the grazed system simultaneously, irrespective of animal species and vegetation type. Studies comparing the two dispersal modes with regard to a single herbivore species within the same grazing system revealed that the two diaspore spectra were more complementary than concordant (Fischer et al. 1995, Stender et al. 1997, Couvreur et al. 2005, Eichberg & Wessels-de Wit 2011).

Both endo- and epizoochory are related to the dispersal-in-time strategy (soil seed bank formation). On the one hand, many studies have shown that the ability of a diaspore to survive gut passage is positively associated with its ability to survive in the soil (Pakeman et al. 2002, Cosyns et al. 2005a, Mouissie et al. 2005, Kuiters & Huiskes 2010, Stroh et al., in press). On the other hand, herbivores take up diaspores externally that are part of the soil seed bank (or litter layer) when grubbing (coats and faeces of pigs; Neugebauer 2004), wallowing (fleece of sheep; Fischer et al. 1996; with high probability, fur of donkeys; Süss & Schwabe 2007), walking (hooves of sheep; Fischer et al. 1995) or resting. Livestock species thus not only disperse diaspores of actually fruiting plants (primary dispersal), they also continue to disperse diaspores that have already been dispersed (secondary dispersal).

For many plant species, retention times of diaspores in the digestive tract or the coat of large herbivores are long enough to expect long-distance dispersal (distance > 100 m, Cain et al. 2000) if the herbivores are allowed to roam the landscape. For various domestic livestock species Cosyns et al. (2005a) revealed mean gut passage times of 2–3 days, allowing long-distance dispersal by endozoochory. Multiplying herbivore travel velocities by diaspore retention times in fur, maximum potential dispersal distances were calculated by Kiviniemi (1996) at nearly 1 km in cattle, and by Fischer et al. (1996) at up to 100 km in sheep. For the grass species *Stipa capillata*, Wessels et al. (2008) showed that there was no significant detachment from sheep fleece during paddock changes (3 km walking distance), but significant diaspore losses within arrival paddocks. This gives experimental evidence that diaspores of habitat-typical species transported by livestock species can indeed reach isolated areas in considerable numbers. Predictions about diaspore arrival in recipient areas must consider that the dropping rate of diaspores from animal fur decreases with time (Bullock et al. 2011). Linking plant traits to landscape history, Purschke et al. (2012) revealed that plant species with a high potential for long distance dispersal are over-represented in Swedish grasslands with a long-term grazing continuity. In this case, cattle zoochory as a direct herbivore effect played an important role; facilitation of anemochorous dispersal is an indirect effect because grazing leads to (semi-)open plant communities (Purschke et al. 2012).

Diaspores transported by large domestic herbivores have a comparatively high probability of reaching suitable sites for germination and establishment. On a large scale, herbivores free-ranging on paddocks comprising vegetation mosaics exchange diaspores between preferred grazing sites (54–61 ha, Belgian coastal dune reserves; COSYNS et al. 2005b). On a fine scale, large herbivores create a variety of safe sites for diaspore germination and seedling establishment, including diaspores that have been transported zoochorously, both pre- (NEUGEBAUER 2004) and post-displacement. EICHBERG et al. (2005) showed that diaspores of the threatened Asteraceae, *Jurinea cyanoides*, risk less post-displacement predation when buried through sheep trampling, and that only then do seedlings establish. In many further cases, the two processes (diaspore dispersal and microsite creation) will likely be directly linked as well (e.g. trampled faeces deposits; FAUST et al. 2011).

In a restoration context, knowledge of the relation between target and non-target species in dispersal spectra is important. Within grazing regimes comprising nutrient-poor and nutrient-rich(er) plant communities, many more diaspores of non-target than of target species were dispersed, both endo- and epizoochorously (FISCHER et al. 1996, MATĚJKOVÁ et al. 2003, RASRAN et al. 2004, MOUISSIE et al. 2005, BAKKER et al. 2008). One explanation for this phenomenon was found in the diet preferences of the livestock species and, as a consequence, the animals' longer presence in productive plant communities (RASRAN et al. 2004, BAKKER et al. 2008). In many cases, small population sizes of target species will be a further reason. The question arises as to whether there is a threat to nutrient-poor, species-rich parts of the grazing area by the zoochorous input of diaspores of invasive generalist species. Although this question requires much more research to be answered fully, we assume that natural abiotic filters will in many cases prevent invasion (Section 5.4). However, to minimize the probability of colonization by competitive species and to enhance the chance of target species inter-habitat exchanges in restoration projects, the donor grazing area should be restricted to well-developed stands (WESSELS et al. 2008).

Among the total numbers of diaspores dispersed by livestock, the proportion of diaspores which establish successfully has rarely been quantified. For a range of species it has been experimentally demonstrated that the (initial) establishment after epi- as well as endozoochorous dispersal is possible (COSYNS et al. 2006, WESSELS-DE WIT & SCHWABE 2010). But it got also clear that the costs of zoochorous dispersal are high: Field studies dealing with the post-dispersal fate of endozoochorous diaspores in open sand ecosystems revealed seedling emergence ≤ 5 % with respect to various livestock species (COSYNS et al. 2006, EICHBERG et al. 2007; see also PAKEMAN & SMALL 2009).

Advantages for colonization of new habitats and/or for mixing of genetic material likely prevail over disadvantages that also are represented by zoochorous dispersal. However, this balance requires testing in fragmented cultural landscapes with small populations of target plant species. In general, knowledge concerning impacts of livestock zoochory at the level of plant genetics remains scarce (but see WILLERDING & POSCHLOD 2002).

It can be stated in conclusion that recent research results offer ample evidence to support the hypothesis that domestic herbivores play a key role in preserving plant species richness in the European landscape. Herbivores function as effective, intra- and inter-habitat diaspore dispersal vectors. For further development of the hypothesis, more intensive studies are needed in order to better understand the mechanisms and net balances of zoochorous colonization. In present day European landscapes, due to increasing constraints on livestock mobility, valuable dispersal infrastructure is disappearing (OZINGA et al. 2009, BEINLICH & PLACHTER 2010, AUFFRET 2011). Short-lived plant species are especially threatened by habitat fragmentation and will profit by any attempt to re-enforce livestock movements (BRUUN & FRITZBØGER 2002, PURSCHKE et al. 2012).

## 4. Grazing impacts on plants and mechanisms of survival

The spatial and temporal variety of grazing impacts and gradients of grazing intensity in (large) pastures is reflected in the occurrence of multiple plant life strategies. Grazing impacts on plants comprise (1) more or less selective destruction and physical removal of plant tissue by feeding and/or trampling (direct effects), (2) the release of resources due to defoliation of competitors, removal of litter and the creation of gaps which reduces competition and provides new opportunities for colonization (GRUBB 1985, PICKETT & WHITE 1985) and (3) a change of environmental conditions and thus a modification of competitive interactions and species rankings (BULLOCK 1996, SUDING 2001). The importance and the interaction of these mechanisms with plant life properties decide on how a plant species will respond to a particular grazing regime and how species diversity will develop (BULLOCK & MARRIOTT 2000, BULLOCK et al. 2001, SAATKAMP et al. 2009): As a rule-of-thumb, the response to increased grazing can be characterized as a change from long-lived to short-lived plant species, from tall to low growth forms, from space monopolizers to colonizers, from large-seeded to small-seeded species, from species with large-sized leaves to species with small-sized leaves and from species with low to species with high plasticity and re-growth potential (BULLOCK et al. 2001, HELLSTRÖM et al. 2003, KLEYER et al. 2004, LOUAULT et al. 2005, DIAZ et al. 2007, PLASSMANN et al. 2010).

An overview on plant resistance strategies (either avoidance or tolerance) and the resulting functional types is given in Table 2. Avoidance of defoliation can be achieved by low stature and rosettes (meristems below the reach of grazing animals), by tall stature above the browse line, by biochemical, anatomical or mechanical defenses and by seasonal avoidance (BOKDAM et al. 2001). An additional effect of selective grazing is that avoided plants concurrently profit from the reduction of more competitive and more palatable neighbors. However, the efficiency of these avoidance strategies depends on grazing management. For instance, in year-round pastures, thistles, which are avoided during summer, will be fed on during winter when the fodder supply is getting short.

Plants growing in nutrient-rich habitats often do not avoid herbivory but develop tolerance traits to minimize its detrimental effects (SKARPE & HESTER 2008). Grazing tolerance can be achieved by a) fast regeneration of lost tissue, b) rapid vegetative or generative re-colonization from the bud bank, soil seed bank and/or seed rain or c) tolerance of changed biotic and abiotic conditions caused by herbivores (Table 2).

