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Selective livestock grazing and its consequences for functional vegetation properties and agronomic services of species-rich grasslands

PhD. Thesis

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Title page: Sheep (Romney-Marsh breed) grazing broad-leaved dry grassland dominated by Tor-grass (Brachypodium pinnatum). Photo: Zdeněk Miklas

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Abstract: Planning of agri-environmental measures requires knowledge of the effects of management regimes on the occurrence of endangered plant and animal species as well as of the effects on grassland agronomic services, i.e. forage quantity and quality. In the face of the renascence of grazing at the end of the 1990s we particularly assessed the causes of selective grazing by livestock and evaluated its consequences for the agronomic value of the extraordinarily species-rich grasslands in the White Carpathian Mts., Czech Republic. In order to understand feedbacks of grazing on vegetation properties, studies of diet selection were reviewed and sheep grazing patterns in productive mesic and low-productive dry species-rich grasslands were analysed. The effects of four management regimes were investigated in long-term experiments using community-weighted means of plant functional traits. In addition, as nature conservation frequently requires postponing of grassland harvest until summer, we were interested to know in which grassland types this measure does not substantially reduce forage quality. Our results indicate that maximising forage quality and maximising forage quantity are alternative diet selection strategies of sheep to exploit food resources in mesic and dry grasslands, respectively. This provided insight into the effects of early-spring grazing in broad-leaved dry grasslands, where sheep grazing unexpectedly eliminated productive but unpalatable grasses. Although mid-July mowing decreased the performance of grasses and enhanced forbs most of all management treatments, a pattern desired by nature conservationists, it cannot be recommended as the optimal low-cost management for broad-leaved dry grasslands due to its adverse effects on forage quantity and quality. Community-weighted mean of leaf dry matter content was a good indicator of seasonal growth pattern and forage quality, but not a suitable predictor of forage quantity when grasslands under different management regimes were taken into account. In two independent studies we evidenced that later-developing species were best supported under long-time grazing pressure, and postponing of defoliation until summer produced the smallest decrease in forage quality in grasslands managed in this way. We propose to establish a one-year late harvest application in permanent pastures as a low-cost agri-environmental measure.

Key-words: agri-environmental measures, species-rich grasslands, agronomic value, late harvest, plant functional traits, selective grazing, mowing, long-term management experiments, White Carpathian Mts.

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Abstrakt: Plánování agro-environmentálních opatření vyžaduje znalosti vlivu managementu na výskyt ohrožených druhů rostlin a živočichů stejně jako vlivu na agronomické servisy travních porostů, tj. množství a kvalitu píce. Vzhledem k renesanci pastvy na konci 90. let 20. století v mimořádně druhově bohatých travních porostech Bílých Karpat (Česká republika) bylo hlavním cílem této práce posoudit příčiny selektivní pastvy dobytka a vyhodnotit její dopady na agronomickou hodnotu. Aby bylo možno lépe porozumět zpětnému vlivu pastvy na vegetaci, byly nejdříve revidovány studie selektivity pastvy a následně analyzovány pastevní preference ovcí v produktivních (mezických) a nízkoproduktivních (suchých) druhově bohatých travních porostech. Byly také založeny dlouhodobé experimenty se čtyřmi typy managementu, na základě kterých byl hodnocen vliv managementu na vegetaci pomocí vážených průměrů rostlinných znaků. Protože ochrana přírody často vyžaduje odložení sklizně travních porostů do letních měsíců, zajímalo nás také, ve kterých typech travních porostů toto opatření výrazně nesnižuje kvalitu píce. Naše výsledky ukazují, že maximalizace kvality píce a maximalizace množství píce jsou alternativní pastevní strategie ovcí pro využití potravních zdrojů v mezických vs. suchých travních porostech. Toto zjištění významně pomohlo objasnit efekt časně jarní pastvy v širokolistých suchých trávnících, kde pastva neočekávaně eliminovala produktivní, ale nechutné trávy. I když sečení v polovině července nejvíce ze všech typů managementu snížilo dominanci trav a zvýšilo proporci bylin (tj. nejvíce podpořilo procesy požadované ochranou přírody), sečení v polovině července nelze doporučit jako optimální nízkonákladový management pro širokolisté suché trávníky z důvodu nepříznivých dopadů na množství a kvalitu dostupné píce. Na základě našich výsledků lze konstatovat, že vážený průměr obsahu sušiny v listech byl dobrým indikátorem sezónního vývoje společenstva i ukazatelem kvality píce, ale nebyl shledán jako vhodný prediktor množství dostupné píce v případě, když byly společně analyzovány travní porosty s různým obhospodařováním. Ve dvou nezávislých studiích jsme dále prokázali, že fenologicky pozdní druhy jsou nejvíce podporovány režimem dlouhodobé časně jarní pastvy, a odložení sklizně do letních měsíců způsobuje nejmenší pokles kvality píce v travních porostech obhospodařovaných dlouhodobě právě tímto způsobem. Navrhujeme tedy zavést jednorázovou pozdní sklizeň na dlouhobých pastvinách jako levné agro-environmentální opatření.

Klíčová slova: agro-environmentální opatření, druhově bohaté travní porosty, agronomická hodnota, pozdní sklizeň, funkční znaky rostlin, selektivní pastva, sečení, dlouhodobé managementové pokusy, Bílé Karpaty

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Declaration

I hereby declare that this thesis has been completely worked out by myself and the named co-authors using the cited references.

Olomouc, 26th May 2011 Jan Mládek

Contributions of the co-authors

- The review paper in **Chapter III** was elaborated approximately equally by P. Hejcmanová and J. Mládek. Authorship of particular subchapters is listed at the first page of the chapter.

- The manuscript in **Chapter IV** was prepared by J. Mládek from data collected by M. Dvorský. P. Mládková helped with data analysis and the other co-authors contributed to correct formulations and terminology.

- The manuscript in **Chapter V** originates from long-term experiments conducted by J. Mládek. Several botanists listed in the acknowledgements helped with field data collection, P. Mládková performed statistical analyses, J. Doležal corrected formulations, and M. Dančák was indispensable in identifying plants in the field.

- The paper in **Chapter VI** was elaborated by J. Mládek from data collected by J. Juráková (MSc. thesis supervised by J. Mládek).

- **Chapter VII** provides the test of the hypothesis suggested by J. Mládek. P. Mládková performed statistical analyses, S. Hejduk helped with field data collection, and the other co-authors contributed to correct formulations and terminology.

- The published paper in **Chapter VIII** is based on an idea suggested by J. Mládek. M. Hejcman substantially helped with the introduction and an interpretation of the results, S. Hejduk contributed to field data collection, M. Duchoslav performed complicated two-way analyses of variance with missing cells, and V. Pavlů helped with agronomical terminology.

- The manuscript in **Chapter IX** was prepared equally by J. Mládek and M. Hejcman. S. Hejduk contributed to field data collection, V. Pavlů helped with agronomical terminology, and M. Duchoslav and P. Mládková gave advice on statistical analyses.

The above-mentioned contributions to published papers or manuscripts were confirmed by all co-authors at e-mail address jan.mladek@upol.cz on 4th May 2011.

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Our long-term management experiments comprise 240 permanent plots, which for monitoring are divided into 9 fields by an iron frame. Thus, monitoring of 2160 squares over six years provided an unimaginable total of 185,000 records of species cover. This amount of data could not have been collected and transcribed into a digital format without the help of the following friends and students: Vendula Křivánková, Michaela Kocyanová, Martin Kočí, Kateřina Čiháková, Jana Juráková, Petr Pavelčík, Miroslav Dvorský, Alena Jírová, Lenka Šafářová, Jana Richterová, Štěpán Slížek, Lenka Králová, Tomáš Berka, Jana Gajdová, Lukáš Chrást, Radim Hédl, Petra Špačková, Zuzana Münzbergová and Karla Vincenecová.

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Motto: Let everything you write find a reader.

(Son Adam studying methodology for grazing management in protected landscape areas – Mládek et al. 2006)

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CHAPTER I

General introduction

In the early 1990s, large-scale land-use changes took place in many countries of Central and Eastern Europe as a result of political transformation (Miklas 2008; Metera et al. 2010). In the Czech Republic, cattle numbers decreased to half and the number of sheep to a quarter in comparison to the 1980s (Hejcman 2005a). In consequence, vast areas of low-productive grasslands were abandoned, especially in the hilly borderlands. Cessation of grassland management led to encroachment of shrubs and expansion of highly competitive grasses (e.g. *Arrhenatherum elatius*, *Brachypodium pinnatum*, *Calamagrostis epigejos*, *Molinia arundinacea, M. caerulea*) and forbs (e.g. *Hypericum maculatum, Polygonum bistorta*), which caused subsequent severe reduction of species richness (Lepš 1999; Klimeš et al. 2000; Klimeš et al. 2001; Mládek et al. 2006; Pecháčková et al. 2010). In 1999 came a turning point in Czech agricultural and nature conservation policy. Several subsidy programmes were introduced. Particularly extensive grazing received considerable support and so became the most profitable tool for grassland maintenance (Miklas 2008). Instead of cutting and haymaking or rotational grazing of dairy cows performed in the past fifty years, farmers increasingly began to apply grazing of large herds of beef cattle and sheep for the entire vegetation season due to its higher profitability. However, at that time there was only little evidence of the effect of grazing regimes on the vegetation structure and occurrence of endangered plant and animal species in various grassland types of the Czech Republic (see Krahulec et al. 2001; Pavlů et al. 2003; Háková et al. 2004).

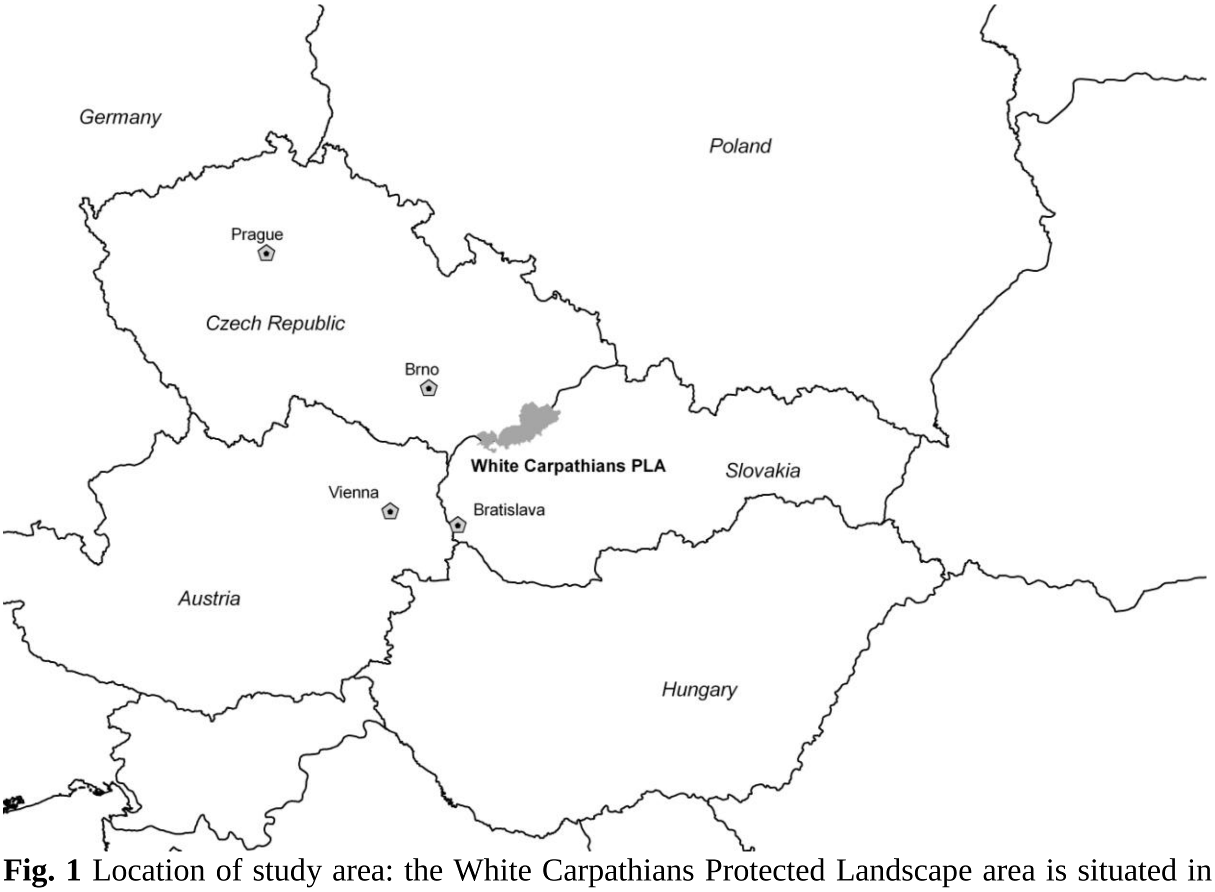

Fig. 1 Location of study area: the White Carpathians Protected Landscape area is situated in Central Europe in the borderland between the Czech Republic and Slovakia (in Czech Republic: Bílé Karpaty, in Slovakia: Biele Karpaty)

