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REVIEW PAPER

Phytodiversity of temperate permanent grasslands: ecosystem services for agriculture and livestock management for diversity conservation

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Abstract Plant diversity has been reported to increase productivity. Farming practices aiming at conserving or increasing plant diversity are, however, usually less profitable than conventional ones. In this review, we aim to find reasons for this discrepancy, discuss ecosystem services of grassland phytodiversity that are useful for farmers, and ways of livestock management most beneficial for diversity. Under agricultural conditions, a clear effect of species richness on a site's primary or secondary production has not yet been demonstrated. Reasons could be that species numbers in permanent grassland are above the threshold of five species found effective in experimental plots or that the conditions are more in equilibrium with management than in weeded experimental plots. Other diversity effects on production stability, nutrient and water retention or product quality might convince farmers to increase diversity. However, these should be tested in agricultural situations, as most research has again been carried out in experimental plots. To enhance phytodiversity, grazing has been found superior over mowing, as selective grazing, treading and excreta deposition increase the heterogeneity of a sward and thus the niches available. Especially rotational grazing with intermediate intensity may be advantageous for phytodiversity. However, complex interactions between environmental conditions, sward composition, management and livestock behaviour make it difficult to forecast grazing effects. Thus, ecological and agricultural researchers should cooperate more, e.g. either in interdisciplinary projects or by hiring researchers from the respective other profession and thus diversifying research groups, in order to integrate agricultural management into biodiversity research and biodiversity measurements into agricultural research to

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advance our understanding of how to make conservation and enhancement of grassland phytodiversity both feasible and sustainable.

Keywords Grazing · Productivity · Nutrient and water retention · Quality · Selectivity · Treading · Excretion

Introduction

Biodiversity has been increasingly in the focus of scientific and public attention over the past decades, culminating in the United Nations declaring 2010 to be the International Year of Biodiversity. Concerning the role of phytodiversity in grasslands, positive effects on ecosystem services have repeatedly been pointed out. Thus, increased diversity has been suggested to lead to an enhanced production (Bai et al. 2007; Bullock et al. 2007; Dodd et al. 2004; Hector et al. 1999; van Ruijven and Berendse 2003; Weigelt et al. 2009; Yachi and Loreau 1999) as well as to an improved stability, sustainability and efficiency of grassland production systems (Caldeira et al. 2001; Hooper et al. 2005; Hooper and Vitousek 1998; Kahmen et al. 2006; Luck et al. 2003; Niklaus et al. 2006; Oelmann et al. 2007; Roscher et al. 2004, 2008; Scherer-Lorenzen et al. 2003; Tilman et al. 2006; Yachi and Loreau 1999).

Despite such promising research results, grassland farming practices aiming at biodiversity conservation are usually regarded as less economically profitable than conventional practices (Pärtel et al. 2005). In temperate regions, grassland is mostly under agricultural management and grassland phytodiversity has developed over centuries in relation to such management (Bender et al. 2005; Isselstein et al. 2005; Moog et al. 2002; Vallentine 2001). Plant communities here are in dynamic equilibrium with utilisation practices. Without management, most temperate grassland would successionally turn into woodland. A regular utilisation is therefore also required for the protection of species-rich grassland (Moog et al. 2002). However, measures aimed at increasing production have usually led to a decline of biodiversity in grassland areas (Bezák and Halada 2010; Henle et al. 2008; Silvertown et al. 2006).

How can ecologists and farmers come to such diverging views regarding the usefulness of biodiversity for production? Is only one of the views correct? Is phytodiversity not useful in the often fertile situation of agricultural grassland (Schmid 2002)? So far, most of the research on grassland diversity and ecosystem functioning has been carried out in low-input experimental grassland plots sown and weeded to yield different species numbers (e.g. Caldeira et al. 2001; Hector et al. 1999; Tilman et al. 2006). Such artificial experimental conditions make it difficult to draw conclusions for agriculturally managed semi-natural grassland (Caliman et al. 2010; Isselstein 2005). Is this the only explanation for the different views of ecologists and farmers? Is species richness not agriculturally usable?

Here, we want to discuss two central questions: (1) What is the agricultural benefit of biodiversity in livestock production? and (2) How can we manage livestock for biodiversity benefits? To this end, we will summarize results of studies on grassland biodiversity and its ecosystem services like productivity and product quality and discuss implications and applicability for livestock farming. In the second part, principle interactions between grazers, sward structure and diversity will be outlined. Against this background, the impact of livestock management on diversity will be investigated. In the last part, we will discuss whether and how the diverging views on diversity of ecologists and farmers can be reconciled and what the implications of this are for both livestock management and biodiversity research. Throughout this text, ‘diversity’ will be used synonymously with ‘plant species richness’ unless indicated otherwise.

Benefits of grassland phytodiversity for livestock production

Grassland is needed as the fodder basis for agricultural herbivores. Of importance to the farmer is therefore only at first instance a high primary production efficiency, i.e. large biomass production per unit of input. Essential is that this biomass can then be made available to the animals (Sanderson et al. 2004). To keep the animals adequately performing and healthy, their diet should provide the necessary energy and nutritional components. Especially in meadows, this may not be straightforward as there may be biomass losses and quality impairments during harvest and conversion into silage or hay (Tallowin and Jefferson 1999). Here, broad-leaved herbs have disadvantages as they undergo larger disintegration losses. Because animals have difficulties avoiding poisonous plants in conserved fodder, these should be absent. Therefore, special care has to be taken concerning grassland quality and composition in meadows and mown pastures. However, diversity may also have positive side effects, which will be discussed in the following.

Diversity and productivity

What can biodiversity of pastures and meadows mean for the farmer who needs biomass for his livestock? Table 1 summarizes results of studies on biodiversity effects on productivity or other ecosystem services. Due to the difficulties involved in transferring results from experimental grassland plots to agricultural situations (Caliman et al. 2010; Isselstein 2005), we will concentrate here mostly on the few studies carried out in agriculturally managed swards.

Results from these studies are conflicting: while some experimental studies found no consistent effect of biodiversity on primary production (de Lafontaine and Houle 2007; Deak et al. 2009; Kahmen et al. 2005; Soder et al. 2006; Tracy and Faulkner 2006), others, both observational (Bai et al. 2007) and experimental (Caldeira et al. 2001; Tracy and Sanderson 2004; van Peer et al. 2004; Weigelt et al. 2009), found a positive effect (Table 1). Despite initially positive impacts on plant production, Tracy and Faulkner (2006) did not measure increased daily liveweight gains of cattle nor could they increase stocking rates in more diverse pastures. Also Soder et al. (2006) found no effects on herbage intake or milk production of dairy cattle with increased plant diversity. In a survey of 854 meadows and pastures in Inner Mongolia, Bai et al. (2007) observed increased primary production with increased plant diversity. However, the authors pointed out that this coincided with patterns of annual rainfall and soil nitrogen. Furthermore, conditions in this area were representative of those in the Eurasian steppe, but not necessarily directly comparable with managed temperate grassland. The voluntary daily dry matter intake of sheep has been found to increase with species richness up to eight species out of 11 in an indoor cafeteria trial (Wang et al. 2010). This should translate into weight gains of the animal, which were however not determined. In a field experiment, no difference in intake was observed between fields with four to six and with more than eight plant species. The authors discuss that this might be due to supplementary corn offered in the field (Wang et al. 2010). Interestingly, the studies finding positive effects were mainly carried out in experimental plots, not in agricultural grassland (Caldeira et al. 2001; Tracy and Sanderson 2004; van Peer et al. 2004; Weigelt et al. 2009). In other studies of experimental plots,

Table 1 Results from studies of biodiversity effects on production and further ecosystem services in grassland with some form of agricultural management

Management	Country	Plant diversity	Production	Further ecosystem services	References
Rotational grazing (dairy cows), no fertiliser, clipping of excessive ungrazed forage	Pennsylvania, USA	2–9 sown species	0 (herbage intake, milk production)	+ (higher conjugated linoleic acid content of milk with more species)	Soder et al. (2006)
Rotational grazing (beef cattle)	Illinois, USA	3–8 sown species	0 (stocking rate, average daily gain, despite initially higher herbage mass in more diverse plots before grazing)	n.d.	Tracy and Faulkner (2006)
Rotational grazing (to different target heights), mowing	Pennsylvania, USA	1–7 sown species	0 (in favourable years higher yields in fertilised monocultures)	+ (more consistent yields in diverging weather conditions, improved CP and IVTDMD at first harvest, more stable quality of complex mixtures over season)	Deak et al. (2009)
Montane semi-natural grassland (78 plots under agricultural management, grazed or cut)	Germany	8–33 species; average of 20 species	0 (for species richness as well as effective diversity and Camargo's evenness) plant community composition explained productivity	n.d.	Kahmen et al. (2005)
Park grass experiment, different fertilisation treatments since 1856 with N, P or K, two cuts (initially one cut followed by grazing)	England	3–44 species per 200 m^2	− (less species numbers with more production)	+ (stability of hay biomass was positively correlated with species number, albeit weakly)	Silvertown et al. (2006)
Experimental restoration sites (sown on arable land, no weeding), late cut with autumn and winter sheep-grazing	England	Mixtures with 6–17 or 25–41 species (species-poor and -rich, respectively)	+ (linear relationship between difference in species number among treatments and increase in hay yield)	0 (no effect on fodder quality)	Bullock et al. (2001)