Species with above-ground runners, typically growing in wet productive pasture communities (e.g. *Ranunculus repens*, *Agrostis stolonifera* and *Potentilla anserina*), are particularly able to search for and quickly propagate into new gaps and thus profit from grazing induced soil disturbances (BULLOCK et al. 1995, SAMMUL et al. 2004). The stoloniferous plant species *Apium repens* even depends on a specific disturbance regime with frequent, but small-sized trampling disturbances, which is almost exclusively realized in flood meadows of large cattle pastures (ROSENTHAL & LEDERBOGEN 2008; Table 3, Photo 3). Frequent extinction and re-colonization result in a strong fluctuation of population density, which generally appears to be a characteristic feature of plant populations in grazed swards (Accordion-succession; OESTERHELD & SALA 1990, BULLOCK et al. 1994). The more efficient re-colonization strategy of *Apium repens* as compared with its tall-growing non-clonal competitors (mainly *Juncus inflexus*) reflects a change in the relative competitive abilities, which depends on differences in propagation speed. Another example of competitive abilities changing with grazing are the effects of soil compaction and water logging by trampling in wet habitats: reduced soil water capacity as a result of trampling gives competitive advantage to plant species that tolerate oxygen deficiency in the soil such as *Juncus effusus* and *Blysmus compressus* (Table 2; SCHRAUTZER et al. 1996, KLEYER et al. 2004).

There are only a few studies available on trampling resistance of plants. According to SUN & LIDDLE (1993), the most important feature accounting for high trampling resistance is high stem flexibility, because this prevents the destruction of meristems. GRABHERR (1982) and COLE (1995) found trampling resistance to be a function of erectness and plant life form, with non-erect grasses being most resistant and chamaephytes and erect forbs being least

Table 2: Avoidance and tolerance strategies of plants associated with grazing impacts in large-scale pasture systems. Plant species are arranged in functional groups (comprising the features life form, growth form, mode of vegetative expansion and physiological attributes) that are typical for grazed open ecosystems. The most important grazing impacts and the ecological effects to which these functional traits are adapted are presented in column 3 (> indicates the process chain from grazing impact to ecological effect).

Tabelle 2: Vermeidungs- und Toleranzstrategien von Pflanzen in großflächigen, extensiven Weiden.
Die Arten sind geordnet nach weidetypischen, funktionellen Gruppen (bestehend aus Lebensformen- und Wuchsformentypen, der Art der vegetativen Ausbreitung und physiologischen Eigenschaften). Charakteristische Weidewirkungen und ihre ökologischen Effekte, auf die die funktionellen Eigenschaften adaptiert sind, finden sich in Spalte 3 (> symbolisiert die Prozesskette zwischen Weidewirkung und ökologischem Effekt).

| Functional group | Habitat | Relevant grazing impacts > ecological effect | Representative plant species | References |
|---|---|---|---|---|
| **Avoidance strategies** | | | | |
| Plants of low stature | All habitats | Reduction of taller plants > reduced competition | *Antennaria dioica, Linum catharticum, Polygala amarella* | 2,9,12,14 |
| Plants with rosettes | All habitats | Reduction of taller plants > reduced competition | *Arnica montana, Hieracium lactucella, Leontodon hispidus, Primula farinosa, Taraxacum palustre* | 2,8,10,12, 16 |
| Plants with mechanical and/or chemical defenses | Low productive, fresh and dry grasslands, heath | Reduction of taller plants > reduced competition | *Crataegus* spp. (juvenile stage), *Gentiana* spp., *Euphorbia cyparissias, Hypericum* spp., *Ononis* spp., *Prunus spinosa, Senecio jacobaea* | 8,17,19 |
| **Tolerance due to efficient regeneration and recolonization strategies** | | | | |
| Plants with stolons | Eutrophic, wet grasslands | Reduction of taller plants, intensive but small-scale soil disturbances > reduced competition, vegetative expansion into gaps | *Agrostis stolonifera, Alopecurus geniculatus, Apium repens, Ranunculus flammula, Trifolium fragiferum* | 4,5,10,13, 14 |
| Small graminoids with rhizomes | Oligo-mesotrophic grasslands | Reduction of taller plants, less intensive soil disturbances than above > reduced competition, vegetative expansion into gaps | *Agrostis capillaris, Carex arenaria, Festuca filiformis* | 2,7,9,10, 13,14,16 |
| Short-lived plants | All grasslands | Heavy soil disturbances > colonization of gaps from diaspores dispersed in time (soil seed bank) or in space | *Bromus racemosus, Medicago minima, Myosurus minimus, Peplis portula, Senecio aquaticus, Trifolium campestre*, *T. dubium* | 1,6,11,12, 15,18 |
| **Tolerance of changed abiotic conditions** | | | | |
| Plants tolerant of waterlogging | Water logged, strongly fluctuating water table | Soil compaction (changing oxic and anoxic conditions) > persistence of temporarily water-logged conditions due to morpho-physiological adaptations | *Blysmus compressus, Carex nigra, C. panicea, Eleocharis uniglumis, Triglochin palustre* | 2,10,11, 12 |
| Floating plant species | Oligo- to mesotrophic calcareous fens | Trampling creates hollows > calcareous oligotrophic water bodies, colonization of less competitive, calciphilous, oligotrophic plants | *Scorpidium scorpioides, Utricularia minor, U. intermedia.* | 2,3 |
| Brown mosses tolerant of (weak) trampling | Transitional mires | Compression of the moss and superficial peat layer, disturbance of *Sphagnum* hummocks > enhancement of calcium-rich groundwater at soil surface, competitive benefit for calciphilous plants | *Bryum pseudotriquetrum, Calliergon trifarium, Campylium stellatum.* | 2,3 |

References: 1, Bullock et al. (1994); 2, Lederbogen et al. (2004); 3, Arnesen (1999); 4, Rosenthal & Lederbogen (2008); 5, Bullock et al. (1994); 6, Rosenthal et al. (1998); 7, Louault et al. (2005); 8, Stroh et al. (2004); 9, von Oheimb et al. (2006); 10, Stammel et al. (2003); 11, Schrautzer et al. (2004); 12, Schley & Leytem (2004); 13, Buttenschøn & Buttenschøn (1982A); 14, Kleyer (2004); 15, Bullock & Marriott (2000); 16, Bakker (1989); 17, Pott (1998); 18, Schwabe et al. (2004A, B); 19, Craig et al. (1992).

Photo 3: *Apium repens* depends on grazing because trampling creates frequent but small-scale soil disturbances and at the same time prevents the competitive superiority of tall growing species, such as *Juncus inflexus*. This type of grazing regime is almost only realized in large low-intensity pastures as in some parts of the pre-alpine region (Upper Bavaria) (photo: G. Rosenthal).

Bild 3: *Apium repens* profitiert von extensiver Beweidung, wie sie z. B. in großflächigen Weiden im Alpenvorland stattfindet. Viehtritt erzeugt häufige aber kleinflächige Bodenstörungen, die die Ausbreitung über Stolonen fördern und gleichzeitig die hochwüchsigen Konkurrenten in Schach halten.

resistant (see also Section 5.2). In pre-alpine pastures the latter were represented among others by *Dactylorhizza incarnata*, *D. maculata*, *Epipactis palustris*, *Polygonum bistorta* and *Phyteuma orbiculare*. In fens, most woody species, forbs and *Sphagnum* species were non-resistant to trampling whereas graminoids such as *Carex panicea*, *Trichophorum cespitosum*, *Equisetum palustre* and *Eriophorum angustifolium* suffered less (Arnesen 1999, Lederbogen et al. 2004). At very low grazer densities trampling selects between species representing the same type of plant life form but representing different trampling tolerances: On sheep trails of the British uplands the dwarf shrub *Calluna vulgaris* was substituted by another, more tolerant dwarf shrub: *Vaccinium myrtillus* (Hester & Baillie 1998).

A specific avoidance mechanism realized in low-intensity pasture systems depends on vegetation structures that are capable of protecting associated plants from grazing such as tree stumps, forest edges and thorny shrubs ('associational resistance'; Bakker et al. 2004) (Fig. 3: area below the curve). The important point is that these less-grazed or even completely ungrazed habitats assure the coexistence of grazing-sensitive plant species which would normally be eliminated from pastures. In upland pastures, it is litter meadow species (*Molinion*), woodland fringe species (*Trifolio-Geranietea*, e.g. *Laserpitium latifolium*, *Fragaria vesca*, *Potentilla sterilis* and *Knautia dipsacifolia*) and species of the forest ground flora (*Querco-Fagetea*, e.g. *Oxalis acetosella*, *Viola reichenbachiana*, *Maianthemum bifolium*, *Aposeris foetida*, *Brachypodium sylvaticum* and *Epipactis helleborine*) that typically profit from that kind of protection (Lederbogen et al. 2004, van Uytvank & Hoffmann 2009). This is also true for tree saplings which, at low grazing intensities can be protected from grazing by thorny shrubs (facilitation by nurse plants; Bakker et al. 2004, Vandenberghe et al. 2009). Characteristic species of the *Molinion*-litter meadows of the Bavarian pre-alpine region which Stammel et al. (2003) found to be completely lacking in small pastures, such as *Veratrum album*, *Rhinanthus glacialis* and *Thalictrum aquilegifolium* were able to coexist in adjacent large pastures (Lederbogen et al. 2004).