As transferability of results of abundant grazing studies from Western Europe is limited due to different species compositions and also due to a discrepancy in effects under variable climatic conditions (e.g. de Bello et al. 2005), in 2000 the Ministry of the Environment started to support monitoring of the influence of grazing regimes on vegetation in Protected Landscape Areas (PLA). Several projects were initiated in the Bílé Karpaty PLA (Fig. 1), which can boast on possessing extremely species-rich grasslands in the European context (Jongepier and Jongepierová 2009). I was fortunate to take part in the first project (VaV 610/10/00), under which I compiled my master thesis focused on the classification of grassland communities with respect to grazing management and its history (published later: Mládek 2008). In 2003, I was approached by I. Jongepierová (Czech Union for Nature Conservation & Administration of the Bílé Karpaty PLA) to conduct a multidisciplinary project as a principal investigator (VaV 620/11/03). This project was aimed at bringing evidence from a wide spectrum of semi-natural grassland communities regarding effects of grazing on plants, insects and soil biota, and simultaneously report on forage quantity and quality, subsequent livestock performance and farming economy in order to facilitate the preparation of Czech agri-environmental measures and nature conservation subsidy programmes. An important output of the project was a complex methodology for management of grasslands with grazing in PLAs (Mládek et al. 2006). As a consequence of all the research issues solved during both previous projects and during the current project, which is dealing with effects of management on plant community functioning (RPV SP/2D3/179/07), I decided to conceive my PhD thesis in a complex manner.

Large herbivores such as cattle and sheep graze selectively responding to many abiotic and biotic factors. Hence, contrary to mowing machines, sward defoliation by grazing is usually not uniform but highly heterogeneous. Especially in species-rich grasslands, the diversity of forage supply enables large herbivores to express their feeding preferences. To understand the causes and consequences of selective grazing I made a survey of all relevant literature sources and compiled a review on diet selection of herbivores in species-rich pastures together with P. Hejcmanová, specialist in large herbivore grazing behaviour (**Chapter III**). Diet selection, in other words foraging strategy, substantially differs between sheep and cattle; and their feeding preferences are modified by availability and spatial distribution of preferred forage as well as by overall grazing intensity. Hence, in order to recognise the underlying mechanisms of diet selection in our species-rich grasslands and regional grazing systems, two separate studies were performed (sheep selectivity in **Chapter IV**; preliminary results of cattle grazing selectivity in: Pavelčík and Mládek 2008). Several researchers tried to find a mechanistic understanding between sheep selectivity and plant response to grazing (e.g. Cingolani et al. 2005; Evju et al. 2009). However, they did not find clear links. This might be attributed to the fact that positive response to a grazing regime is not only exhibit by less defoliated species (avoidance strategy) but also by light-demanding species compensating frequent defoliation by fast regrowth (tolerance strategy). Furthermore, response to grazing is dependent not only on defoliation rate but also on nutrient impoverishment or enrichment (see Rusch et al. 2009). Consequently, selective defoliation together with soil disturbance by trampling and nutrient enrichment with faeces and urine produce a feedback on structure and species composition of the sward.

Recent grassland studies have documented that the effects of grazing (or any other management regime) on community structure and composition can be better understood using ecological knowledge of plant functional traits (de Bello et al. 2005; Cruz et al. 2010). Particularly community-weighted means of traits have proved to be suitable for an identification of functional vegetation properties (see e.g. Doležal et al. 2011). Community-weighted means are based on the ‘biomass ratio hypothesis’ (Grime 1998), which postulates that functional vegetation properties depend on the traits of the most abundant species of the community. Especially leaf traits (specific leaf area, leaf dry matter content – henceforth LDMC) related to fundamental plant resource acquisition – conservation trade-offs are useful to capture the response of a community to factors applied such as management regime (Duru et al. 2010a) as well as to predict community feedback on ecosystem processes such as litter decomposition (Garnier et al. 2004). These are called 'response traits' and 'effect traits', respectively (Lavorel and Garnier 2002). Thus, community-weighted leaf traits are suitable to assess ecosystem services of semi-natural grasslands (Díaz et al. 2007; de Bello et al. 2010). Land-use (i.e. in our case long-term grassland management regime) substantially modifies delivery of ecosystem services by affecting ecosystem properties either directly or indirectly via functional traits (Lavorel et al. 2011); the conceptual framework of all relevant links is presented in Fig. 2.

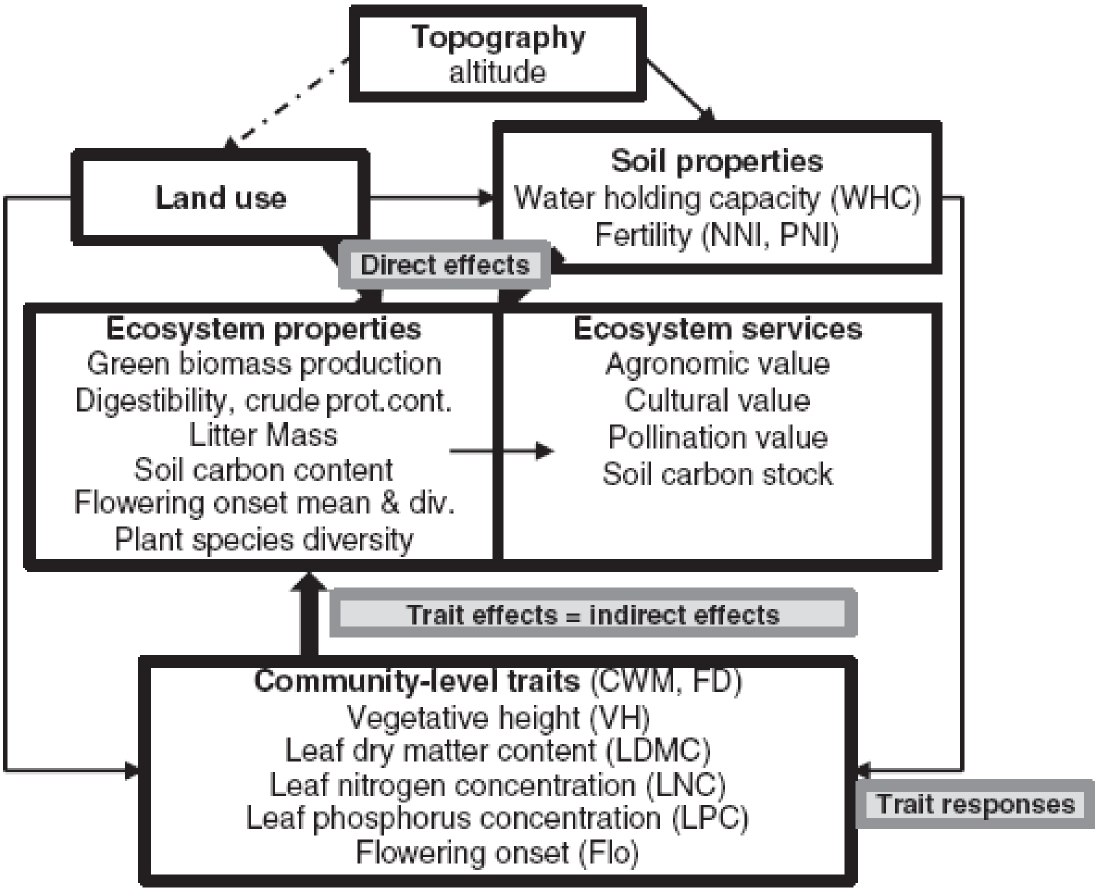

Fig. 2 Ecosystem services of grasslands (including agronomic services – forage quantity and quality) are derived from ecosystem properties. This conceptual framework identifies the direct effects of land use on ecosystem properties; the combined direct effects of land use and abiotic variables on ecosystem properties, and the combination of abiotic effects with indirect effects via plant functional traits (CWM: community-weighted means of functional traits; FD: trait functional divergence) (Lavorel et al. 2011)

Huge areas of grasslands throughout Europe are currently maintained for their biodiversity (pollination, aesthetic and cultural values), but financial resources for biodiversity-targeted management are limited, therefore knowledge of management-induced effects on the agronomic value are of high importance. In consequence, understanding of the relationship between functional traits and seasonal development of forage quantity and quality is crucial for assessing agronomic services of species-rich grasslands. The first steps to reaching this have been made. High LDMC was identified as a suitable marker of low herbage digestibility and productivity (Pontes et al. 2007; Duru et al. 2008; Andueza et al. 2010). Further, diversity of LDMC within a community was acknowledged to identify a seasonal growth pattern (Duru et al. 2010b, c): high diversity was shown to be connected with less variation of herbage mass around the growth peak, thus providing greater flexibility in grassland harvest (Martin et al. 2009).

Although several current studies highlighted the importance of intraspecific trait variability for inspection of community-weighted trait response to environment (e.g. Lepš et al. 2011), for most traits positive covariation between species turnover and intraspecific trait variability was reported. Thus, neglecting intraspecific trait variability results usually only in underestimation of community response to environmental changes, in other words patterns found on the basis of field measurements should be more pronounced than patterns on the basis of ‘fixed’ database values. Thefore, we utilised freely accessible trait values of most European grassland species in databases (BiolFlor – Klotz et al. 2002; LEDA – Kleyer et al. 2008), and elucidated herbivores’ diet selection strategies, effects of grazing regimes on community functioning and agronomic services of species-rich grasslands with the help of community-weighted functional traits.