Table 1 continued

Management	Country	Plant diversity	Production	Further ecosystem services	References
Experimental plots, no weeding, one cut/year, followed over 9 years	The Netherlands	0–15 sown species, on average 10 to 14 species in total	+ (productivity increased with number of sown species) However, if total species number was considered, there was no clear relationship	+ (stability increased with sown species number, but not with total species number)	Bezemer and van der Putten (2007)
Experimental plots, rotational or continuous grazing, initial weeding during establishment	New Zealand	0–8 functional groups	+ (for sown species in spring) 0 (for total species production in spring as well as total and sown species production in autumn)	+ (resistance to invasion, resilience to disturbance)	Dodd et al. (2004)
Indoor cafeteria experiment with sheep	China	1–11 species	+ (more voluntary average daily intake of sheep with higher diversity)	n.d.	Wang et al. (2010)
854 steppe sites, hay fields or grazed	Inner Mongolia, China	Observational study, up to 36 species per m^2	+ (at all scales; at regional scale, this correlated with annual rainfall and soil nitrogen; grazing did not affect form of relationship)	n.d.	Bai et al. (2007)
Experimental plots (cut) as well as survey on 37 pastures	Pennsylvania, USA	1–15 sown species in experimental plots; up to 11 species in surveys	+ (often more production in more diverse pastures)	+ (less weed invasion)	Tracy and Sanderson (2004)
Experimental plots as well as preexisting vegetation invaded by exotic species at four locations, one cut/year	North Dakota, USA	2–32 sown species	Mostly + (in experimental plots) 0 (in preexisting vegetation) Changing relationships over time and sites	n.d.	Guo et al. (2006)

Table 1 continued

Management	Country	Plant diversity	Production	Further ecosystem services	References
Experimental plots, cutting (1–4 times/year), fertilisation (0–200 kg N ha^{-1} a^{-1}), regular weeding	Germany	1–16 sown species	+ (plant production)	n.d.	Weigelt et al. (2009)
Experimental plots, cut twice/year, regular weeding	Germany	1–60 sown species	n.d.	+ (increased carbon storage in soil)	Steinbeiss et al. (2008)
Experimental plots, regular weeding	Portugal	1–14 sown species	+ (plant biomass)	+ (water use)	Caldeira et al. (2001)
Gradient from forest edge to abandoned pasture	Québec, Canada	Observational study, up to 16 species per 0.75 m^2	Different relationships determined by limiting resources affecting productivity; if pooled together: humped relation; however, this may confound determining environmental variables	n.d.	De Lafontaine and Houle (2007)
Microcosm experiment, four harvests from December to May	New Zealand	1–9 sown species	n.d.	+ (less potential nitrification and nitrous oxide production with more species, especially with legumes in mixture), 0 (no effect on methane uptake)	Niklaus et al. (2006)
Microcosm experiment with heat/drought stress	Belgium	1–8 sown species	+ (more plant biomass with more species before drought stress)	+ (better water acquisition with more species),-(less survival of plants in mixtures)	Van Peer et al. (2004)
Meta-analysis of data from 171 studies	n.a.	No range given; local scale (<20 km)	Mostly humped, followed by 0, −, +	n.d.	Mittelbach et al. (2001)

Table 1 continued

Management	Country	Plant diversity	Production	Further ecosystem services	References
Meta-analysis of data from 1339 plots in 12 natural grassland systems	USA (nine systems), Tanzania, India, Finland	0–59 species	– (nonlinear structural equation modelling indicated competitive effects, but no positive effect of species richness on production)	n.d.	Grace et al. (2007)
Meta-analysis of data from 163 studies	n.a.	No range given	Mainly unimodal in temperate zone Mainly + in tropics in total: 60: 0, 46: +, 37 humped, 20: –	n.d.	Pärtel et al. (2007)

'0' no clear effect, '+' positive effect, '–' negative effect, *n.d.* not determined, *n.a.* not applicable, *CP* crude protein, *IVTDMD* in vitro true dry matter digestibility positive effects on production were found when the number of sown species was considered. However, based on the total number of species present (i.e. including weeds), no consistent effects were found (Bezemer and van der Putten 2007; Dodd et al. 2004).

It has been a principle of ecological theory that the assembly of species in a given habitat depends on the niches present. Therefore, within the limits of historical influences and site accessibility for propagules, the available resources determine phytodiversity in the first place. Here, diversity has been found to be maximal at intermediate resource availability (Critchley et al. 2002; Janssens et al. 1998; Schmid 2002). Hautier et al. (2009) could show that a negative effect of fertilisation on phytodiversity of fertilised grassland communities was mainly due to increased competition for light and restriction of light reaching the lower layers of vegetation. In contrast to this, Rajaniemi (2002) did not find an effect of shading on species richness or diversity in an unproductive former field and concluded that the observed significant effects of fertilisation were due to increased total above- and belowground competition. The importance of belowground competition in such a system where light is not limiting could later be confirmed (Rajaniemi et al. 2003).

In agricultural grassland, this initial diversity determined by the available niches is manipulated by management. A new situation develops where species richness is in dynamic equilibrium with the management, if this is constant. In contrast to this, the experimental grassland plots used for biodiversity–productivity research have usually been weeded intensively, inhibiting the establishment of such a dynamic equilibrium. If weeding was terminated, similar species richness developed within 2 years in all plots of initially different richness (Pfisterer et al. 2004).

Taking a closer look at the results from experimental grassland studies, it becomes obvious that observed diversity effects were most pronounced with species numbers increasing from one to two or four. Many studies found that 90% of the productivity effect was reached with five plant species (Roy 2001). In permanent grassland, the plant diversity is usually larger. For example, Sanderson et al. (2004) summarized that American grazing lands comprised between nine and 50 species per 1000 m^2 and European grasslands between 10 and 60 species per 100 m^2, depending on management intensity. Thus, species richness may usually be too large in permanent grassland to find effects of diversity on productivity.

Several studies have pointed out the larger impact of species identity (Hooper and Vitousek 1997) or functional diversity (Díaz and Cabido 2001) than species number on primary production. Here, functional diversity is not necessarily only the presence or absence of legumes, but can encompass the range of traits like leaf sizes, canopy heights, or rooting depths (Díaz and Cabido 2001). These findings should have implications for the assembly of seed mixtures for grassland renovation, where the species number is furthermore usually in the range where species richness-productivity effects have been found. In practice, this principle has already been used and the long-term experience of seed companies and farmers has been found to deliver a superior product to experimental mixtures in Switzerland (Suter et al. 2010).

To sum up, a clear effect of species number on primary or secondary production of grassland under agricultural conditions could not yet be demonstrated. This may be due to primary effects not translating into animal production, vegetation composition developing a dynamic equilibrium with management conditions or higher species richness in permanent pastures than found effective in experimental grassland. If fertilisation was also manipulated in permanent grassland experiments, its effect on biomass production outreached that of diversity [Crawley et al. (2005); Silvertown et al. 2006; but see also

Weigelt et al. (2009) for results in weeded experimental grassland]. Thus, a potential production benefit may not convince farmers to protect diversity in their grasslands.

Diversity and other services for livestock production

Despite an unclear productivity effect, increased diversity can still have benefits for livestock farming. First of all, the production stability has been found to increase, granting good harvests also in years with adverse weather conditions (Deak et al. 2009; Silvertown et al. 2006; Tilman et al. 2006). However, in a comparison of stability of biomass production of plots sown with 0, 4 or 15 different species and not weeded, Bezemer and van der Putten (2007) found a positive relation with sown species number, but not with actual species richness and concluded that the relationship is context-dependent.

Nutrient losses may be smaller under diverse grassland (Mulder et al. 2002; Niklaus et al. 2006), probably due to resource complementarity and a better use of the soil space (Harrison et al. 2007; Weigelt et al. 2005). This can also cause a better water use efficiency of more diverse systems (Caldeira et al. 2001; van Peer et al. 2004). So far, most studies looking at these relationships have been carried out in experimental grassland plots. Research on long-term grassland, where root structures have developed over long time periods, is needed.

Important effects of phytodiversity on product quality and animal health have been found, which will now be discussed in more detail. Grazing, as compared to indoor fattening, results in a different fatty acid composition (higher proportions of linoleic and linolenic acid), darker and redder meat with better sensory qualities and an increased shelf-life (Dieguez et al. 2006; Farruggia et al. 2008; Fraser et al. 2009; Hocquette et al. 2007). Fraser et al. (2009) conducted grazing experiments with different breeds on improved permanent pasture (ryegrass/clover) and semi-natural rough grazing on *Molinia caerulea* dominated swards. Their results indicated a greater influence of the sward type on animal performance, grazing behaviour and meat quality than the breed when beef cattle are produced in less favoured areas. Under rough grazing, loin steaks contained more vitamin E and had a lower lipid oxidation (Fraser et al. 2009).