## 5. Creation of microsites

### 5.1. Importance of grazing-induced soil disturbances for plant regeneration

Phytodiversity of grasslands largely depends on gap dynamics (Bakker & Olff 2003), which comprise cycles of disturbance, local extinction and colonization (Van der Maarel 1996). As large herbivores induce various kinds of gaps, they are capable of mediating such cyclic regeneration processes and encouraging species with different microsite demands and colonization abilities. Spatial and temporal characteristics of soil disturbances (gap size, timing, duration) determine whether re-colonization is realized more dominantly by plants that originate from the soil seed bank or species with vegetative strategies.

This, consequently determines which species composition will persist or develop in grazed grassland swards (Silvertown & Smith 1988, Bullock & Marriott 2000, Pakeman & Small 2005). Year-round grazing, for instance creates larger gaps than only summer-grazing (Silvertown & Smith 1988) and autumn-grazing creates more persistent gaps than spring grazing (Smith & Rushton 1994) which has significant effects on species abundances: Large gaps are preferably colonized by seed colonizers and small gaps by clonal colonizers (Bullock et al. 1995). The size of gaps also decides on the relative competitive advantages of different seed sizes with large gaps particularly favoring small-seeded species (Milton et al. 1997). Correspondingly, grazing of S-Swedish pastures was found to enhance seedling recruitment with the greatest effect for small-seeded species (Eriksson & Eriksson 1997). The co-incidence of the timing of disturbances and seed dispersal is an important factor determining the species composition of gaps and thus spatial and temporal features of regenerative processes within pastures (Watt & Gibson 1988). For instance, summer-disturbed plots had higher rates of re-vegetation and a lower proportion of forbs than winter-disturbed plots which were more dominantly influenced by the soil seed bank (Pakeman & Small 2005).

The interaction of grazing intensity and plant community productivity has been highlighted by Proulx & Mazumder (1998). According to them, highest species diversity is correlated with intermediate to high grazing intensities in productive habitats, but with low grazing intensities in unproductive habitats where the general availability and the persistence of gaps is higher (Kull & Zobel 1991). In productive grassland vegetation, intensive disturbances by animals reduce competition and increase seedling recruitment and small-scale species diversity (Leutert 1983, Milton et al. 1997, Edwards & Crawley 1999), because the density of safe sites is the major constraint for seedling recruitment and increase of species diversity, particularly after some years of abandonment (Oesterheld & Sala 1990, Losvik 1999, Hellström et al. 2003, Pakeman & Marriott 2010). Hence, re-introduction of grazing supports the re-establishment of plant species and the restoration of species-rich grasslands on abandoned sites, with major effects in productive habitats (Losvik 1999, Hellström et al. 2003, Pykälä 2005, Rasran et al. 2007, Marriot et al. 2009).

### 5.2. Trampling effects in large pastures

One major contribution of recent research projects is that the importance of trampling has come more into focus. Influences on the population dynamics of plant species by trampling have so far been underestimated. Trampling effects on plant communities are omnipresent on pastures, and influence as well plant communities in areas where feeding does not take place (Hobbs 2006). Trampling is closely linked to diaspore dynamics: it leads to diaspore burial, activation of soil seed banks and cracking of diaspore-containing faeces pellets. In many cases, these processes facilitate diaspore establishment (Eichberg et al. 2005, Wessels-de Wit & Schwabe 2010, Faust et al. 2011).

Areas providing food, water, salt and shade for animals are highly impacted by trampling. A feature of large pastures is the occurrence of livestock trails linking these sites. Von Oheimb et al. (2006) measured a quickly established and expanding trail system after re-introduction of low-intensity grazing on dry grassland pastures, which, after five years,

Table 3: Examples of grazing-induced soil disturbances and their importance for germination and establishment of plant species in different plant communities of large-scale pasture systems.

Tabelle 3: Beispiele von beweidungsbedingten Bodenstörungen und ihre Bedeutung für Keimung und Etablierung von Pflanzenarten in verschiedenen Pflanzengesellschaften großsflächiger Weidesysteme.

| Grazing-induced soil disturbances and microstructures | Affected plant communities (examples) | Effects on germination and establishment | Representative plant species | References |
|---|---|---|---|---|
| Artificially created cattle hoof prints | Calcareous fens (*Caricion davallianae*) | High abundances of sexually reproduced rosette plants at hoof print edges (no germination at bottom) | *Drosera rotundifolia, Galium uliginosum, Linum catharticum, Primula farinosa* | 1 |
| Hummock-hollow complexes | Calcareous fens (*Caricion davallianae*) | High abundances of sexually reproduced rosette plants at hummock edges | *Parnassia palustris, Pinguicula vulgaris, Primula farinosa* | 2 |
| Trampled flood swards, large disturbances | Eutrophic wet grasslands (*Potentillion anserinae*) | High abundances of stoloniferous grasses and sexually reproduced herbaceous annuals | *Agrostis stolonifera, Glyceria fluitans, Persicaria hydropiper* | 3 |
| Trampled flood swards, small-sized disturbances | Wet grasslands (*Potentillion anserinae, Nano-cyperetalia*) | Strong population fluctuations. Local extinction and re-colonization by means of stolons | *Apium repens, Blysmus compressus, Cyperus flavescens, Trifolium fragiferum* | 4, 5 |
| Sheep trails | Inland sand vegetation (*Sedo-Scleranthetalia*) | Increased species abundances of annuals | *Arenaria serpyllifolia, Erodium cicutarium, Medicago minima, Trifolium campestre* | 6 |
| Donkey wallows | Inland sand vegetation (*Sedo-Scleranthetalia*) | Increased cover of mainly annuals | *Arenaria serpyllifolia, Erodium cicutarium, Silene conica* | 7, 8 |
| Eroded sand slopes (increased shearing forces) | Mesotrophic acidic grasslands (*Cynosurion*) | Safe sites for herbs of less productive habitats and pioneer species | *Aira praecox, Betula pendula, Hieracium pilosella, Ornithopus perpusillus, Vulpia bromoides* | 9 |
| Grazing induced increase of ant and mole hills | Mesotrophic acidic grasslands (*Cynosurion*) | Safe sites for the germination and establishment of dry grassland pioneer species | *Arenaria serpyllifolia, Erophila verna, Spergula morisonii, Teesdalia nudicaulis* | 9, 10, 11 |

References: 1, Stammel & Kiehl (2004); 2, Lederbogen et al. (2004); 3, Sach & Schrautzer (1994); 4, Rosenthal & Lederbogen (2008); 5, Barth et al. (2000); 6, Eichberg et al. (2008); 7, Süss (2006); 8, Süss & Schwabe (2007); 9, von Oheimb et al. (2006); 10, Jentsch (2004); 11, Leutert (1983).

added up to 300 km total trail length on 220 ha. The importance of these trails for plant and animal diversity derives from both their network structure and their microsite function. Reduced litter and vegetation cover favors as well insects (like ground beetles, Von Oheimb et al. 2006) as the seedling emergence and establishment of subordinate plant species from the soil seed bank and/or from diaspores that have been transported by the herbivores themselves (Section 3). On sandy grassland paddocks that were used for only short periods per year, sheep trails covered nearly 1 % of the paddock area and led to an increase of mainly habitat-typical, small stature annuals (e.g. *Medicago minima*, *Trifolium campestre* and *Vulpia myuros*) compared to the less-trampled surrounding grazing area (Eichberg et al. 2008; Table 3, Photo 4). Sonnenburg & Gerken (2004) could show that bryophyte species such as *Anthoceros agrestis, Phaeoceros laevis* and *Jungermannia gracillima* disperse from grassland areas into forest areas along trampling trails of a mixed horse/cattle herd.

Indirectly induced soil disturbances are ant and mole hills which increased from 20,000 to 70,000 (per 220 ha and five years) and from 35,000 to 150,000, respectively, on dry sandy soils following the re-introduction of a low-intensity grazing regime with sheep and cattle (VON OHEIMB et al. 2006; Table 3). The occurrence of ant hills can initialize the development of hummock pastures where low-intensity grazing causes a strong differentiation of species assemblages between hummocks and depressions. In pre-alpine dry calcareous hummock pastures small-growing species like *Gentiana clusii, Thymus polytrichus* and *Antennaria dioica* inhabited intensively grazed hummocks, whereas grazing-prone, tall-growing species such as *Astrantia major* and *Trollius europaeus* occurred in the non-grazed depressions (GUTSER & KUHN 1998).