In order to investigate the effects of grazing regimes on plant species composition and community functioning, long-term experiments were established in several grassland communities (associations as defined in Chytrý (2007)): *Carlino acaulis-Brometum erecti* Oberdorfer 1957 (alliance *Bromion erecti* Koch 1926), *Festuco capillatae-Nardetum strictae* Klika et Šmarda 1944 (alliance *Violion caninae* Schwickerath 1944), *Poo-Trisetetum flavescentis* Knapp ex Oberdorfer 1957 (alliance *Arrhenatherion elatioris* Luquet 1926) and *Anthoxantho odorati-Agrostietum tenuis* Sillinger 1933 (originally included in *Cynosurion cristati* Tüxen 1947, but according to Rozbrojová et al. 2010 rather belonging to *Arrhenatherion elatioris*). In 2004 we selected three sites in the Bílé Karpaty (White Carpathian) Mts. (*Bromion, Cynosurion, Violion*) and in 2006 three sites in the Javorníky Mts. (*Arrhenatherion, Bromion, Bromion*), in which the same experimental design was used. The design included four treatments: (1) mowing in mid-July, (2) extensive rotational sheep grazing starting in June combined with burning of litter every third year in March (traditional management in the region), (3) extensive rotational sheep grazing, and (4) abandonment (lying fallow). Each treatment was 10 times replicated within each site; one replication comprised of a 5 m × 5 m experimental plot. Treatments were arranged in blocks situated within two ‘exclosures’ per site, i.e. one exclosure contained five blocks (Fig. 2).

Six (five) years of vegetation monitoring in permanent subplots 1 m^2 in size (located in the centre of each experimental plot) in broad-leaved dry grasslands (all three *Bromion* sites) were sufficient to reveal marked differences in effects of management treatments on community-weighted functional traits (**Chapter V**). The design of the experiments encompassed factors with random effects so that performing data analysis with traditional repeated measures ANOVA was not eligible. Therefore, all analyses were carried out with linear mixed-effect models using restricted maximum likelihood methods (Crawley 2007; Zuur et al. 2009), in which management and its interaction with year were treated as fixed effects while site, exclosure, block, subplot code and year as random effects.

Grassland managers advising farmers on utilisation of semi-natural grasslands need some simple diagnostic tools to assess grassland agronomic services, i.e. forage quantity and quality. As mentioned above, methods based on functional vegetation properties seem to be very promising (see Ansquer et al. 2009a; Duru et al. 2010c). We decided to test if patterns found for community-weighted LDMC on a large scale of grasslands are valid when differently managed swards are taken into consideration. Low LDMC at the community scale was acknowledged to be connected to high herbage productivity and high nutrient concentrations in biomass (Garnier et al. 2004; Gaucherand and Lavorel 2007). Therefore, considering vegetation in three long-term experiments in the Bílé Karpaty (White Carpathian) Mts. (*Bromion, Cynosurion, Violion*), we asked whether management supporting the lowest community LDMC also provides the highest amount of standing biomass and highest total amounts of nitrogen (N), phosphorus (P) and potassium (K) (**Chapter VI**).

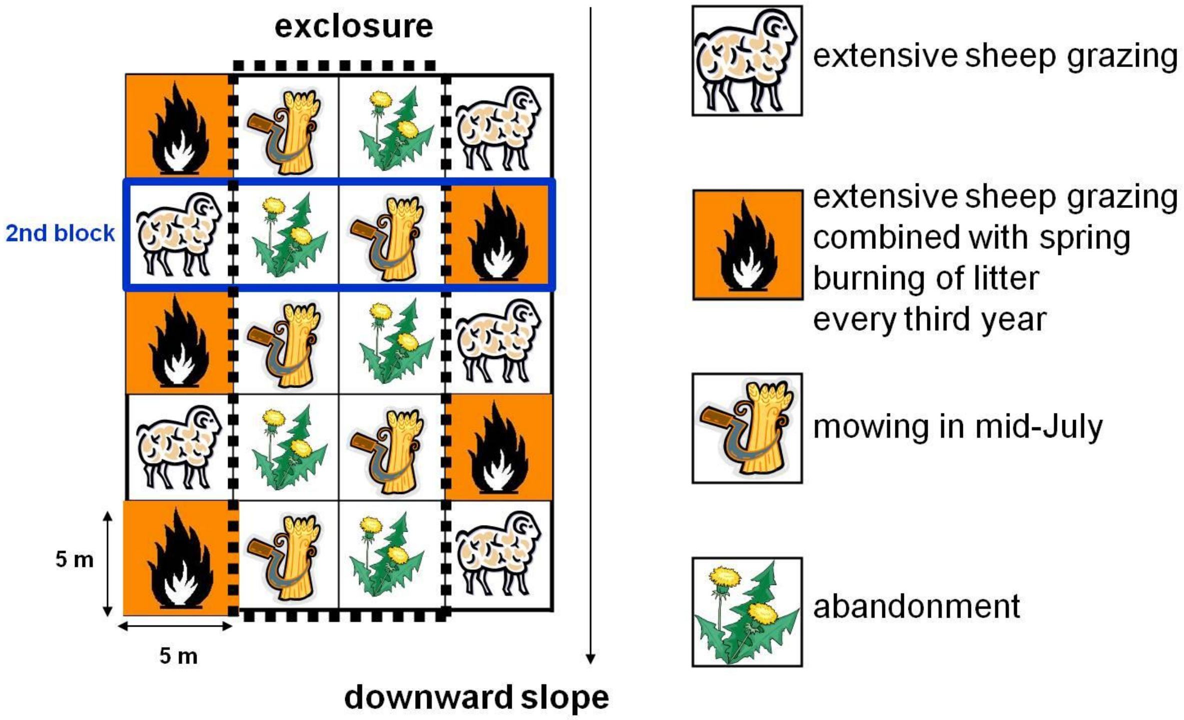

Fig. 3 Experimental design used in 12 grasslands. Management treatments were allocated into five blocks; treatments within blocks were not arranged randomly for reasons of building of an exclosure around the mown and abandoned plots (similarly as in Hejcman et al. 2005b). Moreover, the vicinity of burned and abandoned plots had to be excluded with regard to fire risk

Especially in mountainous and less-favoured areas, farmers have to accommodate timing of grassland management to weather conditions or new agri-environmental schemes. Recently applied schemes usually postpone defoliation activities to June–July in order to assure diaspore production of endangered plant species and reproduction of insects and ground-nesting birds (Kleijn and Sutherland 2003). Thus, farmers often face the problem which grasslands enable a harvest later in the season without a substantial decline in forage quality (Martin et al. 2009). As forage quality decline is particularly driven by the speed of phenological progression of species (Duru et al. 2008); it is a challenging question which factors control this progression. It was found that grassland communities with higher community-weighted LDMC flower later (Ansquer et al. 2009b), however, hitherto no study has answered the question how phenological progression is modified by long-term management (**Chapter VII**). In another study we explicitly asked how postponed defoliation affects biomass production and forage quality in different vegetation types and, therefore, profitability of livestock production systems. In agriculturally improved grasslands summer harvest provides forage of lower digestibility for livestock and lower N, P and K concentrations than spring harvest (Bruinenberg et al. 2002; Gibson 2009). However, semi-natural grasslands occur on a wide range of soils with distinct levels of nutrient availability and their dominant plant species substantially differ in resource economy strategies (Eckstein et al. 1999). Leaf lifespan vs. nutrient resorption strategies may produce distinct seasonal nutrient concentration patterns. The paper in **Chapter VIII** is focused on seasonal changes in crude fibre concentration and organic matter digestibility while manuscript in **Chapter IX** primarily deals with the development of nutrient concentrations in biomass and provides a comparison of these with requirements for optimal cattle nutrition. Furthermore, the presented ratios of nutrient concentrations in biomass help to reveal which nutrients limit biomass production and thus preserve the unique species-richness of grassland communities in the Bílé Karpaty Mts., where flysch bedrock with alternating claystone and sandstone layers (usually rich in Ca and K) predominates. This question is particularly important under increasing levels of atmospheric N deposition and has not received much attention in the Western Carpathians to date (but see Rozbrojová and Hájek 2008).

Understanding of interactions between plants, nutrient flows and large herbivore grazing is of high importance for designing proper agri-environmental schemes and farm plans. The complexity of effects of grassland management on structure and functioning of semi-natural grasslands (including agronomic services) has thoroughly been presented in the Czech Republic by prof. Rychnovská (Rychnovská 1993) and a group led by prof. Hejcman and Dr. Pavlů (Pavlů et al. 2003; Hejcman 2005a; Pavlů et al. 2006), who showed me all the processes in grasslands in a wide context. However, effects of grazing regimes on extraordinarily species-rich grasslands in the Bílé Karpaty Mts. have received almost no attention (but see a short-term study by Lanta et al. 2009), and therefore this thesis provides first complex picture of how these unique grasslands function under grazing regimes.

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CHAPTER II

Aims of the Thesis

As indicated in the title the Thesis deals with selective livestock grazing and its consequences for functional vegetation properties and agronomic services of species-rich grasslands. To understand the causes and consequences of selective grazing we aimed to following issues:

- review studies dealing with diet selection of herbivores in species-rich grasslands
- recognise the underlying mechanisms of diet selection of sheep in productive mesic and low-productive dry species-rich grasslands
- understand the feedbacks of sheep grazing selectivity on functional vegetation properties
- reveal the relationship between community-weighted plant functional traits and forage quantity and quality and their seasonal development
- on the basis of long-term management experiments identify management-induced effects on the agronomic value of broad-leaved dry grasslands
- examine which long-term management produces vegetation with the slowest phenological progression and supports phenological complementarity
- elucidate seasonal development of organic matter digestibility and nutrient concentrations in biomass in species-rich grasslands and compare their absolute values with characteristics of agriculturally improved grasslands and with requirements for optimal cattle nutrition
- identify grassland types in which postponing of the first harvest until summer does not substantially reduce forage quality
- recognise long-term management regime which supports functional vegetation properties providing a potential for late harvest

CHAPTER III

Review: Diet selection of herbivores on species-rich pastures

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Abstract

Understanding of grazing by domesticated ruminants for the animal production is of high economic importance throughout the world and therefore is paramount in designing management strategies for livestock production. The plant-animal interface is the central feature of these systems. Food quantity and quality are major determinants of animal production. Both food quantity and quality herbivores maintain through selective foraging which alters sward structure, modifies plant species composition and thus produces new pattern of plant biomass production. We focus therefore in our chapter on mechanisms of foraging selection which may enable us to insight into grazing decision making and processes. The central question is: what are principle drivers in grazing decision processes leading to high selectivity on species-rich grasslands and this at different spatial and temporal levels? However, before to answer this question we have to precise, what do we mean under selective grazing and to distinguish it from other terms used in the domain of foraging strategies. We will also summarize known methods and quantification of grazing selectivity. Only then we may bring a complex view on various factors affecting diet selection strategies of herbivores in species-rich pastures. Finally, we propose management rules in order to use herbivore foraging selectivity to utilize food resources in semi-natural grasslands most efficiently and simultaneously keeping forage production and quality of grasslands from long-term perspective.

Contents:

Introduction

Pastures and grazing livestock managed by man are an inseparable part of animal husbandry since neolith till present. Pastures form our landscape and give it its high economic value. They provide, furthermore, important regulating ecosystem services and have high intrinsic value for future maintenance as a cultural heritage and as biodiversity hotspots (e.g. Austrheim et al. 1999; Hart 2001; Pavlů et al. 2006; Smit et al. 2008). Species-rich grasslands originate predominantly from large herbivores' grazing at moderate grazing pressure which induce high species richness and enhance occurrence of vulnerable species (Collins et al. 1998; Pavlů et al. 2007). At present, the management of these grasslands fulfil therefore not exclusively economic goals. The role of grazing systems has been widely reassessed and multiple goals have been assigned to current grassland management with strong focus on ecosystem function and biodiversity conservation. Within the terms of animal husbandry, the ultimate goal of livestock producers is therefore to achieve on pastures an environmentally and economically sustainable livestock production and to maintain the forage production. This requires a fundamental understanding of the processes at the plant-animal interface. The knowledge of diet selection is therefore vital for agronomists taking care about animal nutrition and also for grassland specialists managing development of sward structure and species composition.