Some recent studies have demonstrated that dairy products from grazing ruminants have a composition thought to be beneficial to human health, compared to that from animals fed concentrate diets; the content of unsaturated fatty acids in milk, for example, increases with grazing (Cuchillo et al. 2010b; Elgersma et al. 2006). Milk yields and animal productivity are limited by genetic potential, botanical composition and trophic status of the pasture, which needs to meet basic requirements to ensure a sustainable system (Osoro et al. 2007). Extensive grazing on bio-diverse swards for milk production is often characterized by smaller milk yields but more solid contents (Farruggia et al. 2008). Moloney et al. (2008) concluded from a review of several experiments that more phytodiverse pastures produced milk with increased C18:3n-3 and polyunsaturated fatty acid concentrations whereas the saturated fatty acid concentrations were in most cases reduced. Leiber et al. (2005) discussed that changes in the ruminal ecosystem due to energy shortage or specific secondary plant metabolites may be possible causes for the high C18:3n-3 concentrations in alpine milk.

Animals mix plant and biochemical diversity to enhance the nutritive value of the diet as well as to maintain possible toxic concentrations of plants below critical levels (Provenza and Villalba 2010). Certain plants can also have health benefits for the animals. For example, legumes contain condensed tannins that may cause increased production of milk and wool, improve the lambing percentage and reduce bloating risk as well as intestinal parasites (Min et al. 2003). In addition, Martin et al. (2010) point out that adding tannin-rich legumes to animal diets may decrease rumen methanogenesis and thus the production of the greenhouse gas methane. As reducing methane production during rumination also means decreasing energy losses by the animals, this is interesting from a production point of view as well. So far, the importance of diverse grasslands in this respect is not completely understood.

Thus, despite unclear productivity effects, plant richness may have positive effects on product quality, animal health, nutrient and water retention as well as production stability. The latter may be especially important for sustainable production under changing climatic conditions, but has so far mainly been studied in experimental plots.

Livestock management to enhance grassland phytodiversity

Extensive grazing has been suggested to be a good means for enhancing and protecting grassland diversity (Dumont et al. 2007; Hart 2001; Loucougaray et al. 2004; Pykälä 2003; Rook et al. 2004; Scimone et al. 2007; Tallowin et al. 2005). What is the advantage of grazers over mowing? How do the animals influence diversity over time and space?

Grazing animals affect the distribution and occurrence of plants in several ways. Besides directly influencing competition between species, they also introduce more heterogeneity into the sward. The main mechanisms in this respect are selective grazing, nutrient redistribution, treading and seed distribution. As the complex actions of biting/defoliation/selection play the most important role in this process (Illius and Hodgson 1996), we will first concentrate on these before discussing the influences of treading and excreta deposition and bringing this together in a discussion of livestock management for biodiversity.

Selective grazing

Selectively grazing animals preferrably feed on certain pasture areas (horizontal selection) or plant parts (vertical selection) (Arnold and Dudzinski 1978; Elsässer 2000). Given a free choice, they select a mixed diet rather than chosing one fodder species only (Villalba and Provenza 2009). The chosen biomass usually has higher concentrations of nitrogen, phosphorus and energy than avoided material (Wales et al. 1998). Despite the variability in quality and digestibility of herbage on offer in time and space, ruminants aim to select herbage with fairly constant digestibility (Fulkerson et al. 2007; Garcia et al. 2003). Therefore, the degree of selectivity changes with the quality of the herbage on offer. The animals have to resolve the trade-off between feeding on preferred food and the energy required to forage for that food (Rook et al. 2004; Utsumi et al. 2009). A higher selectivity has been found when preferred patches were aggregated (Dumont et al. 2002).

The intensity of vertical selectivity differs between animal species and is related to the actual mechanical way of fodder uptake. Cattle take up plant material with their prehensile tongue into the mouth where it is pressed against the dental plate of the upper jaw and torn off with a move of the head. They can graze tall herbage more easily than sheep because of their physical size (Hodgson 1990; Wilmshurst et al. 2000). Cattle might select separate leaves merely from tall plants, while sheep and goats with their narrower and more pointed muzzles graze more fastidiously and readily select individual leaves and other plant parts (Animut and Goetsch 2008; Arnold and Dudzinski 1978; Dumont 1997).

Table 2 Spatial dimensions of the grazing animal/sward system, following Laca and Ortega (1996) and Vallentine (2001)

Spatial dimension	Description	Unit involved	Temporal dimension
Bite	Area of a bite	Individual (head)	1–2 s
Feeding station	Total of bites of a standing grazer (circular arc of the head)	Individual	5–100 s
Grazing patch	Cluster of feeding stations of the same intake rate	Few individuals	1–30 min
Feeding site	Collection of grazing patches during a grazing interval	Sub-herd	1–4 h
Pasture, habitat/camp	Pasture–in the open landscape related to a central resting and watering place	Herd	1–4 weeks
Habitat/home range	All habitats in an open landscape	Population	1–12 months

Besides determining the potential bite selection of an animal, the body size also influences the size of a feeding station, i.e. the area a standing grazer can reach with its head (Table 2). A cluster of feeding stations with the same intake rate is defined as a grazing patch. The size of this feeding patch depends on the size of the animal as well as the heterogeneity, biomass and quality of fodder available. Thus, the size and selectivity of the animal in interactions with the heterogeneity of the sward will lead to a mosaic of areas with different spatial and temporal dimensions of defoliation (Table 2).

Sight helps the grazing animal to position itself towards the other animals and the environment, but is less important in selecting the diet. In experiments, sheep with their eyes bandaged selected a diet similar to that of sheep allowed to see. However, the preference for certain grassland plants changed when touch, smell and taste were impaired (Arnold and Dudzinski 1978). Animals familiar with a sward or forage were quicker in finding their preferred feeding patches (Bailey and Sims 1998) and using the available forage (Flores et al. 1989a, b), suggesting an influence of learning in patch selection (Dumont 1997).

Besides a spatial and qualitative dimension of selective grazing, there is also a temporal dimension that influences the structure of the sward and helps to establish a mosaic of more or less frequently defoliated patches. Thus, the previous meal an animal had seems to have an influence on the preference for the next one (Dumont 1997; Mote et al. 2008). From experiments on extensive grazing it was concluded that there was a strong diurnal pattern of selectivity: Dumont et al. (2007) found a marked preference of cattle for short, highly digestible bites in the morning and an increased consumption of bite types requiring a greater rumination effort during the second half of the day. Bites of short mixed vegetation consisting of grasses and herbs were generally grazed preferentially, regardless of the offer and time of day (Dumont et al. 2007).

Plant species on a pasture usually exhibit two defence strategies: resistance to (avoidance) and tolerance of herbivory (Briske 1996). Resistance refers to the ability of a plant to reduce the amount of damage. This means reducing the probability and intensity of defoliation by morphological traits like thick hair, sharp leaf blades (silica) and chemical defences. This group is classified as facultative weeds and weed grasses if they are potentially edible (Opitz von Boberfeld 1994). Among these are *Holcus lanatus*, *Deschampsia caespitosa* and *Ranunculus repens*. Also unwanted poisonous and non-edible plants like *Equisetum palustre*, *Cirsium palustre* or *Juncus effusus* show this defence mechanism and may compete successfully for space and nutrients if no agronomic measures are taken (Moretto and Distel 1997, 1999). Tolerance is the ability of a plant to react to defoliation by rapid regrowth and recovery without a reduction in fitness. In this case, growing points for regeneration are located below the grazing level at the shoot basis or along stolons and storage roots may contribute to survival after intense defoliation (Herben and Huber-Sannwald 2002).

Disturbances by the grazer can shift the competition conditions among plants, as varying defoliation frequencies lead to different optima in adaptation to grazing. Generally, intensive grazing will induce the formation of a dense, well-tillered sward (Frame 1992; Matthew et al. 2000; Nelson 2000). As a result, the vegetation composition usually differs between tall and short sward areas (e.g. Correll et al. 2003) and indicator species for the extremes in grazing, i.e. selective undergrazing and selective overgrazing, can be determined (Opitz von Boberfeld 1994).

Treading

The treading of grazing animals can have two effects: it may cause compaction of the topsoil and it can create open gaps without vegetation cover. According to Jacob (1987), the tread of a cattle of 600 kg causes a pressure of 4–5 kg cm^{-2} on the topsoil. The resulting compaction may lead to retarded water infiltration and gas diffusion, increasing the risk of surface runoff and elevated emissions of gases like the greenhouse gas nitrous oxide (Menneer et al. 2005; Mulholland and Fullen 1991; Oenema et al. 1997; van Groenigen et al. 2005). However, compaction can also have positive effects: it is expected that treading might compensate for the prohibition of rolling in spring on nature protected grassland (Benke and Isselstein 2001).