The importance of soil moisture gradients for the inverse correlation between foraging and trampling impacts and their relevance for the micro-topography and species diversity have seldom been considered till now. Wet organic soils are not only more vulnerable to soil wounding than dry soils but also are plastically deformable (HOBBS 2006). Trampling initiates the molding of a micro-relief, which depends on a positive feedback between increased trampling and erosion of hollows, and gradually reduced trampling on initial hummocks. Extensive hummock-hollow complexes are characteristic features of old, wet low-intensity pastures, which has been demonstrated for both calcareous fens in South Germany and acidic fens in northern Germany (QUINGER et al. 1995, VOSS 2001, LEDERBOGEN et al. 2004; Photo 5). Such complexes represent distinct environmental gradients (soil moisture, micro climate) which are responsible for pronounced floristic gradients. Hollows suffer high trampling but low feeding impacts, whereas the reverse is true for hummocks. The micro-climatically favored edges of hummocks provide exceptionally suitable conditions for small-growing and light-demanding rosette species (e.g. *Gentiana clusii, Tofieldia calyculata, Primula farinosa* and *Pinguicula alpina* in pre-alpine calcareous fens; Table 3). Hollows represent wet, shady and frequently disturbed habitats, which inhibit germination and require efficient vegetative regeneration strategies (rhizomes, stolones) as realized by, e.g. *Eleocharis uniglumis,*

Photo 4: Sheep trail on a ruderalized sandy paddock (the photo has been taken shortly after the grazing period; Darmstadt region, Germany, July 2007) (photo: C. Eichberg).
Bild 4: Schaf-Weidepfad auf einer ruderalisierten Sandfläche (das Photo wurde kurz nach der Weideperiode aufgenommen).

Photo 5: Hummock-hollow complexes are characteristic features of old, wet low-intensity pastures (here: calcareous fens in Upper Bavaria). Hummock edges provide micro-climatically suitable conditions for small-growing and light-demanding rosette species (photo: G. Rosenthal).

Bild 5: „Bult-Schlenken"-Komplexe sind charakteristisch für extensive Feuchtweiden mit langer Nutzungstradition (hier: Kalkflachmoore in Oberbayern). Die Bultflanken stellen mikroklimatisch begünstigte Standorte für kleinwüchsige, lichtbedürftige Rosettenarten dar.

Photo 6: Shallow hollows created by trampling of cattle in a transitional fen. The calcareous, oligotrophic water body provides habitats for rare plant species such as *Scorpidium scorpioides* and *Utricularia minor* (photo: G. Rosenthal).

Bild 6: Durch Viehtritt entstandene, mit Wasser flach überstaute Flutmulden in einem Übergangsmoor. Das kalkreiche, nährstoffarme Wasser bietet geeignete Standorte für seltene Pflanzenarten, wie z. B. *Scorpidium scorpioides* und *Utricularia minor.*

*E. quinqueflora* and *Carex viridula* ssp. *oederi* (VOSS 2001, LEDERBOGEN et al. 2004). As opposed to the results of STAMMEL & KIEHL (2004) from seeding experiments with single hoof prints, extensive hummock-hollow complexes thus provide beneficial germination and establishment sites for a diverse plant community on a small spatial scale (Table 3).

In contrast to the relief forming processes in fens, grazing of transitional bogs has a contrary effect, where trampling inhibits the growth of *Sphagnum* hummocks and supports fen species (e.g. *Carex hostiana* and *C. lepidocarpa*) through soil compaction and increased influence of minerotrophic groundwater. It even creates persistent shallow hollows with a calcareous, oligotrophic water body which is a habitat for rare bryophytes such as *Scorpidium scorpioides* and *Calliergon trifarium*, as well as for vascular species such as *Utricularia minor* and *U. intermedia* (Photo 6; WELCH 1997, ARNESEN 1999, LEDERBOGEN et al. 2004). It can be concluded that low-intensity grazing of mires is capable of increasing the small-scale habitat and species diversity and should therefore not be rejected as a management option for mires (GROOTJANS et al. 2002, HOBBS 2006).

### 5.3. Wallows

Wallows are further important examples for livestock-induced soil disturbances that promote the regeneration of mainly subordinate, short-lived plant species. SÜSS & SCHWABE (2007) revealed that donkey wallows in mid-successional stages of inland sand grassland in Germany significantly enhanced the cover values of several target (e.g. *Arenaria serpyllifolia*) and ruderal pioneer species (e.g. *Chenopodium album*), leading to a diversity increase as compared to control areas (Table 3). In wet grasslands, pig-induced wallows are preferential habitats of several plant species: Annuals with a long-term persistent soil seed bank (e.g. *Cyperus fuscus*) accumulated, as did perennial clonal plants (e.g. *Gratiola officinalis*) (POSCHLOD et al. 2002).

### 5.4. Faeces deposits

Plant colonization of faeces deposits depends on both direct effects (embedded endozoochorous diaspores) and indirect effects (physical covering of established plants, nutrient input). In mid-successional stages of inland sand ecosystems, SÜSS & SCHWABE (2007) revealed a high nutrient input on faeces accumulation sites of donkeys (223 kg N $ha^{-1}$), leading to a promotion of nitrophilous and a suppression of target plant species. By contrast, on sheep faeces deposits (290–380 kg N $ha^{-1}$) in pioneer stages of inland sand vegetation, no such ruderalization process was observed, even though diaspores of competitive species were highly abundant in the sheep faeces (EICHBERG et al. 2007). In this study, only stress-tolerant, site-typical plant species were able to establish in low numbers after germinating directly out of faeces, indicating the importance of environmental filters for the final outcome of diaspore distribution. Evidence for environmental establishment constraints has been found also in a Dutch coastal grazing system, where cattle transferred seeds endozoochorously between dune and salt marsh vegetation but no inter-habitat establishment could be observed (BAKKER et al. 2008).

Generally, large faeces deposits (especially cattle dung pats) or faeces accumulation sites (latrines of equids) have stronger effects on local vegetation development than small deposits with multi-pellet form (e.g. sheep faeces deposits). The reasons might be that large deposits have higher destructive effects on the resident vegetation (gap creation), are less prone to desiccation, are in better contact to the soil and often contain higher amounts of viable dia - spores than faeces pellet deposits (MOUISSIE et al. 2005). Another precondition for faeces deposits serving as safe sites for plant species is the presence of low-competition surroundings (e.g. bare-soil gaps; COSYNS et al. 2006) because species of the resident vegetation quickly re-colonize faeces sites (WELCH 1985).

Dung beetles can strongly influence the distribution of nutrients and the fate of diaspores embedded in livestock faeces by deep burial of large portions of faeces deposits (D'HONDT et al. 2008, EICHBERG & WESSELS-DE WIT 2011). In many cases this will lead to reduced germination chances for endozoochorously dispersed diaspores.

## 6. Secondary progressive and regressive successions in large pastures

A specific management target involved with the implementation of large low-intensity pastures is the development of a patchy mosaic of different vegetation structures, which results in an increase of landscape heterogeneity (KLEYER et al. 2004, LEDERBOGEN et al. 2004, STROH et al. 2004). This Section illustrates successional processes which in general contribute to enhance heterogeneity of the vegetation structure in low-intensive pastures. Furthermore, results are presented concerning the development of the vegetation during the first years after introduction of large-scale grazing.

The compilation in Table 4 shows some examples how grazing modifies the pathways of undisturbed progressive successions with distinct impacts on landscape structure. On preferably grazed sites (e.g. mineral soils of common pastures of the alpine foothills in Southern Bavaria), progressive successions occur only on a small spatial scale following the mechanism of 'associational resistance' (BAKKER et al. 2004, SMIT et al. 2005). It allows grazing-sensitive tree species of later successional stages (e.g. *Picea abies*) to establish in the shelter of spiny bushes (e.g. *Crataegus monogyna*, *Prunus spinosa*) which established on temporarily ungrazed patches of the grassland sward (VANDENBERGHE et al. 2009). This type of local facilitation (CONNEL & SLATYER 1977) results in a semi-open, park-like landscape (grassland intermixed with single trees, bushes and forest islands) (VERA 2000, BAKKER et al. 2004, LEDERBOGEN et al. 2004). Grazing-induced facilitation is also realized in the succession of fen grasslands towards alder carrs (*Alnion glutinosae*) in calcareous fens (Table 4). A reduced grazing intensity due to low fodder values combined with a high trampling impact facilitates the germination and establishment of alder (*Alnus glutinosa*) particularly at the edge of hummocks.