The plant species composition and sward structure on species-rich pastures is substantially formed by selective defoliation which changes micro-site conditions, such as light, moisture or temperature and consequently altered competitiveness among plant species in the sward (Bullock and Marriott 2000). Grazing thus offers an important tool for conservation management. The success of maintaining high biodiversity levels lies however on grazing intensity, grazing distribution pattern and specific exploitation of available forage resources by animals. Grazing may both, either increase, or decrease plant species composition and sward heterogeneity (Adler et al. 2001). Hence, the pastoral management needs to predict animals' foraging decisions at various temporal and spatial scales. Given the constraints imposed through management practices, animals are continually faced with a series of short-term decisions about what to forage and where to forage (Taylor 1993). This is fundamental to animal decisions on the trade-off between forage quality and quantity ingested. In intensive production systems with few highly productive plant species, foraging is mainly function of sward characteristics such as height or structure (homogeneous *versus* heterogeneous sward) integrated to particular patches and their spatial distribution (e.g. Wallis De Vries et al. 1999; Griffiths et al. 2003). On species-rich pastures, the animals' decision-making becomes more complex because animals have not only spatially heterogeneous sward structure, but also more variability in rich food resources of divers quantity and quality. The diversity of forage supply enables large herbivores to select their forage in relation to available plant species and their particular quality. Thus, differences among large herbivore species in forage selectivity offer potential for efficient utilization of pastures with diverse arrays of plant species. The knowledge of mechanisms of foraging selection may help us to link the grazing processes with management leading to both effective livestock production and biodiversity conservation.

We focus therefore in our chapter on mechanisms of diet selection of large herbivores which may enable us to insight into grazing decision making and processes. The central question is: what are principle drivers in grazing decision processes leading to high selectivity of animals on species-rich grasslands? However, before to answer this question we have to precise, what we mean under grazing selectivity and to distinguish it from other terms used in the domain of foraging strategies. We will also review methods of evaluating foraging selectivity. Only then we may bring a complex view on various factors affecting diet selection on herbivores with particular attention paying to species richness of the sward. And finally, we emphasize the importance of management of grazing systems for animal performance.

What do we mean under grazing selectivity?

Grazing selectivity presents an important mechanism whereby grazing herbivores search and intake individual food sources. This mechanism helps the animals to respond to changes in actual stage of sward (caused either naturally or by management) and *vice versa*, selective grazing affects plant-species composition and vegetation structure of pasture swards.

First, the terms selective grazing or diet selection can be easily replaceable by diet preferences. There is however a clear distinction between selection and preference which consists in the difference between what the animals eat and what they would eat if given complete freedom of choice (Hodgson 1979). Such a situation is almost impossible on the pastures. Herbivores face various constraints caused by environmental and management factors while foraging on pastures. Then, the animals start to forage selectively, adjusting their choice to the available food resources. Selection is thus a function of preference, but it is clearly affected by the abundance or the availability of both palatable and unpalatable plant species, and by their spatial distribution (Wang et al. 2010a). Selection is further influenced by some of the animals' foraging abilities; for example, their ability to sort one food from the others, to walk long distances and to learn and remember the location of food patches (Dumont 1997; Dumont et al. 2002).

On species-rich pastures, the vegetation is heterogeneous and the grazing pattern interacts with the spatial distribution of vegetation. If the spatial pattern of grazing does not follow the pattern of vegetation, we refer to 'patch grazing' or 'homogeneous grazing'. When grazing pattern closely tracks vegetation pattern, we refer to 'selective grazing' (Adler et al. 2001).

Selective grazing has been described in a conceptual hierarchical model across different spatial and temporal scales. Senft et al. (1987) and Bailey et al. (1996) defined six basic spatial scales for large herbivores in a foraging hierarchy which span from plant level to regional scale and each scale is functionally defined based on characteristic behaviours that occur at different rates: 1. Bite is the smallest spatial as well as temporal scale and is defined as the complete herbage prehension, jaw and tongue movements, and severance by head movements (Laca et al. 1994). 2. Feeding station is a set of plants available to a herbivore without moving their front feet (Novellie 1978). 3. Patch represents a cluster of feeding stations separated from others by a break in the foraging sequence when animals reorient to a new location. 4. Feeding site refers to a set of patches in a contiguous spatial area that animal graze within a foraging bout. It may contain one plant community or even extend beyond. Foraging bout is the time spent continuously foraging without interruption till a complete change of behaviour, for instance to resting, ruminating or other. 5. Camp is a set of feeding sites which involve places where animals drink, rest or seek shelter. 6. Home range represents large scale involving several camps, but usually limited by fencing on pastures or other barriers in the landscape. Temporal scales include short-term (instantaneous or daily scale), medium-term (vegetation season) and long-term (seasonal cycles and inter-annual variability) (O'Reagain and Swartz 1995). At each scale the animals confront a series of decisions. Free ranging herbivores have a free choice within a variety of habitats and food resources. They can independently migrate in an open landscape and to feed selectively to satisfy their energy, nutrient, and minerals requirements (McNaughton 1984; Wallis De Vries and Schippers 1994). At pastures in animal production systems different mechanisms operate because pastures are usually delineated by natural landscape barriers or by a fence imposed by management. In order to obtain adequate and balanced diet the animals must adopt a strategy coping with constraints of limited area affording resources limited in quantity, nutrient and mineral content. Pasture constitutes of one or more camps where animals together drink and rest between feeding bouts (Bailey et al. 1996). Species-rich pastures create implicitly heterogeneous sward with a number of patches and feeding sites. Regarding that the area of pasture is usually small and readily accessible the initial decision where to start grazing at the beginning of bout has a little importance. On the other hand, during the grazing, the animals search and select individual vegetation patches. At this level only bites are aggregated, which animals select only by the head movement in terms of feeding station (Bailey et al. 1996; Bailey et al. 1998). However, whatever the spatial scale, the animals' selectivity seems to be based on maximization of daily energy intake rather than instantaneous/momentary maximization (Wallis De Vries and Daleboudt 1994).

Measuring grazing selectivity in heterogeneous swards

Electivity indices

Although forage value is generally considered to be determined by organic matter digestibility (e.g. Marinas et al. 2003), palatability for herbivores does not strictly follow this plant characteristic and is also influenced by odour and taste of biomass (Provenza et al. 2003). Preference of herbivores differ between (i) cafeteria experiments (e.g. Thomas et al. 2010), in which all food types are equally available, and (ii) field studies, where food types vary in availability, accessibility and divergent spatial distributions (Pérez-Harguindeguy et al. 2003; Wang et al. 2010b). From practical point of view, measurements of palatability from cafeteria trials are mainly useful for planning of animal feeding whereas measurements of grazing selectivity on species-rich pastures enable us to predict under what conditions particular food types will be exploited by herbivores.

Measuring diet selection requires a comparison of the relative abundance of food type available to an herbivore with the relative abundance of food type utilized by an herbivore. For this purpose many electivity indices (e.g. Ivlev 1961; Jacobs 1974; Vanderploeg and Scavia 1979; Johnson 1980) were developed and their suitability has been much debated. But due to their computational simplicity electivity indices have not been superseded by more complex statistical techniques, for instance as resource selection functions (Boyce and McDonald 1999). Lechowicz (1982) analysed strengths and weaknesses of seven most commonly used electivity indices and identified Vanderploeg and Scavia's relativized electivity as the single best, but not perfect electivity index. Its main advantage lies in fact that maximum attainable preference is an increasing function of the number of food types, but on the contrary index is vulnerable to sampling errors. In the last decade diet selection studies on species-rich pastures (e.g. Dumont et al. 2005a; Farrugia et al. 2006; Boulanger et al. 2009; Fraser et al. 2009) most often used Jacobs' modified electivity index (Jacobs 1974) due to its low sensitivity to variations in the relative abundance of food types. However, comparison of diet selection among studies which use different electivity index is needed very often. As every index reacts differently to changes in availability and use of food type, food type may appear preferred according to one index but avoided according to another. Finally, Lechowicz (1982) and Tanentzap et al. (2009) brought empirical evidence that choice of electivity index is unimportant when preference is derived from rank order of species selectivity which is consistent across all electivity indices.

Measuring forage availability

Relative availability of forage (food types) might differ significantly between measurement techniques. Frequency of occurrence represents the presence/absence of food types within a sampling unit. It provides a rapid measure of the spatial patchiness of food types, but Norbury and Sanson (1992) did not recommend it as this measure overemphasizes rare food types. Availability is sometimes expressed as density of food types within a sampling unit (e.g. Van der Wal et al. 2000). However, this measure is unsuitable for food types whose individuals cannot be readily separated, such as grass tussocks. Cover, the perpendicular projection of plants onto the ground, was often used in diet selection studies (e.g. Grant et al. 1985); it may be measured accurately with point quadrat or visually estimated. As neither frequency nor density and cover do account for differences in plant height, more appropriate are techniques based on biomass. Direct assessment of plant biomass in sampling unit by harvesting is the most accurate but precludes the evaluation of the amount of food type utilized by herbivore. In relatively homogeneous pastures this might be surpassed by the use of paired neighbour plots – one for determination of food type availability before grazing and one for determination of food type utilization after grazing (Lepš et al. 1995). Such destructive techniques with harvesting, separating and weighing of each food type can be very labour intensive and thus, the number of replications would be substantially limited. Alternatively, biomass of food types in sampling unit may be obtained much faster using a calibrated weight-estimate method (Tadmor et al. 1975) as follows: visual estimates of the biomass of food types are calibrated by clipping and weighing in several training plots, when consistent estimates are attained, direct estimations of food type biomass of the studied plots are undertaken.

In the case when food type availability is sufficient to be determined at the scale of sward patches, researchers commonly use double-sampling techniques based on calibration of some easily measured patch quantity (i.e. estimators) by clipping and weighing of biomass in several training patches (e.g. Reese et al. 1980). Many instruments for forage estimation have been developed and adapted for day-to-day on farm management. Among the most commonly used biomass estimators belong Robel pole (Robel et al. 1970), electronic capacitance meter (Currie et al. 1973), rising plate meter (Castle 1976) and sward stick (Stewart et al. 2001). The visual obstruction method measures the lowest point on the Robel pole which is not visually obstructed by vegetation. The capacitance meter measures the capacitance of the air–herbage mixture (Curie et al. 1987) and responds mainly to the surface area of the foliage. The rising plate meter integrates sward height and density into one measure, often called bulk density (Michalk and Herbert 1977). Sward stick relies on a positive relationship between biomass yield and canopy height. Commercial products using above mentioned methods are usually calibrated and enable quick assessment of grassland biomass which is needed for whole farm simulation models in order to ensure economic management of grasslands (Sanderson et al. 2001). Nevertheless, these calibrated commercial instruments operate reliably only in relatively homogeneous grasslands (e.g. Currie et al. 1987; Murphy et al. 1995) while species-rich pastures consist of patches of distinct structure and phenology. Harmoney et al. (1997) quantified effectiveness of four indirect methods across heterogeneous pastures and found Robel pole and rising plate meter to be most efficient biomass estimators but with fairly low coefficients of determination, 0.63 and 0.59 respectively. On that account most researchers (e.g. Virkajärvi 1999; Sanderson et al. 2001) recommend calibrating all these devices separately for each measurement occasion. Therefore Martin et al. (2005) conducted measurements on naturalized cattle pastures and used local and time-specific calibrations; however, they were not able to identify a method that was consistently accurate to approximate standard quadrat harvesting. Thus, estimating forage biomass in mixed-species pastures is still a challenge. The effectiveness of indirect methods in heterogeneous pastures may be improved by construction of separate calibration curves for distinct patch types in the pasture.