Damages of the vegetation leading to patches of bare soil may offer space for propagation of seeds from the seed bank and invasion by other species. This can be desirable, but can also promote the growth of unwanted species. Kohler et al. (2006) found that gaps were colonized by species with small seeds, unspecialized seed dispersal, a persistent seed bank and high vegetation spread. The role of other grazing effects (feeding, dung deposition and trampling) on the recolonisation was only secondary, modifying the competition between recolonisers.

Plant species react differently to treading. Jacob (1987) found that *Poa annua* had increasing yield proportions at heavily frequented pasture gate areas while proportions of *H. lanatus* decreased. In line with this, Graf Bothmer (1953) ascribed a community at a zone close to pasture gates of permanent pastures showing highest frequency and dominance of *P. annua*, *Polygonum aviculare*, *Plantago major* and *Lolium perenne* to larger influences of treading in these areas.

Excreta deposition

The grazing animal transforms vegetation biomass into animal biomass and performance; however, with considerable losses and a rather low efficiency. In cattle, about 75–95% of the ingested N is returned via excreta (Whitehead 1995). In this transformation, nutrients are redistributed from relatively large areas where the animals feed to small excreta patches. These excreta patches have high input of nutrients, but also experience a grazing pattern different to the rest of the pasture area.

Dung patches might cover 5–10% of the grazed area each year in dairy farming, but the affected area can be much greater and, depending on weather conditions, be one to six times the covered area (Bao et al. 1998; Bastiman and van Dijk 1975; Haynes and Williams 1993). Herbage growing in the vicinity of dung patches is unattractive to stock, also due to the dung smell, and is avoided unless the grazing pressure is very high (Frame 1992; Gillet et al. 2010). This behaviour is explained by hygienical/sanitary advantages of avoidance (Hutchings et al. 1998). As a result, micro-areas with a tall sward develop, especially under extensive grazing.

Urine patches can cover up to 24% (at 700 cow-days ha^{-1}) of the pasture and the area affected may be up to double that size (Haynes and Williams 1993; Whitehead 2000). The vegetation at urine patches may be grazed preferentially (Day and Detling 1990; Steinauer and Collins 2001), probably due to high concentrations of minerals in the herbage.

The nutrient return with excreta is large. It is unevenly distributed within the pasture and often accumulates at feeding, rest and water places (König 2002; Owens et al. 2003). This results in further differentiation in sward structure and soil conditions. In the process of grazing and excretion, a decoupling of major plant nutrients takes place. Usually, more K is excreted in urine than in dung (Whitehead 2000); while P is mainly excreted in dung. A certain amount of N is excreted with dung, the rest with urine (e.g. Schellberg et al. 2007). Thus, the more N cattle take up, the higher the ratio of N in urine versus N in dung (Whitehead 1995).

On urine patches, legumes are especially negatively affected. White clover competes only poorly for mineral N with grasses and is more susceptible to scorch. N_2 fixation can be markedly depressed in the urine patch (Ball et al. 1979; Ledgard et al. 2001). Therefore, urine patches become grass dominated (Ledgard et al. 1982), but the degree of clover reduction and N_2 fixation is dependent on the time of urine application as well as the clover content of the sward (Ball et al. 1979; Ledgard et al. 1982). Thus, Norman and Green (1958) did not find an effect of a single urine application on the botanical composition of a pasture.

Dung patches may lead to an increase in the total yield of grasses around the pats (MacDiarmid and Watkin 1971; Norman and Green 1958). This effect was shown to be stronger when the excretion was combined with defoliation. Underneath the cow pat, the vegetation died (MacDiarmid and Watkin 1971). Dung patches were found to decrease species turnover and thus have a stabilizing effect on plant composition in their direct surroundings in mountain pastures (Gillet et al. 2010).

Grazing management and diversity

The development of a specific sward structure is induced by the behaviour of the grazing animal as discussed above and by agricultural management (pasture maintenance) on a background of site characteristics. Important with respect to grazing management is the grazing intensity, grazing system and the type and breed of grazing animal. The effects of grazing are further modified and partly determined by the level of nutrient input (fertilization; additional feeding), and the intensity of intermittent management like cutting or topping, rolling and harrowing, usually intended to decrease grazing effects. However, these secondary management effects will not be considered in more depth here.

High grazing intensity has often been blamed for negative effects on diversity (Dumont et al. 2009; Henle et al. 2008; Plantureux et al. 2005; Vallentine 2001). With increasing intensity, animals become less selective in the choice of their diet in order to obtain sufficient intake (Dumont et al. 2007). Thus, defoliation will be more homogeneous than on less intensively grazed paddocks, creating less diverse niches. Furthermore, the frequency of defoliation will be high, allowing only pasture plants adapted to this to survive. With very high grazing pressure, animals may harm vegetation points by removing too much biomass, especially from preferred plant species. This happens more easily by animals being able to remove biomass close to the soil, such as horses, sheep or goats rather than cattle (Animut and Goetsch 2008; Benavides et al. 2009; Menard et al. 2002). With high grazing intensity, effects due to treading and gap creation will also be more serious. In contrast to selective grazing, gap creation and compaction will not be maximal at low grazing pressures, but increase with increasing intensity. However, colonisation of new gaps will be retarded with high grazing intensity due to frequent disturbances of newly emerging propagules. Excreta patches will affect larger pasture areas (White et al. 2001) and more nutrients can be lost by run-off, leaching or gaseous losses. However, increased grazing pressure decreases the size of dung pats as the animals tend to feed closer to and sooner after an excretion event.

The grazing system may have large effects on diversity, even if the annual stocking density is the same for different systems. Most important in this respect are rotational grazing and permanently stocked pasture. Permanently stocked pasture requires less work from the farmer, as the animals are put on the pasture in spring and removed at the end of the grazing season. In rotational grazing, animals have less space per unit of time, but are transferred to a new paddock at regular time intervals. Thus, at a given time, the stocking density is higher with rotational grazing, but the vegetation is then allowed time to recover until the animals rotate back to the same paddock. Therefore, the pressure on preferred species is less intense than in permanently stocked pastures (Pavlu et al. 2003). It has been found that grazing at intermediate intensity may allow more plants to get to the flowering stage (Correll et al. 2003; Sahin Demirbag et al. 2009) and may thus have positive effects on the vegetation, but also on the abundance of insects (Dumont et al. 2009; Kruess and Tscharntke 2002).

As permanently stocked pastures can only be grazed with relatively few animals to allow them to find enough fodder even in times of little vegetation growth, different areas develop with very different frequency of use. The seasonal vegetation development of a continuously grazed pasture (set stocking) in temperate areas can be divided into three parts, namely the spring/early summer period, the summer, and the late summer/autumn period based on the development of herbage mass (Jacob 1987). Figure 1 gives an overview of the interactions of grazing cattle and sward structure during a grazing period. The spring/early summer period is characterized by a surplus of herbage mass of good quality allowing a high performance of livestock. As grazers initially use only relatively small areas on continuously grazed pastures with set stocking, other areas develop into a generative state where feed quality deteriorates. During the summer period, grazing cattle therefore have to invest time to select herbage and are also forced to use overripe parts of the pasture. As a result, performance of the individual animal decreases (Baumont et al. 2000). Towards the end of the grazing period, in late summer/autumn, the relation between herbage on offer (standing crop) and intake by the grazing cattle synchronizes again. At this time, the variability in quality and sward height is reduced, causing less need for the animal to select. This will allow, weather conditions permitting, a moderate increase in animal performance during that period. Overall, preferred patches are defoliated very frequently and experience the same pressure as on pastures with high grazing intensity. However, other pasture areas are hardly influenced by the animals during long parts of the grazing season. Here, competition between species will drive diversity development.

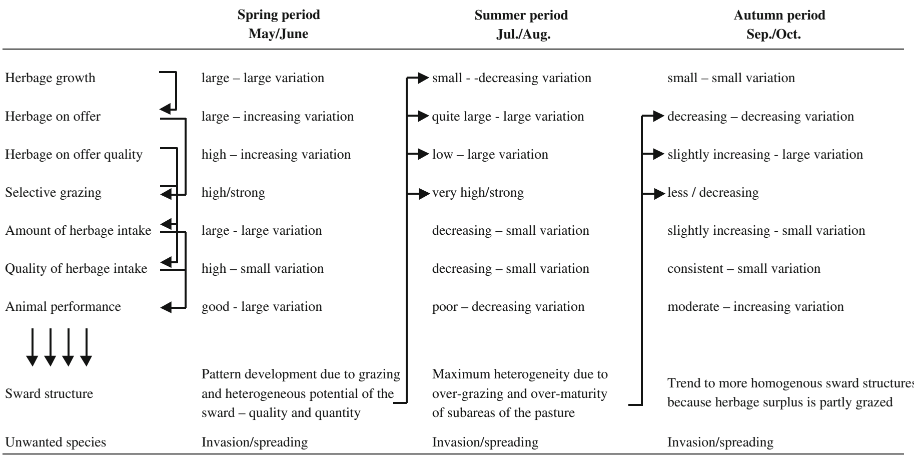

Fig. 1 Schematic overview of the phases of developments and of the interactions of grazing cattle and sward structure under conditions of selective grazing on extensively grazed grassland

Usually, farmers would choose to cut or mulch surplus vegetation at the end of a grazing season.