However, selective grazing may also result in inhibition mechanisms. As opposed to the case of fen succession, and because trampling destroys *Sphagnum* hummocks (WELCH 1997, WAGNER 2000), low-intensity cattle grazing in transitional bogs (*Caricion lasiocarpae*) inhibits the succession (detrophication) towards ombrotrophic plant communities. Such trampling stabilizes minerotrophic stages of *Caricion lasiocarpae* communities consisting of

Table 4: Succession processes on large-scale pastures induced by low-intensive grazing of large herbivores. Mechanisms according to CONNEL & SLATYER (1977).

Tabelle 4: Durch große Weidetiere gesteuerte Sukzessionsprozesse in großskaligen, extensiv genutzten Weidesystemen. Bezeichnung der Mechanismen nach CONNEL & SLATYER (1977).

| Type of succession | Initial successional stage | Successional trend, mechanism | Successional stage attained with low-intensity grazing | References |
|---|---|---|---|---|
| „Thorny shrub" succession | *Cynosurion*, *Genistion pilosae* | progressive, facilitation | *Cynosurion*, *Genistion pilosae* spatial complex with *Prunetalia* communities | 1,2,3,4,5 |
| Carr succession, establishment of alders | *Caricion davallianae*, *Calthion* | progressive, facilitation | *Alnion glutinosae* | 5,6 |
| Detrophication and development of bogs | *Caricion lasiocarpae* | stabilization | *Caricion lasiocarpae* | 5 |
| Development of stages with dominant rhizomatous herbaceous plant species | a *Calthion*<br>b *Cynosurion* | progressive, inhibition of forest succession | a *Magnocaricion*, *Filipendulion*<br>b *Aegopodion* | 6 |
| Breaking of dominance | a *Magnocaricion*<br>b *Aegopodion*<br>c *Calamagrostis epigejos* stage | regressive | a *Calthion*<br>b *Cynosurion*<br>c *Koelerion glaucae* | 6,7,8 |

References: 1, BUTTENSCHØN & BUTTENSCHØN (2001); 2, OLFF et al. (1999); 3, HOLSTEN (2003); 4, BAKKER et al. (2004); 5, LEDERBOGEN et al. (2004); 6, SCHRAUTZER et al. (2004); 7, SÜSS et al. (2004); 8, SCHWABE et al. (2004a, b).

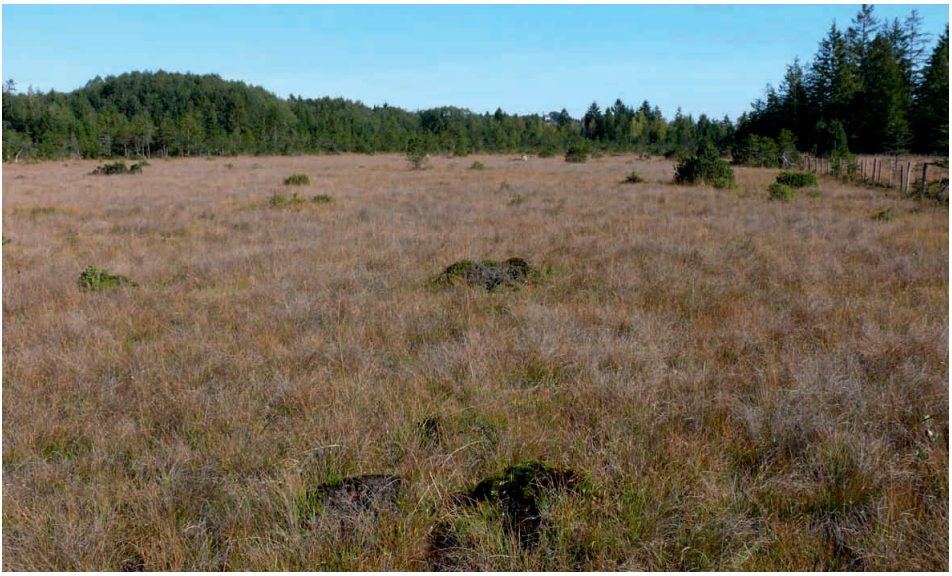

Photo 7: Minerotrophic stages of *Caricion lasiocarpae* communities with a mosaic of remnant *Sphagnum* hummocks, water filled hollows and brown moss vegetation. Minerotrophic conditions are stabilized by soil compaction due to cattle trampling (photo: G. Rosenthal).

Bild 7: Minerotrophes Stadium der *Caricion lasiocarpae*-Gesellschaft mit einem Mosaik aus reliktären Torfmoosbulten, Flutmulden und Braunmoos-Teppichen. Die minerotrophen Bedingungen werden durch trittbedingte Bodenverdichtung stabilisiert.

a mosaic of remnant hummocks, water-filled hollows and brown moss vegetation (Photo 7, LEDERBOGEN et al. 2004). In wet eutrophic grasslands (*Calthion*), inhibition occurs in dominant patches of unpalatable species (e.g. *Carex acutiformis*). They develop species-poor, persistent, non-woody successional stages, which not only reduces local plant species richness, but also inhibits further progressive succession to forests (DIEMER et al. 2001, LOUAULT et al. 2005, SCHRAUTZER & JENSEN 2006, ROSENTHAL 2010a).

Grazing is also capable of supporting regressive successions and breaking the dominance of tall-growing rhizome species which characterize for instance plant communities of the *Magnocaricion* (Table 4, Photo 8). This kind of succession leads to a degradation of the vegetation structure ('retrogression' sensu GLAVAC 1996) and thus enhances the habitat (light) conditions for low-growing species.

Short-term effects of low-intensity grazing have been demonstrated in an experimentally re-installed large cattle pasture on wet grassland sites in northern Germany. On the community scale, grazing involved both progressive and regressive successions, which resulted in an increase of vegetation heterogeneity within only a few years (Fig. 4). Some species-poor, previously intensively used *Potentillion anserinae* stands passed into more species-rich *Calthion* stands.

Changes in vegetation structure and the development of a spatial mosaic of successional stages on low-intensive pastures imply the broadening of environmental and floristic gradients (Photo 9). Thus, in large old pastures of southern Germany, β- and γ-diversities are significantly higher when all successional stages are considered (Fig. 5A, B; ROSENTHAL 2010b). The γ-diversity increased by ca. 30 % when late stages (forests) occur in addition to early stages (*Cynosurion* and *Calthion* communities). The loss of each of these successional stages, e.g. due to abandonment or deforestation, would lead consequently to a decrease of β- and γ-diversities. In contrast to the existing complete series of successional stages in old traditional South German pastures, recently established large pastures in northern Germany still lack the late stages. Hence, β- and γ-diversities were significantly lower (Fig. 5C, D).

Photo 8: Grazing cattle invade *Magnocaricion* communities from drier habitats at the valley edges and reduce dominant tall growing *Carex acutiformis* and *Glyceria maxima*. New established large pasture in the Eider valley (Schleswig-Holstein, Germany) (photo: J. Schrautzer).

Bild 8: Weidevieh dringt in *Magnocaricion*-Gesellschaften von trockeneren, am Rande der Aue gelegenen Standorten her ein und reduziert hochwüchsige Arten wie *Carex acutiformis* und *Glyceria maxima*. Neu eingerichtete großflächige gemeinschaftliche Weide im Eidertal (Schleswig-Holstein).

Photo 9: Large-scale grazing creates heterogenous landscapes. Spatial mosaics consisting of different succession stages provide manifold habitats allowing a high species diversity (Hessisches Ried, Germany) (photo: C. Eichberg).

Bild 9: Großflächige extensive Beweidung erzeugt heterogene Landschaftsstrukturen. Räumliche Mosaike aus verschiedenen Sukzessionsstadien stellen vielfältige Mikrostandorte für eine hohe Artendiversität zur Verfügung (Hessisches Ried).