Measuring diet composition

Quantification of diet composition can be generally implemented by three approaches: (i) analysing plant parts consumed by herbivores either with the help of oesophageal fistulation (e.g. Woji and Iji 1996), by disassembling of stomach contents (e.g. Homolka and Heroldová 1992, Bee et al. 2009) or by analysing animal faeces (e.g. Fraser et al. 2009; Hejcmanová et al. 2010); (ii) recording grazing behaviour of foraging animals (Dumont et al. 2007a; Hejcmanová et al. 2009) and (iii) recording utilization of vegetation (e.g. Lepš et al. 1995; Hejcman et al. 2008; Mládek et al. 2011a). Only the last two approaches appear suitable for quantification of diet selection in species-rich swards composed of many plant species because small masticated or digested particles are almost impossible to identify to species level (Norbury and Sanson 1992). Moreover, exact feeding trials made by McInnis et al. (1983) showed that diets determined by stomach content analysis and faecal analysis significantly overestimate proportions of grasses on the account of forbs. Cell walls of forbs are more readily digested, thus forbs gradually disappear as they pass through digestive tract. Hence, the least proportions of forbs are usually detected in faeces.

Direct observation of individual animals and recording their grazing behaviour belongs to the most common technique (e.g. Bailey 1995; Wallis De Vries et al. 1998; Dumont et al. 2007a; Farrugia et al. 2008; Hejcmanová et al. 2009). Sampling grazing time, biting rate and bite size (weight) gives complex information on grazing behaviour pattern. On species-rich swards marked by their heterogeneity and patchy character, observing directly the animals enables to embrace the spatial pattern of grazing and movements on pastures at different scales. Another advantage of direct animal behaviour sampling consists in recording social interactions among animals which may mutually compete for available forage resources or in turn, they may cooperate in terms of vigilance against potential predators. Measuring diet composition on species-rich pastures requires the advanced knowledge of the sward and its components (plant species). In order to identify precisely the plant parts, plant species or defined sward types/patches, the observers have to approach the animals to rather close distance. For such type of behaviour sampling the animals have to be trained, although the risk of bias by observer presence remains relatively high. A flat well-arranged pasture render the investigation possible using a binocular with appropriate parameters. The biggest advantage of direct observation however reposes in the possibility to determine motivation of a concrete animal for the choice of concrete food items at a given moment (and for how long time); and this in relation to their actual physiological state (age, reproduction), abilities or experience. Consequently, the method enables to reveal proper mechanisms of diet selection.

Vegetation utilization techniques provide clear picture where and to what degree a pasture is being used (Laycock et al. 1972); therefore these methods render information on grazing intensity which may substantially contribute for clarification of possible different patterns of diet composition. Yet, these techniques have been denominated unsuitable for quantification of diet composition due to the possible bias caused by losses of plant parts by trampling, weathering or grazing by other animals than those of interest (e.g. Holechek et al. 1982). However, only these techniques enable accurate determination of neighbourhood effects on diet selection (e.g. Arnold 1987). Moreover, knowledge of plant species utilization in permanent plots is extremely important for assessment of impact of grazing selectivity on community functioning (e.g. Cingolani et al. 2005). Principally, there are two approaches for quantification of vegetation utilization. The first approach relies on evaluating biomass differences between grazed and ungrazed (caged) plots (e.g. Lepš et al. 1995), however, this method is dependent on the assumption that species biomass in both grazed and ungrazed plot is the same and this might be difficult to ensure in heterogeneous pastures. The second approach is based on the comparison of species biomass or height in the same plots before and after grazing (Arnold 1987). The repeated observation of the same plots should exclude omitting utilization of plants grazed totally (without leaving aboveground residues) which may occur when researcher relies on single shot after grazing observation of plot (Laycock et al. 1972). Another advantage of observing foraging traces on vegetation consists in evaluation of selection of diet of the flock of grazing animals as a whole. The method can be practised in variable terrain where the visibility of individual animals is restricted. Plant species can be easily classified according to selection by herbivores even in less accessible pastures in mountain areas (Hejcman et al. 2008).

Drivers of grazing selectivity

Foraging comprises four key phases that can be considered as approach, appraisal, defoliation and ingestion (Griffiths et al. 2003). Each of these phases is subject to key cues and rules controlling animal’s decision making. The animal behaviour is driven by an array of factors of different nature and result in a variety of grazing response patterns. Foraging response mechanisms issue essentially from animal characteristics and abilities, from sward characteristics, environmental conditions, the management intervention of man, and interactions among them.

Animal as a predictor of diet selectivity

Foraging processes are basically predetermined by intrinsic morphological and physiological characteristics of the animal. Then, they are constrained by animal cognitive abilities, capacity of adaptation to concrete conditions and social intra- and interspecies environment.

Morpho-physiological adaptation and body size

Herbivore ungulates represent a group highly diverse in body size (ranging from very small Royal antelope of 25 cm at shoulder to 5 m tall giraffe). They fill a wide variety of ecological niches and play a key role in ecosystems all over the world, from tropical rain forest to tundra beyond polar circle. Their dietary preferences are equally varied. We recognize main foraging types according to their adaptations for consuming (i) a roughage diet composed primarily of grasses - grazers, and (ii) a concentrate diet of browse or forbs – browsers. Transient types consuming various diets are generally known as mixed or intermediate feeders. Varied forage of the animal is reflected in morpho-physiological adaptations in the structure and function of individual parts of the digestive system (Hofmann and Stewart 1972, Hofmann 1989; Gagnon and Chew 2002). Hofmann’s nutritional and physiological interpretations of anatomical differences among ruminants were, however, subjected to a series of tests and appear not supportable. For instance, Pérez-Barbería and Gordon (1999) examined 21 morphological traits of the jaw and skull of 94 species of ungulates to test the differences in of the jaw and skull morphology among feeding types (browsers, grazers, mixed feeders, frugivorous, omnivorous). Results of this study showed that phylogeny has a stronger influence in explaining the differences in jaw and skull morphology which exert in mechanics of chewing than the feeding-type classification. After excluding omnivorous species, there were no differences among the rest of animal feeding types.

On the other hand, the animal feeding types differ in body size and morphological traits functionally related to the ability of forage selection (muzzle width, incisor-arcade shape, incisor shape), prehension of food (incisor protrusion), food comminution (molar occlusal surface area), hypsodonty (high-crowned molar), and intake rate (incisor breadth) (Pérez-Barbería and Gordon 2001). The grazers are usually ranked among large and heavier species and browsers among smaller ones. However, the organs related to food intake and digestion are positively related to body weight and body size rather than to feeding. Gordon and Illius (1994) found that African ruminants with different morphological adaptations of digestive tract display comparable digestive strategy. Their wet and dry mass of the rumen and hindgut contents, fermentation rate in the rumen and retention time of digesta within digestive tracts do not differ between feeding types and are positively related with the body weight. Similar relation of ruminant digestion to body weight showed Robbins et al. (1995). They found no difference in the efficiency of fiber digestion between feeding type and proved that fiber digestion increases as body weight increases. Salivary glands size is approximately four times larger in browsers than grazers and their weight increased linearly with body weight (Robbins et al. 1995). Body size (and weight) of individual herbivore species cannot be therefore considered a good predictor of the differences between feeding types. Body size, however, regardless of feeding type, represents an important driver of diet selection. Body size is the main variable in determination of differences in the oral traits related to food selection and processing of food in the individual herbivore's species. So food selection process is similar for species with similar body size and various feeding styles (smaller species are more selective regardless of feeding style). This emphasizes the importance of food structural characteristics in definition of oral morphology.

Small-sized herbivore species are generally more selective spending more time searching for high-quality forage than larger-body-sized species. The larger herbivores are forced to feed less-quality forage in order to maintain a certain level of forage intake (Bailey et al. 1996). However, both small and large animals adopt relatively selective strategies if adequate available food resources. For instance Schwartz and Ellis (1981) compared foraging behaviour, diet selection and diet overlap of two native herbivores (American bison (*Bison bison*) and pronghorn (*Antilocapra americana*)) and two domestic herbivores (sheep and cattle). They revealed that both small and large animals carry out relatively selective strategies when the forage conditions allow it. They found out that sheep, the smallest of the investigated species, were always less selective than pronghorn and even they were less selective than large cattle in season with most abundant forage. Schwartz and Ellis (1981) relate this behaviour by human selection which makes sheep to be food and habitat generalists despite their relatively small size. Generally-respected fact that smaller-body size animals are more selective than larger may therefore not always be valid.

Another important driver of foraging pattern and selectivity represent physiological state of individual animals, namely age, sex, and reproductive state. The animals adjust their forage intake according to physiological requirements related to growth rate. Growing animals have higher demands on diet quality and have higher energetic demands. For instance suckling calves and yearling heifers have generally higher crude protein content in their diet than mature steers (Grings et al. 2001). In sexually dimorphic animals such as Bighorn sheep (*Ovis canadensis*), subadult males have higher forage intake than adult ones, while females do not show any difference between age classes (Ruckstuhl et al. 2003). For females the most important driver in foraging pattern is reproduction. Lactating females have to compensate the energy invested in lactation and face the tradeoffs between foraging and vigilance over predation risk of their offspring. Consequently, they increase the food intake by increasing bite rate, daily grazing time or by increased selectivity for high quality and energy forage (Ruckstuhl et al. 2003; Lamoot et al. 2005; Farrugia et al 2006). However, differences in foraging patterns and selectivity between animals of various physiological states are reduced by changes in forage availability and quality during the course of season (Grings et al. 2001). Scarce food sources can create diet overlap which occurs among native and domestic or introduced animals (Schwartz and Ellis 1981; Fritz et al. 1996; Baldi et al. 2004; Campos-Arceiz et al. 2004), among animals with similar body size (Schwartz and Ellis, 1981) and among animals with the same feeding ecology (Fritz et al. 1996).

Animal's cognitive abilities

Cognitive abilities facilitate animals to use effectively their environment and to detect and remember the distribution of high and poor quality food resources. Cognitive mechanisms of diet selection comprise animal’s individual ability of learning and spatial memory that both rely on visual, olfactory, and auditory senses. Learning provides to animals the flexibility not only to satisfy nutrient requirements, but most of all to maintain homeostasis in environments where nutrient content and toxicity of potential foods is variable (Bryant et al. 1991).

Mechanisms of diet selection associated with learning processes evolve during an individual’s ontogeny from maternal observation, peer interaction and nutritional post-ingestive consequences (Provenza 1995). Social learning, and learning from dams in particular, enables young animals to get critical information about their specific foraging environment, such as the location of food, water and cover resources (Provenza and Balph 1988). For instance, lambs avoid the food which causes post-ingestive distress much sooner than those without mother example (Provenza 1994). Ganskopp and Cruz (1999) found that naive cattle graze on a broader array of forage and harvest fewer bites than their experienced congeners. Social learning therefore increases not only diet selection, but the efficiency of learning about nutritious foods and reduces risk of over-ingesting toxic foods (Bryant et al. 1991; Provenza 1995). The early experience in life affects animals’ distribution on pasture, as for instance cattle returns in areas where early in the life foraged with their dams (Howery et al. 1998).

Herbivores associate food items with their nutritional consequences. Animals learn about post-ingestive consequences of foods through two interrelated systems, affective and cognitive. The affective system integrates the taste of food and its post-ingestive consequences, and changes in the amount of ingested food, depending on whether the post-ingestive consequences are aversive (toxicity) or positive (nutritious food). Thus, the affective system provides feedback so animals can learn to ingest nutritious and avoid intoxication. The cognitive system integrates the taste and sight to select or to avoid particular foods. For instance, livestock associate visual cues with feeding sites and if the animals are trained to associate high quality food with some visual cue, they are able to generalise the cue to selecting initial patches regardless their quality (Renken et al. 2008). The post-ingestive effects of nutrients and toxins from food are therefore integrated with the plant’s odour, taste, and texture and results in palatability of food resource. Species-rich pastures provide a variety of food resources of different quality offering thus a mixed diet. Such diversity stimulates food intake (see Wang et al. 2010c) and encourages the animal to maximize and balance intake of (macro- and micro-) nutrients and to regulate intake of different toxins (Provenza et al. 2003).