The type of grazing animal has important implications for phytodiversity, especially due to different feeding preferences. The mechanical prerequisites for selective grazing and their differences between animal species have already been discussed above. Requirements of the animals for energy and quality further determine their influence on the vegetation. Impacts due to treading and excretion vary between species. Treading is especially important where a lot of weight is carried on a small area or where animals are very mobile. Apart from small differences in nutrient retention between animal species, excretion mainly differs with respect to the amounts excreted at a given time and the distribution of excreta patches. Thus, depending on the size of the pasture, horses may show latrine behaviour, excreting always at the same points (Lamoot et al. 2004), while cattle may distribute excreta more evenly over the pasture area (White et al. 2001). This has implications for the nutrient return to the plants and mining of nutrients versus accumulation at other places.

Interestingly, the choice of the breed, apart from size and weight restrictions, seems generally to be of less importance in cattle (Fraser et al. 2007; Isselstein et al. 2007), but effects have been reported for sheep and goats (Osoro et al. 2007, 2002). Larger breeds might achieve better performance rates but have higher requirements for maintenance (protein, energy, minerals etc.).

Different effects of grazers on swards are sometimes utilized in co-grazing. Thus, grazing by goats has been found to have positive effects on following sheep grazing, as the proportion of clover in the pasture increased (del Pozo et al. 1998). Sheep may feed on dung pats of cattle and vice versa, decreasing the amount of nutrient and pasture space lost (Abaye et al. 1994; Forbes and Hodgson 1985; Fraser et al. 2007). Co-grazing may also lead to increased daily liveweight gains of both animal species involved (Nolan and Connolly 1989). A combination of species in co-grazing may lead to the development of a more uniform sward with respect to height. However, due to the distinct effects on plant species by selective grazing, treading and excretion, the underlying heterogeneity might be larger with co-grazing, allowing the creation of more diverse niches.

To sum up, grazing is regarded as a most efficient way of utilizing and maintaining less intensive and semi-natural grasslands. However, the interactions of soil and site characteristics, hydrology, plant communities, and grazing management are complex and the situation is often further complicated by restrictions in grazing time, nutrient return and market demands. A thorough understanding of the grazing process will help to properly address the problems arising in a specific environmental/agricultural/socio-cultural context and to combine benefits of extensive grazing concepts for improved or maintained biodiversity, landscape scenery, soil protection and farm income (Soder et al. 2007). In order to achieve these tasks, it is likely that management restrictions need to be adapted to local conditions, especially by adjusting grazing intensity to productivity, by allowing some form of nutrient return or by mulching, to avoid cases where the process of selective grazing might lead to abandonment of parts of the pasture. In a complex situation like extensive grazing what may be beneficial for one objective may have damaging consequences for another (Mills et al. 2007).

Discussion

Farmers and ecologists have contrasting ideas about the usefulness of biodiversity for grassland production. As outlined above, these seem to be based on contrasting experiences in different environments: experiments have often been conducted in experimental grassland plots or newly sown grassland where the vegetation composition is not (yet) in equilibrium with the resources, where management and harvests are rarely comparable with agricultural situations and where the focus is on primary production. In contrast, in low to moderate management situations the farmer is dealing with permanent grasslands comprising species numbers that are in dynamic equilibrium with the environment and is engaged in the sometimes difficult task of matching primary production with the needs of the animals.

Results from experimental grassland plots may still have implications for agricultural systems managed in a way similar to these plots, e.g. in ley farming. Here, the growing of cash crops is alternated with legume or grass pastures. The grassland species are sown in and the pasture is kept for a few years to increase soil fertility and disrupt pest cycles before it is ploughed for another round of cash crops. This system may be improved by using more diverse species mixtures. Research is needed to investigate the transferability of results on impacts of diversity on productivity and other services from experimental studies to ley farming conditions.

To make results applicable for more permanent grassland use, research should focus on established grasslands with species numbers and management comparable to agricultural situations. Next to primary production, the nutritional quality of the biomass should be considered as well as harvest losses in case of meadows. The selectivity of grazers has to be investigated in permanent pastures comprising more than just one or two species. Here, further research has to focus on animal-sward interactions and on the effects of breed, physiological stage and grazing experience on the process of selective grazing. By grazing at different densities, the plant species richness can be—at least partly—determined, but little is known about the potential to create and maintain structurally varying grasslands (Adler et al. 2001; van Wieren and Bakker 1998). Furthermore, a closer look needs to be taken at soil biology and interactions between above- and belowground diversity. In this context, the consideration of organic livestock systems may be interesting, as these may have a higher plant diversity and rely more on services of diversity than conventional systems (Hole et al. 2005; Rundlöf et al. 2010).

For grassland farming, diversity can still have advantages, albeit maybe not the desired production effect. Several other services of biodiversity are also of importance to farmers, e.g. increased stability of production, resilience to changes, improved use of nutrients and water, or influences on product quality. Here as well, more research is needed under more realistic agricultural conditions to better understand the magnitude of these effects. Although in experimental plots more species have been found to be necessary for multiple ecosystem services (Hector and Bagchi 2007), species numbers in permanent grassland might already be high enough to allow such multifunctionality.

For biodiversity conservation, agricultural management is important in temperate grasslands as diversity has developed over the last centuries in line with management. Here, grazing systems with intermediate stocking densities seem to have the largest potential for recreation of diversity. Grazing creates a more heterogeneous sward than mowing as the animals affect sward composition by a mixture of selective grazing, treading and excretion.

Generally, biodiversity-adapted grazing systems might only be economically viable if the costs for maintenance, fertilizer and leasing, especially, can be kept to a minimum. In other cases, the potential of the pasture needs to be utilized better to be profitable. Animal performance is a result of herbage intake and quality. Due to selective grazing, animals might select diets of a better quality than the mean of the herbage on offer (Rook et al. 2004; Wales et al. 1998). Therefore, with reduced stocking, even less productive grassland might be used for efficient livestock farming (Isselstein et al. 2007). In investigations on extensive grazing with oxen on fen grassland in northwest Germany, Benke and Isselstein (2001) found relatively high individual daily live weight gains of 418–871 g head^{-1} with an average of 699 g head^{-1} during 1993–2000. The potential gross biomass growth was about 80 GJ NEL ha^{-1}, while the net pasture performance amounted to 14.3 GJ NEL ha^{-1} in 1999 and 21.3 GJ NEL ha^{-1} in 2000. Thus, the grass leavings of about 80% in 1999 and 73% in 2000 were very high. The farmer has to decide whether he wants to maximize production per animal, which is usually largest on extensively used pastures, or production per area, which increases with increasing intensity up to the carrying capacity.

Production of milk and meat from extensive grazing on more bio-diverse pastures is naturally limited and the economic success usually depending on some form of subsidies for conservation of biodiversity, bird breeding, landscape conservation, tourism, and cultural heritage among others (Kemp and Michalk 2007). Ideally, the products can be marketed through special brands and secure premium prices for milk and meat (Mills et al. 2007; Traill et al. 2008). Bermingham et al. (2008) found that products from pastoral production with properties or constituents related to human health were well accepted by the consumer, a promising fact for extensive grazing enterprises. However, sufficient information on production, regional origin and processing is demanded by the consumer. Generally, the positive influence of botanically diverse swards on grazing animals goes beyond grazing as a means of animal welfare and being a natural process, but includes side effects of antiparasitism and antioxidant activity by phytochemicals transmitted from plant to animal (Cuchillo et al. 2010a; Farruggia et al. 2008; Moloney et al. 2008). Moloney et al. (2008) have reviewed the implications of botanically diverse forage-based rations for cattle on product composition, product quality and consumer health. They conclude that, as information accumulates on the effect of individual plant species on milk and meat quality, opportunities will arise to maintain and develop bio-diverse pastures. Furthermore, other ecosystem functions that could not be covered in this review, like landscape beauty, meadow bird breeding, soil protection, or abundance of pollinators, have to be taken into account when deciding on the fate of phytodiverse grassland.