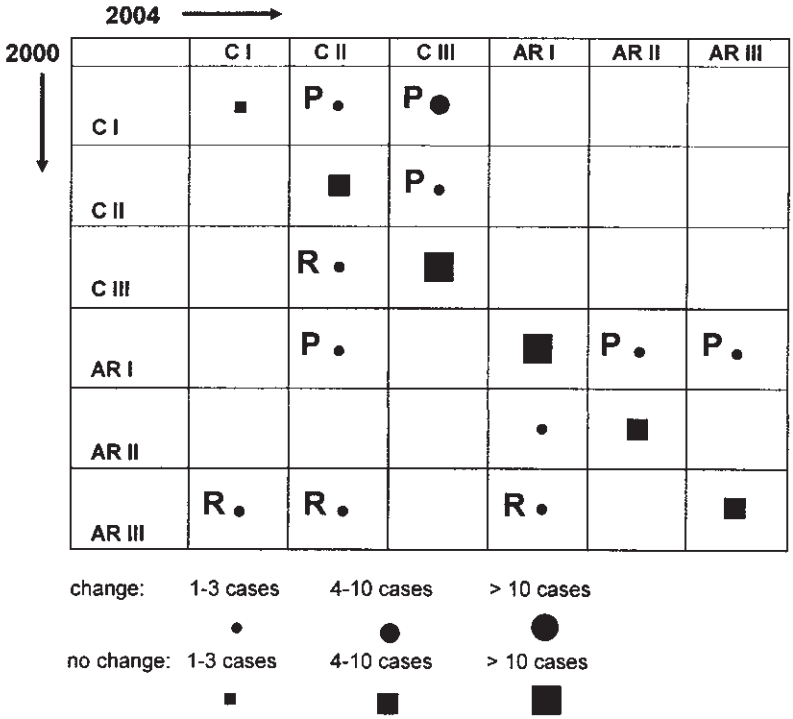


Fig. 4: Vegetation dynamics (years 2000–2004) on permanent plots (25 m$^2$, n = 105) in fen areas of three cattle pastures of the Eider valley, Germany. The matrix is read in each row from left (initial type 2000) to right (types 2004), e.g. in 4–10 cases C I changed to C III. C: *Calthion*, AR: *Potentillion anserinae*. Successional stages (I–III) are characterized by low dominance of tall-growing species (I); high dominance of tall-growing species (> 35 % coverage) (II); and the immigration and establishment of herbaceous ruderal species (e.g. *Urtica dioica*) (III). P: progressive succession, R: regressive succession; after JENSEN & SCHRAUTZER (1999).

Abb. 4: Vegetationsdynamik (Jahre 2000 bis 2004) auf Dauerflächen (25 m$^2$, n = 105) in Niedermooren von drei Weiden im Eidertal (Deutschland). Die Matrix zeigt in jeder Reihe die Veränderung der Vegetationstypen von links (initiale Typen 2000) nach rechts (Typen 2004), z. B. wandelt sich C I in 4–10 Fällen in C III um. C: *Calthion*, AR: *Potentillion anserinae*. Die Sukzessionsstadien (I–III) werden durch geringe Deckungsgrade hochwüchsiger Arten (I), die Dominanz hochwüchsiger Arten (> 35 % Deckung) (II) und die Einwanderung und Etablierung krautiger Ruderalarten (z. B. *Urtica dioica*) (III) charakterisiert. P: progressive Sukzession, R: regressive Sukzession; nach JENSEN & SCHRAUTZER (1999).

However, short-term successions observed for only four years in permanent plots not only indicated an increase of structural diversity (Fig. 4), but also a (slight) increase of β- and γ-diversities. Such short-term positive effects were also shown by PYKÄLÄ (2003) from a comparison of different-aged pastures in Finland.

The control of dominant non-woody plant species, which have the potential of developing species-poor persistent stages, is an important issue of nature conservation in order to avoid further spread into adjacent earlier successional stages consisting of light-demanding species (SCHRAUTZER & JENSEN 2006). Some of the most problematic plant species in low-intensity grazing systems in Central Europe are presented in Table 5 (Photo 10). Decreasing their competitive vigor must aim at disrupting internal nutrient allocation, biomass accumulation and propagation (ROSENTHAL 2010a). The efficiency of grazing in achieving this target correlates with the frequency of defoliation and trampling during the growing season, with temporarily high stocking rates being more efficient than long-term grazing at low intensities (GRANT et al. 1996, BAKKER 1998, LOUAULT et al. 2005).

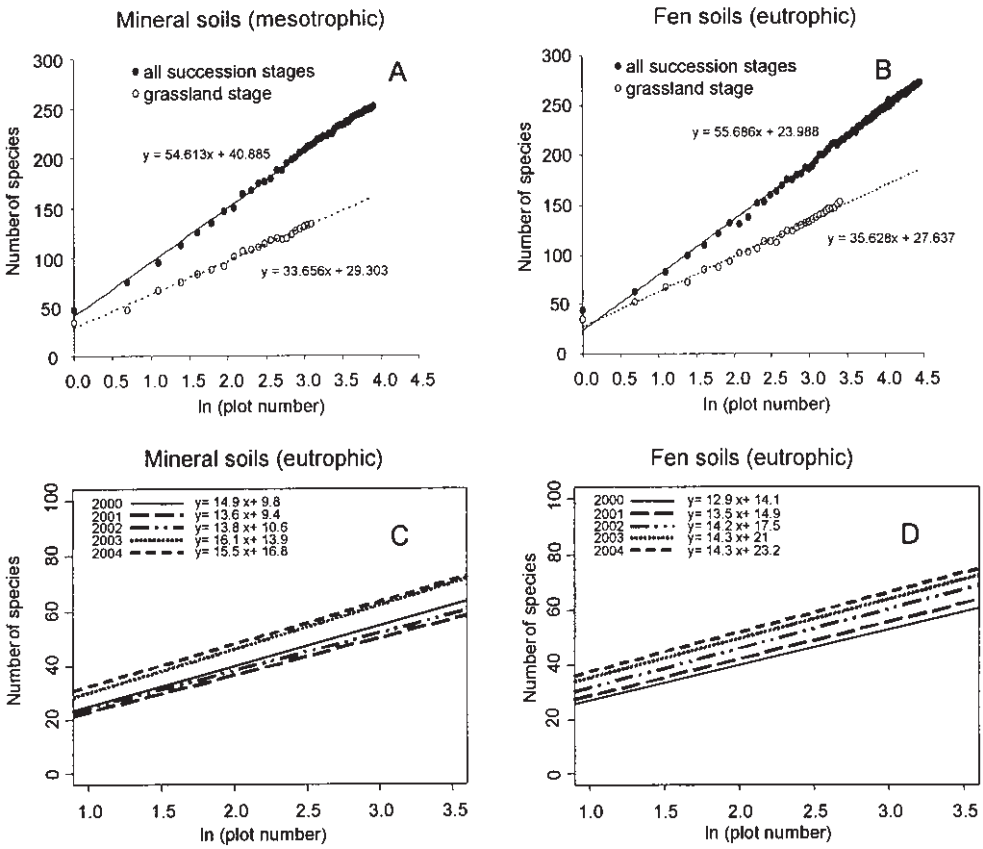


Fig. 5: Species-area curves of ecotones and time series, respectively, using the model of species diversity of RICOTTA et al. (2002). We used data from several-hundred-year-old, pre-alpine common pastures in southern Germany, Upper Bavaria (A, B) and young, recently established pastures in northern Germany, Eider valley (C, D). Habitat types: A: ecotones from mesotrophic mineral soils (grassland stage = mesotrophic *Cynosurion* communities, later successional stages = *Berberidion* and *Fagion* communities), B: ecotones from eutrophic fen soils (grassland stage = *Calthion*, later successional stages = *Alno-Ulmion* communities), C: time series from eutrophic *Cynosurion* habitats (2000–2004), D: time series from eutrophic *Calthion* habitats (2000–2004). Y [number of species] = β-diversity * ln (no. of plots) + -diversity. The α-diversity represents the species richness of equal-sized homogenous plots. The β-diversity represents the slope of the species-area curve and the increase of species richness while increasing the plot number. The γ-diversity represents the total species richness. Data basis: A, B (vegetation relevés from ecoton transects à 25 $m^2$; A: n = 50, B: n = 86); C, D (permanent plots à 25 $m^2$; C: n = 25, D: n = 40); after IRMLER et al. (2010) and ROSENTHAL (2010b).

Abb. 5: Arten-Areal-Kurven von Ökotonen und Zeitreihen nach dem Diversitätsmodell von RICOTTA et al. (2002). Die Daten stammen von jahrhundertealten süddeutschen Allmendweiden (A, B) und von norddeutschen, in jüngerer Zeit eingerichteten Weiden (C, D). Habitattypen: A: Ökotone von mesotrophen Mineralböden (Grünlandstadium = mesotrophe *Cynosurion*-Gesellschaften, späte Sukzessionsstadien = *Berberidion*- und *Fagion*-Gesellschaften), B: Ökotone von eutrophen Niedermoorbereichen (Grünlandstadium = *Calthion*, späte Sukzessionsstadien = *Alno-Ulmion*-Gesellschaften), C: Zeitreihen von eutrophen *Cynosurion*-Flächen (2000–2004), D: Zeitreihen von eutrophen *Calthion*-Flächen (2000–2004). Y [Artenzahl] = β-Diversität * ln (Flächenanzahl ) + α-Diversität. Die α-Diversität repräsentiert die Artenzahl homogener, gleichgroßer Flächen. Die β-Diversität wird durch die Steigung der Arten-Areal-Kurve und den Anstieg der Artenzahl mit zunehmender Flächenanzahl ausgedrückt. Die γ-Diversität repräsentiert die Gesamtartenzahl. Datengrundlage: A, B (Vegetationsaufnahmen von Transekten à 25 $m^2$; A: n = 50, B: n = 86); C, D (Dauerflächen à 25 $m^2$; C: n = 25, D: n = 40); nach IRMLER et al. (2010) und ROSENTHAL (2010b).