Another cognitive ability, spatial memory allows animals to remember where they have foraged and to use that information to determine where they will travel and forage. Spatial memory operates as a two-part code: working (short-term) memory and reference (long-term) memory. The functional value of working and reference memory is determined according to temporal and spatial scales of forage and habitat availability (Laca and Ortega 1996).Working memory serves for remembering and avoiding recently grazed areas within grazing bouts where food resources are depleted. The spatial information is retained only long enough to complete a particular task and then is discarded as no longer necessary. Working memory is used at the scale of feeding station, patch or feeding site, which were visited during preceding grazing bout, and in cattle lasts for eight hours at least (Bailey et al. 1989). On contrary, reference memory is retained for longer periods and works from patch level deciding on daily basis, through feeding sites with their particular abiotic and biotic characteristics to the level of home range remembering the relative value of the habitats for month or even years (Howery et al. 1999).

Nevertheless grazing herbivores are faced to changes in patch quality and resource distribution in the natural, heterogeneous environment. In the face of such unpredictability, remembering the exact location and the previous quality of patches may be of little informative value (Illius and Gordon 1990). Instead, investing time in exploring patches to determine their quality may reduce the cost of feeding on a low-quality patch where a high-quality alternative is available. Such sampling behaviour helps the forager overcome the problem of ‘incomplete information’ (Stephens and Krebs 1986) by tracking environmental fluctuations and thereby increasing foraging efficiency. An ability to switch between strategies would allow greater foraging success under unpredictable conditions (Bateson and Kacelnik 1998; Inglis et al. 2001). So in stable and predictable environments, grazing herbivores can use spatial memory to increase foraging efficiency, while in more variable environment, spatial memory can be replaced by sampling behaviour (Hewitson et al. 2005).

Interspecies interactions

Diet composition and selectivity of herbivores may be influenced by the presence of other herbivore species and their trophic interactions. On natural pastures, where different species of free ranging herbivores share a long evolutionary history, the animals adopted strategies to cope with inter-species competition and to share available common food resources. Competition is considered to be a major selective force leading to resource partitioning (Schoener 1983). The resource partitioning among sympatric herbivores implies the differential temporal and spatial use of available resources, called also niche segregation and resource partitioning which enable species coexistence despite overlap of ecological, namely dietary and nutritional, requirements. Trophic inter-species interactions are mediated largely through their grazing and browsing impacts on vegetation. Generally, at high density and limited food resources the animals with high diet similarity compete, whereas removal of only part of the biomass by one species may facilitate another species access to forage of an adequate height or quality (Vesey-Fitzgerald 1960; Bell 1970; McNaughton 1979). Facilitation occurs in two different manners (i) when grazing by one species makes more grass accessible to another species, e.g. by reducing grass height and removing stems or (ii) when grazing by one species stimulates grass regrowth, thereby enhancing the nutritional quality of forage for another species (Arsenault and Owen-Smith 2002). The resource partitioning has been widely described in temperate zones (Jenkins and Wright 1988; Putman 1996; Johnson et al. 2000; Mysterud 2000) as well as tropical native large herbivore assemblages in Africa (Vesey-Fitzgerald 1960; Bell 1970; McNaughton 1979; Jarman and Sinclair 1979; Voeten and Prins 1999; Woolnough and du Toit 2001; Cromsight and Olff 2006) and Asia (Dinerstein 1980; Martin 1982, Johnsingh and Sankar 1991; Bagchi et al. 2003; Steinheim et al. 2005; Wegge et al. 2006).

The patterns of resource partitioning may be however disrupted by introducing into natural system an exotic species such as cattle or sheep inducing thus strong competitive interactions. For instance, in Tanzania the cattle introduced in an area with wildebeest and zebra selected feeding sites with forage characteristics similar to those of both wild native herbivores, while their selection for feeding sites did not overlap (Voeten and Prins 1999). Similar potential for competition resulting in spatial displacement was observed among mule deer, elk and introduced free-ranging cattle in the Blue Mountains in Oregon, USA. Two native cervids avoided areas used by cattle and their mutual overlap of used habitats resulted in partitioned use of vegetation communities within habitats (Stewart et al. 2002).

Still another situation occurs on managed species-rich pastures limited by fencing. Domestic animals such as cattle, sheep or goat differ in dietary and nutritional requirements and intrinsic abilities of diet selection (Van Soest 1994; Gordon et al. 1996; Fraser and Gordon 1997; Fraser et al. 2009). The species-rich sward enables them therefore to select different items and mitigate potential competition or increase efficient utilization of available herbage on pasture. Sheep and goats consume more forbs than cattle (Rodriguez-Iglesias and Kothman 1998). Cattle, in comparison with sheep, graze more grasses with proportionally more stems and less leaves, or even dead material, and with high content of cellulose. Whilst sheep co-grazing with cattle is able to select sward components low in the profile, selecting grass parts or forbs with higher content of total protein, carbohydrates and phosphorus (Cook et al. 1967; Grant et al. 1985). Goats consume more forbs and browse than sheep (Bartolome et al. 1998), the co-grazing of these two species implies the resource partitioning at pasture. However, the diet selectivity may change in response to different grazing pressure. Animut et al. (2005) found that grazing pressure had no effect on selectivity of goats and sheep neither for, nor against grasses, but influenced selectivity for some forbs, namely ragweed (*Ambrosia* spp.).

Vegetation as a determinant of diet selection

Species-rich pastures present for animals exceptional swards with high diversity of plant species which create a mosaic of patches of different vegetation structure varying in forage availability and nutritive value (Dumont et al. 2005b). Heterogeneity of the vegetation is the fundamental factor in the mechanisms and dynamics of selectivity and grazing behaviour on pastures (Adler et al. 2001). The heterogeneous species-rich swards generate high spatial and temporal variability which frequently mutually interacts (Rychnovská 1993; Mládek et al. 2011b). Herbivores, on the contrary, require a relatively constant intake of nutrients to satisfy metabolism, growth, and reproduction (Prins and Langevalde 2008). They are therefore faced with the problem of obtaining relatively constant supply of nutrients in a relatively variable and fluctuating environment (Frank 2006). The basic trade-off between quality of forage and ingested quantity therefore differs according to actual conditions at each scale of spatial and temporal variability (Griffiths et al. 2003).

Diet selection from bite to landscape

The animals on species-rich swards respond to heterogeneity in food resources by adopting divers foraging strategies. At small scale such as feeding station (*sensu* Senft et al. 1987) the animals make short-term decisions to maximize instantaneous nutrient intake, whereas at larger temporal scale the animals decide on daily intake basis (Fryxell 1991; Wallis De Vries et al. 1999). At plant part level the animals select the most accessible plant parts offering the largest bite size or rate of nutrient intake. Arnold (1960) conducted a series of experiments where the rate of stocking was such that consumption exceeded growth. Sheep continuously selected leaf in preference to stem where this was physically possible. Within both leaf and stem fractions of the plants, the animals selected for material of the highest available nitrogen content. Further, plant level is highly variable within plant species and the animals respond to it by selecting individual plants which maximise their intake of digestible nutrients. For instance, Ganskopp et al. (1992) experimentally proved that cattle prefer to graze individual grass bunches without stems. At the level of feeding station, selectivity is limited by the degree of resource depletion. Grazing animal simultaneously evaluates remaining available forage in reach and costs of travelling to another feeding station and then takes a decision to stay or to move on (Bailey et al. 1998). Therefore, differential defoliation of feeding stations within a paddock is ruled by the marginal forage value (Charnov 1976) which needs to be determined first by sampling (Dumont et al. 2005a). When the best remaining item at the feeding station is below a certain threshold, or when the rate of forage acquisition at that station falls below that threshold, the animal moves forward, establishing a new feeding station at which diet selection proceeds again. Diet selection is further improved by using spatial memory (e.g. Edwards et al. 1996). As grazing progresses and the resources are gradually depleted, herbivores are forced to get back to sampling and searching a new threshold value (Hewitson et al. 2005). Heterogeneous sward on species-rich pastures creates typical patchy arrangement of vegetation (Correll et al. 2003; Parsons and Dumont 2003;

Pavlů et al. 2007). The animals consistently select for high quality and productive patches, rejecting those of low quality (Garcia et al. 2003; Rossignol et al. 2011). Large pastures may involve a mosaic of different plant communities which we find at landscape level. The utilization of these communities and particular landscape units strongly depends upon animal species (larger herbivores assemble their diet from more units than smaller herbivores, Prins and Langevalde 2008) and the particular constraints within which it operates. For instance, Frank (2006) identified a production threshold (34 g m^{-2}) below which plant communities were not grazed in his study system and further showed that ungulates behave in landscape units by increasing the intake as above-ground production of a unit area increases. The selection of units within landscape is a complex process involving a trade-off between nutrient requirements, distance to water and predation risk (O'Reagain and Schwartz 1995). The temporal variability in the sward quality may be either arising naturally through normal changes in plant physiology, phenology, and growth associated with seasonal changes in environmental conditions (Albon and Langvatn 1992, Mládek et al. 2011b) or may be supported by selective grazing. The defoliation by grazing determines the pattern of organic matter digestibility, biomass growth, and accumulation of senescent material (Illius 1986). Both natural and grazing induced temporal variability in forage quality and availability occur at short term scales over few seconds to several hours, at medium term scale over few days to weeks within a vegetation season, and at long term including seasonal cycles (O'Reagain and Schwartz 1995) and inter-annual variability due to rainfall variability (Pavlů et al. 2006).

Sward characteristics and plant functional traits

Basic parameter characterising the sward on species-rich pasture is the high diversity of plant species composition. Species-rich swards stimulate large herbivore generalists to make decisions which plant species to consume. On the one hand, the animals have more opportunity to choose palatable plants and optimize their nutrient intake, and on the other hand higher diversity of food resources make foraging decisions more complex and may make it difficult to determine from which one the animal can obtain the highest nutritional benefit (see experimental study by Wang et al. 2010a). Comparing different livestock species, sheep in contrast to cattle substantially distinguish plant species and select their diet at plant species and even at plant part level with preference for forbs and avoiding grass stems (Grant et al. 1985). Sheep on the species-rich pasture graze on a wide range of present plant species. When meeting a new, unknown plant species, they consume a small quantity and wait for post-ingestive response. Only then, the animals start to graze it in higher quantity (Provenza et al. 2003). Sheep is able to learn to select species within several days and recognize favoured species again after six month (Hejcman et al. 2008). Mixed species diet in contrast to a single diet positively stimulates voluntary daily intake (it means quantity) and enhances nutrient intake (Wang et al. 2010c) and both are positively reflected in animal performance (Atwood et al. 2001).

Diet selection, however, reposes mainly on the interactions of quantity and quality parameters of the sward (Mládek et al. 2011a). The main indicators of forage quantity are biomass yield, sward height or plant density, and indicators of forage quality consist in nutrient content, organic matter digestibility, and/or maturity of the sward (phenological stage of plants). Animals respond to changes in sward characteristics by changes in their grazing behaviour such as total grazing duration, frequency and numbers of grazing bouts or by changes in the mechanisms of diet selection and intake rates (number of ingested bites, number of steps in searching diet sources or bite - step ratio).