Conclusions

Biodiversity in pastures has developed over a long time in line with agricultural management. Therefore, the potential of using grazers for biodiversity enhancement of pastures seems good. However, by modern standards, agricultural management has to be adapted, usually extensified to increase diversity. Diversity does not seem to have the often acclaimed production increasing effect on permanent pastures. Although there can still be other advantages for farmers, like production stability and better use of nutrients and water, farmers still need to be compensated for production losses due to extensification measures. To be able to make full use of biodiversity in agriculture, it is of foremost importance to integrate agricultural management into biodiversity research and to understand the focus and interests of farmers. This may be done by close cooperation between agriculturalists and ecologists, either in interdisciplinary projects or by diversification within working groups through hiring of scientists originally from the respective other discipline. Here, rangeland science may serve as an example where such cooperation seems more common, maybe due to the larger impact of natural processes on production in these usually larger-scale and less intensively managed systems, compared to temperate permanent grassland systems.

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References

Abaye AO, Allen VG, Fontenot JP (1994) Influence of grazing cattle and sheep together and separately on animal performance and forage quality. J Anim Sci 72:1013–1022

Adler PB, Raff DA, Lauenroth WK (2001) The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128:465–479

Animut G, Goetsch AL (2008) Co-grazing of sheep and goats: benefits and constraints. Small Rumin Res 77:127–145

Arnold GW, Dudzinski ML (1978) Ethology of free-ranging domestic animals. Elsevier, Amsterdam

Bai Y, Wu J, Pan Q et al (2007) Positive linear relationship between productivity and diversity: evidence from the Eurasian Steppe. J Appl Ecol 44:1023–1034

Bailey DW, Sims PL (1998) Association of food quality and locations by cattle. J Range Manag 51:2–8

Ball R, Keeney DR, Theobald PW et al (1979) Nitrogen balance in urine-affected areas of a New Zealand pasture. Agron J 71:309–314

Bao J, Giller PS, Stakelum G (1998) Selective grazing by dairy cows in the presence of dung and the defoliation of tall grass dung patches. Anim Sci 66:65–73

Bastiman B, van Dijk JPF (1975) Much breakdown and pasture rejection in an intensive paddock system for dairy cows. Exp Husb 28:7–17

Baumont R, Prache S, Meuret M et al (2000) How forage characteristics influence behaviour and intake in small ruminants: a review. Lives Prod Sci 64:15–28

Benavides R, Celaya R, Ferreira LMM et al (2009) Grazing behaviour of domestic ruminants according to flock type and subsequent vegetation changes on partially improved heathlands. Span J Agric Res 7:417–430

Bender O, Boehmer HJ, Jens D et al (2005) Analysis of land-use change in a sector of upper Franconia (Bavaria, Germany) since 1850 using land register records. Landsc Ecol 20:149–163
Benke M, Isselstein J (2001) Extensive landwirtschaft auf niedermoorgrünland-probleme und chancen. In: Kratz R, Pfadenhauer J (eds) Ökosystemmanagement für Niedermoore, Strategien und Verfahren zur Renaturierung. Ulmer, Stuttgart
Bermingham EN, Roy NC, Anderson RC et al (2008) Smart foods from the pastoral sector-implications for meat and milk producers. Aust J Exp Agric 48:726–734
Bezák P, Halada L (2010) Sustainable management recommendations to reduce the loss of agricultural biodiversity in the mountain regions of NE Slovakia. Mt Res Dev 30:192–204
Bezemer TM, van der Putten WH (2007) Ecology: diversity and stability in plant communities. Nature 446:E6–E7
Briske DD (1996) Strategies of plant survival in grazed systems: a functional interpretation. In: Hodgson J, Illius AW (eds) The ecology and management of grazing systems. CAB International, Wallingford
Bullock JM, Pywell RF, Burke MJW et al (2001) Restoration of biodiversity enhances agricultural production. Ecol Lett 4:185–189
Bullock JM, Pywell RF, Walker KJ (2007) Long-term enhancement of agricultural production by restoration of biodiversity. J Appl Ecol 44:6–12
Caldeira MC, Ryel RJ, Lawton JH et al (2001) Mechanisms of positive biodiversity-production relationships: insights provided by $\delta^{13}C$ analysis in experimental Mediterranean grassland plots. Ecol Lett 4:439–443
Caliman A, Pires A, Esteves F et al (2010) The prominence of and biases in biodiversity and ecosystem functioning research. Biodivers Conserv 19:651–664
Correll O, Isselstein J, Pavlu V (2003) Studying spatial and temporal dynamics of sward structure at low stocking densities: the use of an extended rising-plate-meter method. Grass Forage Sci 58:450–454
Crawley MJ, Johnston AE, Silvertown J et al (2005) Determinants of species richness in the park grass experiment. Am Nat 165:179–192
Critchley CNR, Chambers BJ, Fowbert JA et al (2002) Plant species richness, functional type and soil properties of grasslands and allied vegetation in English environmentally sensitive areas. Grass Forage Sci 57:82–92
Cuchillo HM, Puga DC, Navarro OA et al (2010a) Antioxidant activity, bioactive polyphenols in Mexican goats' milk cheeses on summer grazing. J Dairy Res 77:1–7
Cuchillo MH, Puga CD, Wrage N et al (2010b) Feeding goats on scrubby Mexican rangeland and pasteurization: influences on milk and artisan cheese quality. Trop Anim Health Prod 42:1127–1134
Day TA, Detling JK (1990) Grassland patch dynamics and herbivore grazing preference following urine deposition. Ecology 71:180–188
de Lafontaine G, Houle G (2007) Species richness along a production gradient: a multivariate approach. Am J Bot 94:79–88
Deak A, Hall MH, Sanderson MA (2009) Grazing schedule effect on forage production and nutritive value of diverse forage mixtures. Agron J 101:408–414
del Pozo M, Osoro K, Celaya R (1998) Effects of complementary grazing by goats on sward composition and on sheep performance managed during lactation in perennial ryegrass and white clover pastures. Small Rumin Res 29:173–184
Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. Trends Ecol Evol 16:646–655
Dieguez CF, Hornick J-L, Cabaraux J-F et al (2006) Less intensified grazing management with growing fattening bulls. Anim Res 55:105–120
Dodd MB, Barker DJ, Wedderburn ME (2004) Plant diversity effects on herbage production and compositional changes in New Zealand hill country pastures. Grass Forage Sci 59:29–40
Dumont B (1997) Diet preferences of herbivores at pasture. Annals Zootechnol 46:105–116
Dumont B, Carrère P, D'Hour P (2002) Foraging in patchy grasslands: diet selection by sheep and cattle is affected by the abundance and spatial distribution of preferred species. Anim Res 51:367–381
Dumont B, Rook AJ, Coran C et al (2007) Effects of livestock breed and grazing intensity on biodiversity and production in grazing systems. 2. Diet selection. Grass Forage Sci 62:159–171
Dumont B, Farruggia A, Garel J-P et al (2009) How does grazing intensity influence the diversity of plants and insects in a species-rich upland grassland on basalt soils? Grass Forage Sci 64:92–105
Elgersma A, Tamminga S, Ellen G (2006) Modifying milk composition through forage. Anim Feed Sci Technol 131:207–225
Elsässer M (2000) Wirkungen extensiver und intensiver weidenutzungsformen auf die verwertbarkeit von Grünlandaufwüchsen. Berichte über Landwirtschaft 78:437–453