Table 5: Competitive plant species that have the potential of becoming dominant under low-intensity grazing and grazing regimes that successfully reduced their dominance. Plant strategies and plant height according to GRIME et al. (2007) (C, competitor; SC, stress tolerant competitor; CR, competitive ruderal; CSR, CSR-strategist), growth forms according to SCHIEFER (1981) (rept rhiz: propagation by means of rhizomes, cesp: building tussocks).

Tabelle 5: Konkurrenzstarke, zur Dominanzbildung befähigte Pflanzenarten und Beweidungsregimes, die zur Verdrängung derselben geeignet sind. Pflanzenstrategien und Wuchshöhen nach GRIME et al. (2007), Wuchsformen nach SCHIEFER (1981) (rept rhiz: Ausbreitung durch Rhizome, cesp: horstbildend).

| Species | Plant life strategy, growth form, height (cm) | Target community | Appropriate measure to control dominance | References |
|---|---|---|---|---|
| **Dry to semi-moist grasslands/heathlands** | | | | |
| *Brachypodium pinnatum* | SC, rept rhiz, 30-60 | *Bromion erecti* | short-term intensive goat grazing | 1 |
| *Calamagrostis epigejos* | C/SC, rept rhiz, 60-100 | Mesotrophic *Cynosurion*, *Koelerion glaucae*, *Allio-Stipetum* | low-intensity sheep grazing, mixed sheep/cattle grazing, intensive sheep grazing | 2,3,4 |
| *Elymus repens* | C/CR, rept rhiz, 30-60 | Mesotrophic *Cynosurion* | low-intensity sheep/cattle grazing | 3 |
| *Pteridium aquilinum* | C, rept rhiz, 100-180 | Mesotrophic *Cynosurion*, *Genistion pilosae* | no success, neither with low-intensity nor intensive grazing | 3,4 |
| *Urtica dioica* | C, rept rhiz, 100-150 | Mesotrophic *Cynosurion* | low-intensity cattle grazing | 5 |
| **Moist to wet grasslands/fens** | | | | |
| *Carex acutiformis* | C/SC, rept rhiz, 100-150 | *Calthion* | low-intensity cattle grazing | 5 |
| *Deschampsia cespitosa* | SC/CSR, cesp, 50-120 | Acidic *Molinion* | low-intensity horse grazing | 6 |
| *Juncus effusus* | C/SC, cesp, 30-150 | *Calthion*, acidic *Molinion* | intensive grazing, preferably by horses | 6 |
| *Juncus inflexus* | SC, cesp, 30-150 | *Calthion*, wet *Cynosurion* | intensive grazing, preferably by horses | 7 |
| *Molinia caerulea* | SC, cesp, 45-120 | *Caricion nigrae* | low-intensity cattle grazing, intensive sheep and goat grazing | 4,8 |
| *Phragmites australis* | C, rept rhiz, 100-300 | *Caricion davallianae*, *Calthion* | low-intensity cattle grazing | 7 |

References: 1, RAHMANN (2000); 2, SCHWABE et al. (2004A,B); 3, OHEIMB et al. (2006); 4, BURKART (2006); 5, SCHRAUTZER et al. (2004); 6, ROSENTHAL (1992); 7, LEDERBOGEN et al. (2004); 8, WITTIG (1999).

Effective reduction of dominant grass or herb species has been demonstrated in different European grassland ecosystems (Fig. 6A, Photo 10 and 11). This creates open space for germination and establishment of less competitive species, which results in an almost immediate increase of α-diversity (Fig. 6B). Thus, species numbers of light-demanding *Festuco-Brometea* species increased in calcareous grasslands (RAHMANN 2000), of *Sedo-Scleranthetealia* species in sandy grasslands (SCHWABE et al. 2004b), of *Caricion nigrae* species in wet heath lands (WITTIG 1999) and of *Molinietalia* species in fen grasslands (SCHRAUTZER et al. 2004) (Fig. 6B). This increase evolves asymptotically as observed in Danish large pastures, where six years after the re-introduction of grazing, species richness remains more or less constant (HALD & VINTHER 2000, VAN UYTVANCK et al. 2008).

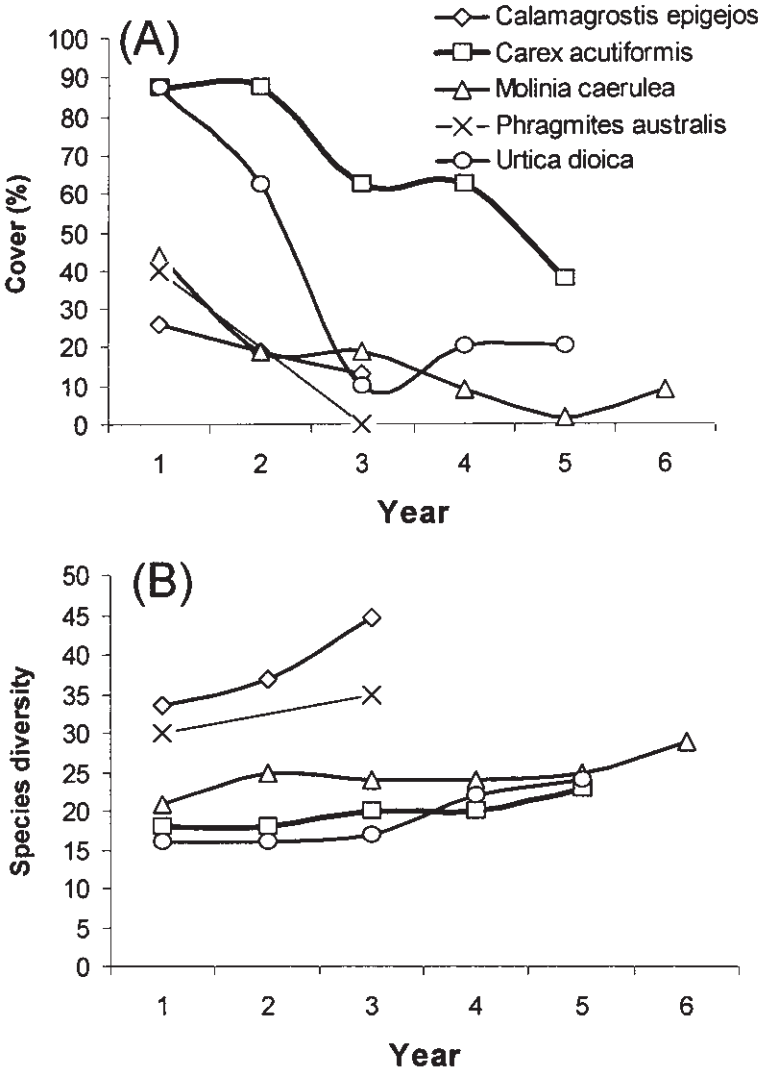


Fig. 6: Examples of successful dominance control by means of low-intensity grazing on large-scale pasture systems from different parts of Germany. (A) cover percentages and (B) species diversities on permanent plots from different study sites which were recorded for 3–6 years. Development of *Calamagrostis epigejos* populations on sheep-grazed inland dunes in the Upper Rhine Valley (*Allio-Stipetum* complex; SCHWABE et al. 2004a), *Phragmites australis* on a cattle pasture in Upper Bavaria (*Caricion davallianae*; LEDERBOGEN et al. 2004), *Carex acutiformis* and *Urtica dioica* on a cattle pasture in Schleswig-Holstein (*Calthion* and *Cynosurion*, respectively; SCHRAUTZER et al. 2004) and *Molinia caerulea* on a cattle pasture in Lower Saxony (*Caricion nigrae*; WITTIG 1999).