Forage availability, reflected for instance by sward height, determines bite size (weight) and biting rate (Forbes 1988; Wallis De Vries et al. 1994; Wallis De Vries et al. 1998; Griffiths et al. 2003). Generally, on short swards bite size is small and animals display high biting rate (Wallis De Vries and Daleboudt 1994; Barrett et al. 2001), increasing approximately by two bites per minute for each 1 cm decrease in sward height (Hejcmanová et al. 2009). The animals compensate decreasing forage by increase of daily grazing time or biting rate or by both. If abundant forage, the animals selectively feed on high quality patches (Bailey 1995; Wilmshurst et al. 1995; Coppedge and Shaw 1998; Ginane et al. 2003; Dumont et al. 2007a; Dumont et al. 2007b). When better quality forage becomes restricted below a certain threshold, for instance due to seasonal dynamics and reproductive state of the sward (Ginane et al. 2003), the animals adjust their grazing time and/or biting rate in order to maintain daily intake (Forbes 1988; Funston et al. 1991; Wallis De Vries et al. 1994; Hejcmanová et al. 2009). In other words, when forage is abundant and offers a choice of highly nutritious species, the strategy of maximizing forage quality appears to be the most favourable. On the contrary, if sward consists mainly of species of low forage value the strategy of maximizing forage quantity seems to be more efficient in maximizing energy gain (Schwartz and Ellis 1981; Dumont et al. 2005a; Mládek et al. 2011a).

Species-rich pastures represent for animals a complex, heterogeneous and continually changing environment where various types of patches may occur. The animals thus continually assess potential costs and benefits and are flexible in adopting their foraging strategy. For instance, Ginane et al. (2003) offered to the heifers an alternative between a tall (14 cm) abundant reproductive sward with high biomass gradually decreasing in nutritive value and a vegetative sward (of two heights: tall – 14 cm and short – 8 cm) with lower biomass and higher nutritional value. They revealed that the choice between quality and quantity of offered sward depended on the magnitude of difference between nutritive values. When the difference was moderate, the animals increased their grazing time on more available reproductive sward patches of lower quality and higher quantity. As the difference in quality widened, the animals switched their preference for vegetative, better quality sward. The animals responded to seasonal changes by changes in foraging behaviour in order to maintain their total intake as well as the diet digestibility (Ginane et al. 2003). However, when animals face a grazing time constraint, they show considerable flexibility in their grazing behaviour compensating for the restricted time by grazing, for instance, for fewer and longer foraging bouts (Iason et al. 1999). The animals seem to prioritise quality over intake (Ginane and Petit 2005).

In species-rich grasslands diet selection strategies of domesticated herbivores have rarely been compared between plant communities, because direct assessment of quantity (biomass yield) and quality (digestibility) in fine-grained heterogeneous environment is costly and laborious. Therefore indirect approaches for quantification of both quality and quantity of herbivore's diet are needed. Most papers from last 20 years based assessment of foraging strategies in semi-natural grasslands on the following assumptions (i) most legumes have higher forage quality than other plant species (Bruinenberg et al. 2002), (ii) leaves provide more digestible biomass than stems including inflorescence in both monocotyledons and dicotyledons (Duru 1997). For instance, Fraser and Gordon (1997) made a comparison of diet of goats, red deer and guanacos in three contrasting Scottish upland vegetation communities. They classified diet composition of oesophageal-fistulated animals into several forage groups as broad- and fine- leaved grasses, clover and dicotyledons, all further divided to green leaf parts and stem/flower parts. Dumont et al. (2007b) in their multi-site study inspecting diet selection of commercial vs traditional livestock breeds categorized bite types according to their broad botanical classification (grass, legumes, forbs), height (tall or short) and vegetation stage (vegetative, reproductive or dead). Both studies used Jacobs selectivity index (Jacobs 1974) and confronted selectivity patterns between different domesticated ruminants. These studies were important for recognition of feeding overlap or possible complementary resource use, and facilitated vegetation management using multispecies grazing systems. But these studies did not provide clear picture how herbivore's selectivity is related with the plant's ability to tolerate or to resist herbivory, and therefore they did not infer how selectivity affects resource use. All these links might be investigated with the help of plant functional classification (Cingolani et al. 2005; Evju et al. 2009; Rusch et al. 2009) and freely accessible trait values in databases, for common European species in BiolFlor (Klotz et al. 2002) and LEDA (Kleyer et al. 2008). Plant trait approach enables considerably easier comparison of diet selection strategies between communities of distinct floral composition; on condition we are able to determine forage availability and diet composition to the plant species level. Quantity-quality dilemma in herbivore's selection may be addressed at the plant species level or at the community level, for which community-weighted mean of particular trait is calculated by abundance weighing of species trait values (Cingolani et al. 2005). At the plant species level forage quantity was recognized to be correlated with canopy height (Cornelissen et al. 2003). However, forage quality in species-rich grasslands is difficult to assess with a single functional trait. Organic matter digestibility, at least for grass species, negatively correlates with leaf dry matter content (LDMC) and positively with specific leaf area (SLA) (Al Haj Khaled et al. 2006). An herbivore's selectivity for these leaf traits, which are considered the best indicators of resource exploitative vs conservative strategies, remains largely untested. To our knowledge only one cafeteria experiment evaluated preference of ungulates with respect to leaf traits, Lloyd et al. (2010) ranked palatability of 44 New Zealand native grass species for deer and sheep. They concluded that deer had a greater tendency to select grasses with high SLA but this trait was not a good predictor of sheep preference. Similarly, two studies of sheep diet selection in semi-natural grasslands (Cingolani et al. 2005; Mládek et al. 2011a) consistently reported that SLA was not related to sheep selectivity at the plant species level. But surprisingly, both studies showed that sheep selected species with tougher leaves or with higher LDMC. This could be partially explained by higher amounts of chemical defences in the softer leaves of dicotyledons compared to tougher leaves of grasses (Long et al. 1999). Forage quality is also modified by the stage of species maturity (Thomas et al. 2010), which is principally ruled by flowering period. Indeed, in alpine grassland Evju et al. (2009) demonstrated that sheep selected species with a later onset of flowering. Probably the most informative measure of forage quality would be the forage indicator value (Klapp et al. 1953). This expert-based ordinal classification of grassland species, which is included in BiolFlor database (Klotz et al. 2002), is based on information of protein and mineral biomass concentrations, leaf/stem ratio, palatability, accessibility and seasonal duration of the plant's forage value for livestock. Mládek et al. (2011a) showed that sheep grazing mesic semi-natural grasslands selected sward patches and even plant species within patches with higher forage indicator value.

Plant defence against herbivory and neighbourhood effects

Especially grasslands with long evolutionary history of grazing host a variety of species which survive herbivore pressure due to defence strategy (Díaz et al. 2007). A basic idea of plant defences is that a plant should gain protection from the investment it allocates to its own physical or biochemical defence (Milchunas and Noy-Meir 2002). Plant's physical defence is represented by structural characteristics which can cause injury (spines, thorns, awns), substantially reduce digestion (silica) or can influence searching time (plant crypticity), cropping time (plant fibrousness, tensile and shear strength) and bite size (plant canopy structure); all these effects depend on the morphology of the herbivore (Laca et al. 2001). For instance, Canada thistle [*Cirsium arvense* (L.) Scop.] represents highly defended weed of cattle and sheep pastures with prickly leaves, but C. thistle is preferentially grazed by goats and these are used for its elimination (see review by Popay and Field 1996). Plant's chemical defence constitutes secondary compounds – toxins, which can cause poisoning or reduce digestion. Some secondary metabolites are toxic in very small quantities such as alkaloid colchicine in Meadow saffron (*Colchicum autumnale* L.), but most compounds as tannins become noxious for livestock only after considerable plant consumption (Robbins et al. 1987; Frohne et al. 2005). Virtually every species in pastures contains at least low concentrations of secondary compounds, even forages sown to agriculturally improved grasslands: saponins in alfalfa (*Medicago sativa* L.), alkaloids in tall fescue (*Festuca arundinacea* Schreb.) and reed canarygrass (*Phalaris arundinacea* L.), tannins in the trefoils (*Lotus* spp.), and cyanogenic glycosides in the clovers (*Trifolium* spp.) (Provenza et al. 2007). But grazing herbivores seldom consume enough toxins to result in poisoning because they regulate their intake through post-ingestive feedback and quickly learn to eat mixes of plants that mitigate toxicity (Villalba et al. 2004). For instance, tannins contained in many wild plants may interact in rumen with highly toxic alkaloids from the other plants, thus neutralizing their negative effects (Lisonbee et al. 2009). Therefore no plant species is protected absolutely against herbivory (Provenza et al. 2003). Some species have been long reported as very poisonous for livestock, such as White hellebore (*Veratrum album* L.) due to high content of toxic alkaloids. This species achieves local dominance in cattle pastures in the Alps (Kleijn and Steinger 2002), but Hejcman et al. (2008) surprisingly found that white hellebore was highly selected by sheep after introduction to abandoned mountain grassland despite of general believe that sheep are particularly susceptible to its poison (Frohne et al. 2005). Similarly, above mentioned high toxicity of Meadow saffron was not an obstacle for sheep which readily grazed its soft spring leaves in species-rich pasture with dominance of unpalatable Tor-grass [*Brachypodium pinnatum* (L.) P. B.] (Mládek unpublished).

However, field consumption of plant species by herbivores depends not only on its physical and chemical characteristic, abundance and spatial distribution, but is greatly influenced by the characteristics of neighbouring vegetation (e.g. Atsatt and O’Dowd 1976). In other words, species susceptibility to grazing is altered by association with alternative forage species. This phenomenon has been debated in vast amount of literature under a variety of names – plant defence guilds, associational avoidance, a. defence, a. refuge, a. resistance, a. susceptibility, neighbour contrast defence, n. c. susceptibility, shared defence or s. doom. In last few years researchers studied neighbourhood effects (e.g. Bergvall et al. 2006; Miller et al. 2009; Bee et al. 2009) agreed on that these effects rely on different underlying mechanisms according to spatial scale, and suggested to unify terminology. Principally, herbivores can be selective or unselective between or within patches of plants and this can rise to four different scenarios (Bergvall et al. 2006; Rautio et al. 2008), which are involved in two alternative hypotheses first explicitly introduced by Hjältén et al. (1993). *Repellent – plant hypothesis* operates for selection between patches in the absence of within patch selectivity and predicts: (i) if there are some less defended, palatable plants within the avoided patch, they would then gain protection from the defended plants (referred as associational defence) or (ii) highly defended, unpalatable plant within patch of palatable plants would be eaten more than if it occurred in a patch of mainly unpalatable plants (referred as associational susceptibility). *Attractant – decoy hypothesis* was proposed for situation when herbivore is unselective between patches and selective within a patch and asserts: (i) a defended, unpalatable plant in a patch of mainly palatable plants would be less eaten than in a patch with plants of its kind (referred as neighbour contrast defence – opposite to associational susceptibility) or (ii) a palatable plant would be eaten more when growing in a patch of mainly less palatable plants than in a patch with plants of its kind (referred as neighbour contrast susceptibility – opposite to associational defence).