Farruggia A, Martin B, Baumont R et al (2008) Quels intérêts de la diversité floristique des prairies permanentes pour les ruminants et les produits animaux? INRA Prod Anim 21:181–200
Flores ER, Provenza FD, Balph DF (1989a) The effect of experience on the foraging skill of lambs: importance of plant form. Appl Anim Behav Sci 23:285–291
Flores ER, Provenza FD, Balph DF (1989b) Role of experience in the development of foraging skills of lambs browsing the shrub serviceberry. Appl Anim Behav Sci 23:271–278
Forbes TDA, Hodgson J (1985) The reaction of grazing sheep and cattle to the presence of dung from the same or the other species. Grass Forage Sci 40:177–182
Frame J (1992) Improved grassland management. Farming Press, Ipswich
Fraser MD, Davies DA, Vale JE et al (2007) Effects on animal performance and sward composition of mixed and sequential grazing of permanent pasture by cattle and sheep. Lives Sci 110:251–266
Fraser MD, Davies DA, Vale JE et al (2009) Performance and meat quality of native and continental cross steers grazing improved upland pasture or semi-natural rough grazing. Lives Sci 123:70–82
Fulkerson WJ, Neal JS, Clark CF et al (2007) Nutritive value of forage species grown in the warm temperate climate of Australia for dairy cows: grasses and legumes. Lives Sci 107:253–264
Garcia F, Carrère P, Soussana J-F et al (2003) The ability of sheep at different stocking rates to maintain the quality and quantity of their diet during the grazing season. J Agric Sci 140:113–124
Gillet F, Kohler F, Vandenberghe C et al (2010) Effect of dung deposition on small-scale patch structure and seasonal vegetation dynamics in mountain pastures. Agric Ecosyst Environ 135:34–41
Grace JB, Michael Anderson T, Smith MD et al (2007) Does species diversity limit productivity in natural grassland communities? Ecol Lett 10:680–689
Graf Bothmer HJ (1953) Der Einfluß der Bewirtschaftung auf die Ausbildung der Pflanzengesellschaften niederrheinischer Dauerweiden. Zeitschrift für Acker- und Pflanzenbau 96:457–476
Guo Q, Shaffer T, Buhl T (2006) Community maturity, species saturation and the variant diversity–productivity relationships in grasslands. Ecol Lett 9:1284–1292
Harrison KA, Bol R, Bardgett RD (2007) Preferences for different nitrogen forms by coexisting plant species and soil microbes. Ecology 88:989–999
Hart RH (2001) Plant biodiversity on shortgrass steppe after 55 years of zero, light, moderate, or heavy cattle grazing. Plant Ecol 155:111–118
Hautier Y, Niklaus PA, Hector A (2009) Competition for light causes plant biodiversity loss after eutrophication. Science 324:636–638
Haynes RJ, Williams PH (1993) Nutrient cycling and soil fertility in the grazed pasture ecosystem. Adv Agron 49:119–199
Hector A, Bagchi R (2007) Biodiversity and ecosystem multifunctionality. Nature 448:188–190
Hector A, Schmid B, Beierkuhnlein C et al (1999) Plant diversity and productivity experiments in European grasslands. Science 286:1123–1127
Henle K, Alard D, Clitherow J et al (2008) Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe-a review. Agric Ecosyst Environ 124:60–71
Herben T, Huber-Sannwald E (2002) Effects of management on species richness of grasslands: sward scale processes lead to large-scale patterns. Grassland Sci Eur 7:635–643
Hocquette JF, Tesseraud S, Cassar-Malek I et al (2007) Responses to nutrients in farm animals: implications for production and quality. Animal 1:1297–1313
Hodgson JG (1990) Grazing management: science into practice. Longman, Essex
Hole DG, Perkins AJ, Wilson JD et al (2005) Does organic farming benefit biodiversity? Biol Conserv 122:113–130
Hooper DU, Vitousek PM (1997) The effects of plant composition and diversity on ecosystem processes. Science 277:1302–1305
Hooper DU, Vitousek PM (1998) Effects of plant composition and diversity on nutrient cycling. Ecol Monogr 68:121–149
Hooper DU, Chapin FS, Ewel JJ et al (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35
Hutchings MR, Kyriazakis I, Anderson DH et al (1998) Behavioural strategies used by parasitized and non-parasitized sheep to avoid ingestion of gastro-intestinal nematodes associated with faeces. Anim Sci 67:97–106
Illius AW, Hodgson J (1996) Progress in understanding the ecology and management of grazing systems. In: Hodgson J, Illius AW (eds) The ecology and management of grazing systems. CAB International, Wallingford
Isselstein J (2005) Enhancing grassland biodiversity and its consequences for grassland management and utilisation. In: McGilloway DA (ed) XX international grassland congress, keynote lectures. Wageningen Academic Publishers, Wageningen

Isselstein J, Jeangros B, Pavlu V (2005) Agronomic aspects of extensive grassland farming and biodiversity management. In: Lillak R, Viiralt R, Linke A, Geherman V (eds) Integrating efficient grassland farming and biodiversity, 13th International occasional symposium of the European grassland federation, vol 10. Grassland Science in Europe, Tartu, pp 427–430

Isselstein J, Griffith BA, Pradel P et al (2007) Effects of livestock breed and grazing intensity on biodiversity and production in grazing systems. 1. Nutritive value of herbage and livestock performance. Grass Forage Sci 62:145–158

Jacob H (1987) Weidenutzung. In: Voigtländer G, Jacob H (eds) Grünlandwirtschaft und Futterbau. Ulmer, Stuttgart

Janssens F, Peeters A, Tallowin JRB et al (1998) Relationship between soil chemical factors and grassland diversity. Plant Soil 202:69–78

Kahmen A, Perner J, Audorff V et al (2005) Effects of plant diversity, community composition and environmental parameters on productivity in montane European grasslands. Oecologia 142:606–615

Kahmen A, Renker C, Unsicker SB et al (2006) Niche complementarity for nitrogen: an explanation for the biodiversity and ecosystem functioning relationship? Ecology 87:1244–1255

Kemp DR, Michalk DL (2007) Towards sustainable grassland and livestock management. J Agric Sci 145:543–564

Kohler F, Gillet F, Gobat J-M et al (2006) Effect of cattle activities on gap colonization in mountain pastures. Folia Geobot 41:289–304

König HP (2002) Stickstoffumsatz und N_{min}-Anreicherung auf Grünland während des Winters bei ganzjähriger Außenhaltung von Fleischrindern. In: agricultural sciences. University of Göttingen, p 125

Kruess A, Tscharntke T (2002) Contrasting responses of plant and insect diversity to variation in grazing intensity. Biol Conserv 106:293–302

Laca EA, Ortega IM (1996) Integrated foraging mechanisms across spatial and temporal scales. Proc Internat Rangel Cong 5:129–132

Lamoot I, Callebaut J, Degezelle T et al (2004) Eliminative behaviour of free-ranging horses: do they show latrine behaviour or do they defecate where they graze? Appl Anim Behav Sci 86:105–121

Ledgard SF, Steele KW, Saunders WHM (1982) Effects of cow urine and its major constituents on pasture properties. N Z J Agric Res 25:61–68

Ledgard SF, Sprosen MS, Penno JW et al (2001) Nitrogen fixation by white clover in pastures grazed by dairy cows: temporal variation and effects of nitrogen fertilization. Plant Soil 229:177–187

Leiber F, Kreuzer M, Nigg D et al (2005) A study on the causes for the elevated n-3 fatty acids in cows' milk of alpine origin. Lipids 40:191–202

Loucougaray G, Bonis A, Bouzille J-B (2004) Effects of grazing by horses and/or cattle on the diversity of coastal grasslands in western France. Biol Conserv 116:59–71

Luck GW, Daily GC, Ehrlich PR (2003) Population diversity and ecosystem services. Trends Ecol Evol 18:331–336

MacDiarmid BN, Watkin BR (1971) The cattle dung pat 1. Effect of dung patches on yield and botanical composition of surrounding and underlying pasture. J British Grassland Soc 26:239–245

Martin C, Morgavi DP, Doreau M (2010) Methane mitigation in ruminants: from microbe to the farm scale. Animal 4:351–365

Matthew C, Assuero SG, Black CK et al (2000) Tiller dynamics of grazed swards. In: Lemaire G, Hodgson J, de Moraes A, Carvalho PCF, Nabinger C (eds) Grassland ecophysiology and grazing ecology. CABI Publishing, Wallingford

Menard C, Duncan P, Fleurance G et al (2002) Comparative foraging and nutrition of horses and cattle in European wetlands. J Appl Ecol 39:120–133

Menneer JC, Ledgard S, McLay C et al (2005) Animal treading stimulated denitrification in soil under pasture. Soil Biol Biochem 37:1625–1629

Mills J, Rook AJ, Dumont B et al (2007) Effect of livestock breed and grazing intensity ongrazing systems: 5. Management and policy implications. Grass Forage Sci 62:429–436

Min BR, Barry TN, Attwood GT et al (2003) The effect of condensed tannins on the nutrition and health of ruminants fed fresh temperate forages: a review. Anim Feed Sci Technol 106:3–19

Mittelbach GG, Steiner CF, Scheiner SM et al (2001) What is the observed relationship between species richness and productivity? Ecology 82:2381–2396

Moloney AP, Fievez V, Martin B et al (2008) Botanically diverse forage-based rations for cattle: implications for product composition, product quality and consumer health. Grassland Sci Eur 13:361–374

Moog D, Poschlod P, Kahmen S et al (2002) Comparison of species composition between different grassland management treatments after 25 years. Appl Veg Sci 5:99–106

Moretto AS, Distel RA (1997) Competitive interactions between palatable and unpalatable grasses native to a temperate semi-arid grassland of Argentina. Plant Ecol 130:155–161

Moretto AS, Distel RA (1999) Effects of selective defoliation on the competitive interaction between palatable and unpalatable grasses native to a temperate semi-arid grassland of Argentina. J Arid Environ 42:167–175

Mote TE, Villalba JJ, Provenza FD (2008) Sequence of food presentation influences intake of foods containing tannins and terpenes. Appl Anim Behav Sci 113:57–68

Mulder CPH, Jumpponen A, Högberg P et al (2002) How plant diversity and legumes affect nitrogen dynamics in experimental grassland communities. Oecologia 133:412–421

Mulholland B, Fullen MA (1991) Cattle trampling and soil compaction on loamy sands. Soil Use Manag 7:189–193

Nelson CJ (2000) Shoot morphological plasticity of grasses: leaf growth vs. tillering. In: Lemaire G, Hodgson J, de Moraes A, Carvalho PCF, Nabinger C (eds) Grassland ecophysiology and grazing ecology. CABI Publishing, Wallingford

Niklaus P, Wardle D, Tate K (2006) Effects of plant species diversity and composition on nitrogen cycling and the trace gas balance of soils. Plant Soil 282:83–98