Abb. 6: Beispiele erfolgreicher Dominanzkontrolle in großflächigen Extensivweiden aus unterschiedlichen Gebieten Deutschlands. (A) Deckungsgrade und (B) Artenvielfalt auf Dauerflächen von unterschiedlichen Standorten, die 3–6 Jahre lang untersucht wurden. Die Entwicklung von *Calamagrostis epigejos*-Populationen auf mit Schafen beweideten Binnendünen der Oberrheinebene (*Allio-Stipetum* complex; SCHWABE et al. 2004a), *Phragmites australis* auf einer Rinderweide in Oberbayern (*Caricion davallianae*; LEDERBOGEN et al. 2004), *Carex acutiformis* und *Urtica dioica* auf einer Rinderweide in Schleswig-Holstein (*Calthion* und *Cynosurion*, SCHRAUTZER et al. 2004) und *Molinia caerulea* auf einer Rinderweide in Niedersachsen (*Caricion nigrae*; WITTIG 1999).

Photo 10: Low-intensity cattle grazing reduces dominant populations of *Phragmites australis* (calcareous fens in Upper Bavaria): the left hand side of the fence represents fen vegetation where grazing had been re-introduced three years before; the right hand side represents the reference which was not grazed (photo: G. Rosenthal).

Bild 10: Extensive Rinderbeweidung reduziert dominante *Phragmites australis*-Populationen in Kalkflachmooren Oberbayerns: links des Zauns seit drei Jahren beweidete Flachmoorvegetation, rechts des Zauns die unbeweidete Referenzfläche.

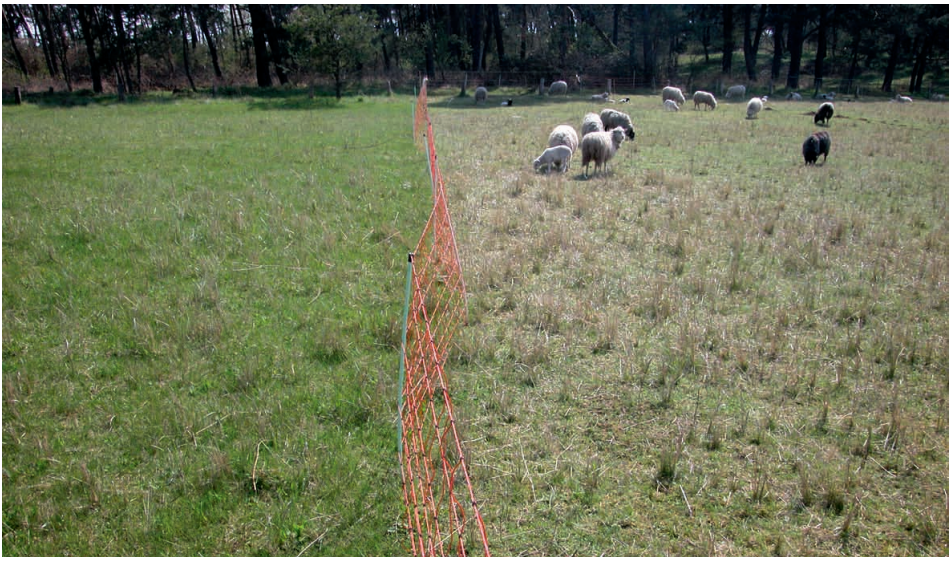

Photo 11: Sheep grazing on a ruderalized sandy paddock (left: paddock part not yet grazed, right: paddock part currently under grazing). Cover of competitive graminoids, such as *Calamagrostis epigejos*, can be reduced by low-intensity grazing (Darmstadt region, Germany, April 2006) (photo: C. Eichberg).

Bild 11: Schafbeweidung auf einer ruderalisierten Sandfläche (links: noch nicht beweidetes Teilstück einer größeren Koppel, rechts: aktuell beweidetes Koppelstück). Die Deckung von Graminoiden, wie *Calamagrostis epigejos*, kann durch Beweidung reduziert werden.

## 7. Conclusions and management implications

Large-scale grazing has many advantages with respect to maintaining or enhancing biodiversity: (i) Characteristics of specific animal behavior and its interaction with specific site conditions (e.g. proportions of different vegetation types) are more distinctly considered as compared to rotational grazing; this opens up new management options (e.g. multi-species grazing) in order to achieve specific goals. (ii) It enhances existing habitat gradients with respect to nutrient and light availability, soil acidity and soil moisture, and generates multiple-disturbance patterns on various spatial scales resulting in a high habitat and hence species diversity (β-, γ-diversity). (iii) It creates extended ecotones, i.e. borderlines between different landscape types (e.g. open land and forest), which is of particular benefit to some animal species with complex structural demands (e.g. birds as *Lanius collurio*, LEDERBOGEN et al. 2004; arthropod groups, IRMLER et al. 2010). (iv) Large domestic herbivores serve as effective vectors for diaspore dispersal improving the connectivity of otherwise widely or totally isolated (threatened) plant populations and the re-colonization of degraded habitats. (v) Chances for fulfilling various nature protection targets in one area are enhanced, e.g. the promotion of threatened plant species from both early and later successional stages.

The latter point, however, has several requirements if these conflicting aims are to be reconciled. On the one hand, size of pasture and herd must allow typical herd behavior to enable the development of a structurally diverse landscape. On the other hand, this bears in many cases the risk of abandonment of less-productive, threatened habitats. Consequently, site-specific management adjustments will be necessary. This can be realized by simultaneously using various herbivore species with different diet preferences (multi-species grazing), by extending the grazing period and enforcing fodder shortages to a certain degree, by (temporarily) subdividing grazing areas in small, successively grazed portions or by additional non-grazing measures such as shrub clearance and mowing. High proportions of productive grasslands stabilize a grazing system as a whole, but again bear the risk of abandonment of less-productive habitats or undesired transfer of nutrients and non-target diaspores from the former to the latter.

As a general conclusion, it should be stressed that an expert management is the key to successfully managing biodiversity by means of low-intensity grazing; it must accurately be adjusted to nature conservation aims and to the natural conditions of the pasture: severe as well as weak grazing pressure over longer time periods can be counterproductive (BUNZEL-DRÜKE et al. 2008, SÜSS et al. 2011). Several invertebrate taxa, for instance, are associated with specific vegetation structures which are given only within grazing regimes that realize an appropriate level of disturbance (TALLOWIN et al. 2005).

There are some further limitations in the concept of large-scale grazing which have to be mentioned: species which require large homogenous habitats, for instance, such as some bird species (e.g. *Vanellus vanellus*), can suffer from a development towards tall vegetation structures (ROSENTHAL et al. 1998). Another limit of the concept is the failure of low-intensity grazing in re-establishing plant diversity on soils with high N concentrations. In heathland ecosystems of NW-Germany, sheep grazing has the potential to compensate atmospheric N inputs, if the animals rest over night in pens (FOTTNER et al. 2007). However, since the net P output is much higher than the net N output, in the long term this grazing system will lead to a shift from N to P limitation which might facilitate competitive grass species (HÄRDTLE et al. 2009). In small populations of threatened plant species, grazing might enhance the risk of local extinction; with respect to species with unidentified grazing tolerance, as a precaution, other management measures should be preferred (BUNZEL-DRÜKE et al. 2008).

The implementation of large-scale grazing systems could contribute to the retardation of the dramatic biodiversity losses co-occurring with the abandonment of land use, e.g. on military training areas, in core areas of nature and biosphere reserves, on commonages of low mountain ranges, and in traditional pasture landscapes. Such landscapes often provide large connected areas and have a high relevance for nature protection. The still ongoing withdrawal of agriculture from marginal sites provides further chances. In Germany, for instance,

4.4 % of the land area would potentially be qualified for the implementation of large, low-intensity pastures, notwithstanding the practical constraints (KALLIES et al. 2003). The recovery of biodiversity via restorative grazing is a very slow process (PYKÄLÄ 2005, MARRIOTT et al. 2009, ROSENTHAL 2010b). Therefore, in every case, the conservation of traditional and existing large-scale grazing systems such as those of the common pastures in the pre-alpine range should be prioritized.

Future research on large-scale pasture systems should focus on (i) long-term succession processes on landscape levels and a mechanistic understanding of succession processes, including changing spatial mosaics, (ii) analyses of herd behavior (especially selectivity and stochasticity) as controlled by herbivore species, breeds, mixed herds and grazing regime, (iii) responses of rare plant species vs. ubiquitous species to grazing, (iv) impacts of livestock zoochory on the genetic level over a broad range of plant species, (v) post-dispersal fate of zoochorously dispersed diaspores, particularly the invasibility of target communities by non-target species and the potential of threatened species to re-colonize restored habitats, (vi) temporal dimensions in restoration of previously intensively used grasslands by means of large-scale grazing, (vi) changes of species diversity at different spatial scales, also with respect to age and biogeographical conditions, and (vii) possibilities and constraints in combining ecological and economic targets as a precondition to guarantee long-term management of many threatened habitats.

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