Nolan T, Connolly J (1989) Mixed v. mono-grazing by steers and sheep. Anim Prod 48:519–533

Norman MJT, Green JO (1958) The local influence of cattle dung and urine upon the yield and botanical composition of permanent pasture. Grass Forage Sci 13:39–45

Oelmann Y, Kreutziger Y, Temperton VM et al (2007) Nitrogen and phosphorus budgets in experimental grasslands of variable diversity. J Environ Qual 36:396–407

Oenema O, Velthof GL, Yamulki S et al (1997) Nitrous oxide emissions from grazed grassland. Soil Use Manag 13:288–295

Opitz von Boberfeld W (1994) Grünlandlehre: biologische und ökologische Grundlagen. Ulmer, Stuttgart

Osoro K, Martínez A, Celaya R (2002) Effect of breed and sward height on sheep performance and production per hectare during the spring and autumn in Northern Spain. Grass Forage Sci 57:137–146

Osoro K, García U, Jáuregui BM et al (2007) Diet selection and live-weight changes of two breeds of goats grazing on heathlands. Animal 1:449–457

Owens LB, Van Keuren RW, Edwards WM (2003) Non-nitrogen nutrient inputs and outputs for fertilized pastures in silt loam soils in four small Ohio watersheds. Agric Ecosyst Environ 97:117–120

Pärtel M, Sammul M, Bruun HH (2005) Biodiversity in temperate European grasslands: origin and conservation. Grassland Sci Eur 10:1–14

Pärtel M, Laanisto L, Zobel M (2007) Contrasting plant productivity–diversity relationships across latitude: the role of evolutionary history. Ecology 88:1091–1097

Pavlu V, Hejcman M, Pavlu L et al (2003) Effect of rotational and continuous grazing on vegetation of an upland grassland in the Jizerske Hory Mts., Czech Republic. Folia Geobot 38:21–34

Pfisterer AB, Joshi J, Schmid B et al (2004) Rapid decay of diversity-productivity relationships after invasion of experimental plant communities. Basic Appl Ecol 5:5–14

Plantureux S, Peeters A, McCracken D (2005) Biodiversity in intensive grasslands: effect of management, improvement and challenges. Agron Res 3:153–164

Provenza FD, Villalba JJ (2010) The role of natural plant products in modulating the immune system: an adaptable approach for combating disease in grazing animals. Small Rum Res 89:131–139

Pykälä J (2003) Effects of restoration with cattle grazing on plant species composition and richness of semi-natural grasslands. Biodivers Conserv 12:2211–2226

Rajaniemi TK (2002) Why does fertilization reduce plant species diversity? Testing three competition-based hypotheses. J Ecol 90:316–324

Rajaniemi TK, Allison VJ, Goldberg DE (2003) Root competition can cause a decline in diversity with increased productivity. J Ecol 91:407–416

Rook AJ, Dumont B, Isselstein J et al (2004) Matching type of livestock to desired biodiversity outcomes in pastures—a review. Biol Conserv 119:137–150

Roscher C, Schumacher J, Baade J et al (2004) The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. Basic Appl Ecol 5:107–121

Roscher C, Thein S, Schmid B et al (2008) Complementary nitrogen use among potentially dominant species in a biodiversity experiment varies between two years. J Ecol 96:477–488

Roy J (2001) How does biodiversity control primary productivity? In: Roy J, Saugier B, Mooney HA (eds) Terrestrial global productivity. Academic Press, San Diego

Rundlöf M, Edlund M, Smith HG (2010) Organic farming at local and landscape scales benefits plant diversity. Ecography 33:514–522

Sahin Demirbag N, Röver K-U, Wrage N et al (2009) Herbage growth rates on heterogeneous swards as influenced by sward-height classes. Grass Forage Sci 64:12–18

Sanderson MA, Skinner RH, Barker DJ et al (2004) Plant species diversity and management of temperate forage and grazing land ecosystems. Crop Sci 44:1132–1144

Schellberg J, Südekum K-H, Gebbing T (2007) Effect of herbage on N intake and N excretion of suckler cows. Agron Sustain Dev 27(4):303–311
Scherer-Lorenzen M, Palmborg C, Prinz A et al (2003) The role of plant diversity and composition for nitrate leaching in grasslands. Ecology 84:1539–1552
Schmid B (2002) The species richness productivity controversy. Trends Ecol Evol 17:113–114
Scimone M, Rook AJ, Garel JP et al (2007) Effects of livestock breed and grazing intensity on grazing systems: 3. Effects on diversity of vegetation. Grass Forage Sci 62:172–184
Silvertown J, Poulton P, Johnston E et al (2006) The park grass experiment 1856–2006: its contribution to ecology. J Ecol 94:801–814
Soder KJ, Sanderson MA, Stack JL et al (2006) Intake and performance of lactating cows grazing diverse forage mixtures. J Dairy Sci 89:2158–2167
Soder KJ, Rook AJ, Sanderson MA et al (2007) Interaction of plant species diversity on grazing behavior and performance of livestock grazing temperate region pastures. Crop Sci 47:416–425
Steinauer EM, Collins SL (2001) Feedback loops in ecological hierarchies following urine deposition in tallgrass prairie. Ecology 82:1319–1329
Steinbeiss S, Beßler H, Engels C et al (2008) Plant diversity positively affects short-term soil carbon storage in experimental grasslands. Glob Ch Biol 14:2937–2949
Suter D, Huguenin-Elie O, Nyfeler D et al (2010) Agronomically improved grass-legume mixtures: higher dry matter yields and more persistent legume proportions. Grassland Sci Europe 15:761–763
Tallowin JRB, Jefferson RG (1999) Hay production from lowland semi-natural grasslands: a review of implications for ruminant livestock systems. Grass Forage Sci 54:99–115
Tallowin J, Rook AJ, Rutter SM (2005) Impact of grazing management on biodiversity of grasslands. Anim Sci 81:193–198
Tilman D, Reich PB, Knops JMH (2006) Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441:629–632
Tracy BF, Faulkner DB (2006) Pasture and cattle responses in rotationally stocked grazing systems sown with differing levels of species richness. Crop Sci 46:2062–2068
Tracy BF, Sanderson MA (2004) Forage productivity, species evenness and weed invasion in pasture communities. Agric Ecosyst Environ 102:175–183
Traill WB, Arnoult MHP, Chambers SA et al (2008) The potential for competitive and healthy food chains of benefit to the countryside. Trends Food Sci Technol 19:248–254
Utsumi SA, Cangiano CA, Gallo JR et al (2009) Resource heterogeneity and foraging behaviour of cattle across spatial scales. BMC Ecol 9. doi:10.1186/1472-6785-1189-1189
Vallentine JF (2001) Grazing management, 2nd edn. Academic Press, San Diego
van Groenigen JW, Velthof GL, van der Bolt FJE et al (2005) Seasonal variation in N_2O emissions from urine patches: effects of urine concentration, soil compaction and dung. Plant Soil 273:15–27
van Peer L, Nijs I, Reheul D et al (2004) Species richness and susceptibility to heat and drought extremes in synthesized grassland ecosystems: compositional vs physiological effects. Funct Ecol 18:769–778
van Ruijven J, Berendse F (2003) Positive effects of plant species diversity on productivity in the absence of legumes. Ecol Lett 6:170–175
van Wieren SE, Bakker JP (1998) Grazing for conservation in the twenty-first century. In: WallisDeVries MF, Bakker JP, Van Wieren SE (eds) Grazing and conservation management. Kluwer, Dordrecht
Villalba JJ, Provenza FD (2009) Learning and dietary choice in herbivores. Rangel Ecol Manag 62:399–406
Wales WJ, Doyle PT, Dellow DW (1998) Dry matter intake and nutrient selection by lactating cows grazing irrigated pastures at different pasture allowance in summer and autumn. Aust J Exp Agric 38:451–460
Wang L, Wang D, He Z et al (2010) Mechanisms linking plant species richness to foraging of a large herbivore. J Appl Ecol 47:868–875
Weigelt A, Bol R, Bardgett RD (2005) Preferential uptake of soil nitrogen forms by grassland plant species. Oecologia 142:627–635
Weigelt A, Weisser WW, Buchmann N et al (2009) Biodiversity for multifunctional grasslands: equal productivity in high-diversity low-input and low-diversity high-input systems. Biogeosciences 6:1695–1706
White SL, Sheffield RE, Washburn SP et al (2001) Spatial and time distribution of dairy cattle excreta in an intensive pasture system. J Environ Qual 30:2180–2187
Whitehead DC (1995) Grassland nitrogen. CAB International, Oxon
Whitehead DC (2000) Nutrient elements in grassland. CAB International, Wallingford
Wilmshurst JF, Fryxell JM, Bergman CM (2000) The allometry of patch selection in ruminants. Proc R Soc Lond B Biol Sci 267:345–349
Yachi S, Loreau M (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. Proc Natl Acad Sci USA 96:1463–1468