However, foraging of herbivore in natural grasslands has been described as a nested hierarchy of decisions, from landscape to plant level (Senft et al. 1987). Moreover, large herbivores continually sample and evaluate food instead of either consuming or rejecting food items (Hewitson et al. 2005). Therefore it is not easily predictable which scenarios from the opposite pairs will take place in a given species assemblage. The foraging selectivity of herbivores is determined not only by species composition within a patch and patch characteristics but also by the contrast between patches within a community (Wallis De Vries et al. 1999). When the patches are clearly apparent, large herbivores should graze optimally according to 'patch-use theory' (e.g. Stephens and Krebs 1986) and select food at the stand level exclusively. Indeed, when herbivores have an opportunity to choose at both, patch and plant level, individual species are utilized in relation to the quality of the stand; this was evidenced in several bioassay studies (Rautio et al. 2008; Miller et al. 2009). Also a few field studies described directly decreased plant defoliation in its natural environment due to associational defence; for instance exceptional study by McNaughton (1978) in East African grasslands provided clear picture that unpalatable plants protected a palatable grass (*Themeda triandra* Forsk.) from grazing by unselective herbivores. Furthermore, Palmer et al. (2003) performed a field study in mountain pasture in Scotland and brought an example of associational susceptibility; unpalatable heather (*Calluna vulgaris* L.) was much more utilized by sheep and deer in patches of forage grasses than growing alone. On the contrary, opposite scenarios following *attractant – decoy hypothesis* might be expected according to bioassay studies (Bergvall et al. 2006; Rautio et al. 2008) when differences between patches are hardly discernable. In real plant communities, nevertheless, large herbivores usually discern between patches, therefore exclusive within patch selectivity is seldom found. Hjältén et al. (1993) suggested that food selection at the plant level become more important where the scale of patchiness is much larger than the home range size of the herbivore, forcing animals to live within just one vegetation patch. Correspondingly, Bee et al. (2009) proposed food selection at the plant level might strengthen at high population densities when herbivores are not distributed across patches in the proportion to the food available, those herbivores in the poorer quality patch may browse the few palatable plants particularly heavily. On the other hand, food selection at the plant level (within patches) applied when domesticated animals grazed poor quality pasture with a few palatable plants under very low stocking rate (Provenza 2003). This lead to neighbour contrast susceptibility scenario: 'cattle ate the best and left the rest' which repetition for many years evoked that toxin-containing woody plants such as sagebrush (*Artemisia* spp.) and juniper (*Juniperu*s spp.) have come to dominate over 39 million hectares of land in the Western USA (West 1993). Up to now we are uncertain what environmental conditions in natural grassland systems facilitate either between or within patch selection. First step towards elucidation of herbivore's motives were brought by Miranda et al. (2011), who illustrated that in spring abundant forage on pastures enabled large herbivores to select palatable shrubs. In this case, unpalatable plants in the vicinity of browsed palatable shrubs were less consumed, which refers to neighbour contrast defence. Conversely, in scrubland with limited forage resources, herbivore consuming a given palatable shrub continued, using the same feeding station, foraging on unpalatable neighbours, which refers to association susceptibility. This feeding behaviour takes place whenever searching and finding a new, optimal, more nutritive patch is more costly than feeding on unpalatable resources. Miranda et al. (2011) consequently outlined opposite associational effects can be explained by optimal foraging theory (McArthur and Pianka 1966). Courrant and Fortin (2010) asked more explicitly and tested if above mentioned alternative associational scenarios may be clarified by quantification of energy gain. They recorded foraging behaviour of free-ranging bison and assessed how spatial patterns of occurrence of highly profitable sedge (*Carex atherodes* Spreng.) could control the risk of herbivory for seven other plant species. Bison had higher energy gain in feeding station where this sedge was consumed while avoiding plant species that experienced neighbour contrast defence (generally shorter species); whereas energy gain in feeding station was higher by consuming instead of avoiding the plant species for which they detected associational susceptibility (tall species). Moreover, risk of herbivory for short species experiencing on average neighbour contrast defence increased notably in that feeding stations where their difference in height with *C. atherodes* become smaller. Thus, even large generalist herbivores as bison make simultaneously foraging decisions at both stand and plant level, and individual plant species (here *C. atherodes*) can cause opposite neighbouring effects for different species and these are dependent on the spatial variation in sward structure. Overall, alternative neighbourhood scenarios can be predicted by simple foraging rules of energy gain maximization.

Another issue is what spatial patterns of neighbour relationship contribute most to defence against herbivory, i.e. provide support for both palatable and unpalatable species which is a prerequisite for stable coexistence between herbivores and plants in grasslands ecosystems (Provenza et al. 2003). Wang et al. (2010a) conducted a manipulative experiment using sheep and three native plant species with different palatability. Their principal finding lies in fact that palatable plants cannot effectively defend themselves against herbivory if the constituted spatial pattern between plant species only compels herbivores to make foraging selection at one scale, either between or within patches. They concluded, particularly high complexity of spatial neighbourhood reduce herbivore’s selectivity, thereby vulnerability of palatable plants decrease. Remarkably, experimental studies from last five years showed that particularly high complexity of grassland sward satisfies best both nutrient and total food requirements of herbivores (Wiggins et al. 2006; Wang et al. 2010b,c).

Animal performance on species-rich pastures

The ultimate goal of livestock producers is to achieve an environmentally and economically sustainable livestock production and to maintain the forage production on grasslands. Pastures rich in plant species evolve mostly, if not sown *a priori* with a mixture of plant species (e.g. Hofmann and Ries 1989), in traditional grazing systems under low and moderate grazing intensity. Livestock producers may manage grazing systems favouring diversity of plant species by applying both the rotational or continuous grazing (Pavlů et al. 2003). The management have not any remarkable effect on grazing behaviour patterns and forage intake (Sharrow 1983; Hejcmanová unpublished data on heifers). If the grazing intensity between the systems is similar, both rotational and continuous grazing allows attaining similar outputs in terms of livestock daily live-weight gain (Hepworth et al. 1991; Hart et al. 1993; Manley et al. 1997; Kitessa and Nikol 2001). The key management variable appears the grazing intensity. Grazing intensity represents the intensity of grassland exploitation in relation to productivity of the sward. Comparing pastures with plant communities of similar biomass production, the intensity may be expressed as stocking rate, and this in terms of number of animals per hectare (Gillen and Sims 2002) or as livestock unit (LU) per hectare: 1 LU = 600 kg live-weight in studies from Western Europe, e.g. Dumont et al. (2007a), or 1 LU= 500 kg live-weight in Central European studies, e.g. Pavlů et al. (2006). Under high grazing intensity many plant species are not able to tolerate the grazing pressure and the amount of available forage becomes restricted (Bullock and Marriott 2000; Hofmann et al. 2001; Pavlů et al. 2007). Low and moderate grazing intensities enable the sward to attain high structural heterogeneity and plant species to co-exist. On the other hand, at very low intensity the plant species diversity declines as a result of competition among plants, namely for light (Marriott et al. 2004; Pavlů et al. 2007). One of the most important and widely used parameters which reflect grazing pressure is the sward height. Tall sward offers more available forage and despite its lower nutritive value the livestock displays positive linear response of daily live-weight gains to the sward height (Manley et al. 1997; Realini et al. 1999; Barthram et al. 2002). Most of these studies, however, have investigated the animal performance on improved pastures with few highly productive plant species, mostly mixture of perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.). Fraser et al. (2009) compared the performance of steers grazing ryegrass/white clover-dominated improved and semi-natural pastures in three experiments and found out higher live-weight gains and meat quality on the improved one. On the other hand, another studies from Finland revealed no difference in the daily gain of beef calves grown on an intensively managed fertilized and natural multi-species pastures (Niemelä et al. 2008). Further, in Central Europe animal performance on species-rich pastures was studied by Pavlů et al. (2006). They conducted a long-term grazing experiment with two grazing intensities (intensive and extensive for target sward height of 5 and 10 cm, respectively), and revealed that daily live-weight gains per animal were relatively similar under both extensive and intensive management, but slightly higher under extensive grazing with higher sward height of lower nutritive value. This was in concordance with cow and calf performance on *Nardus*-dominated semi-natural grassland in Scotland as reported by Common et al. (1998). However, if the animal performance was recalculated to unit land area, seasonal live-weight output per hectare was approximately 1.5 times higher under more intensive than under extensive grazing management (Pavlů et al. 2006). A series of grazing experiments with moderate and low grazing intensities on pastures across Europe brought very similar results; livestock performance per hectare was lower on low than moderate grazing intensity (Isselstein et al. 2007). Similarly, daily live-weight gains per animal do not differ between given grazing intensities (Isselstein *et al*. 2007; Dumont et al. 2007a). Different situation may, however, occur under different climatic and ecosystem conditions. On sand sagebrush (*Artemisia filifolia* Torr.) rangelands (with a mixture of grasses and forbs), only calf birth weight and weaning weight was a negative function of stocking rate, while cow live-weights remained similar among stocking rates. In years of drought the situation changed and cow live-weight declined as stocking rate increased (Gillen and Sims 2002). In semi-arid conditions, for instance in Mediterranean ecosystems, an early-season deferment of grazing may be applied as effective management measure. This allows the forage to grow sufficiently and consequently, to support moderate stocking rate with satisfactory daily live-weight gains of calves and cows per hectare. The deferment presents an economically sound option there, despite the additionally costs of supplementary feed during the deferment period (Gutman et al. 1999).

As already stated, multi-species pastures, namely at lower grazing intensities, stand out by high heterogeneity of swards. If the area available for animals is too large, some places may remain underutilised and decreasing the efficiency of grazing system. To ensure an even livestock utilisation of pasture additional management measures may be adopted. These measures may include, for instance, reducing distance to water on too extent pastures (Hart et al. 1993), providing shade and shelter for resting sites (Senft et al. 1985), placing mineral licks or feed supplements or improving forage quality by burning (all measures reviewed by Bailey et al. 1998).

Conclusions

Experimental studies in last decade have pointed out that domesticated ruminants perform better when offered a variety of food types (e.g. Villalba et al. 2010). Thus, livestock can better meet their needs for energy, intake of nutrients and regulate their intake of toxins in species-rich than in species-poor swards (Provenza et al. 2003; Wang et al. 2010c). It has been shown that in the absence of high quality species the nutrient intake is maintained under high functional group richness, e.g. a combination of legumes, grasses and forbs (Wang et al. 2010c). As natural grasslands are generally low productive and support mainly species of lower nutritional quality than standard forage plants in agriculturally improved grasslands, plant species richness will critically influence herbivore food intake and nutrition. Overall, production per animal in species-rich pastures could benefit by low grazing intensity which allows animals to manifest their feeding preferences. However, absolute feeding preferences for plant species, which may be obtained from cafeteria trials, may not be applicable on species-rich pastures. On pastures, herbivore's diet selection is substantially modified by species availability, spatial distribution and neighbourhood effects as described in chapters above.

Pattern of selection is generally subjected to body-size of herbivore; small herbivores as sheep and goats are generally more selective than large as cattle. The larger herbivores are forced to feed less-quality forage in order to maintain a certain level of intake. However, both small and large animals adopt relatively selective strategies if there are adequate available food resources. It has been suggested that the coarser the grain of vegetation the more likely animals select food at the stand level, i.e. highly exploit forage at high quality/quantity patches and omit other less profitable patches. In the case of fine-grained vegetation heterogeneity selective herbivores choose exclusively palatable plant species on condition these provide sufficient forage intake. However, even large generalist herbivores make simultaneously foraging decisions at both stand and plant level, and the risk of herbivory for every individual plant in the feeding station can be predicted by simple foraging rules of energy gain maximization (Courrant and Fortin 2010).

Let us consider. If structure of the sward and grazing intensity enable high selectivity of foraging herbivore for palatable species, and these plant species are not able to compensate defoliation by fast regrowth (which occur in most unproductive ecosystems – Harrison and Bardgett 2008), pasture become gradually dominated by unpalatable well defended species such as sagebrush (*Artemisia* spp.) (Provenza 2003). Thus, although selectivity enhances animal performance, i.e livestock production per animal, high selectivity often cause adverse effects on forage quality and livestock production per unit land from long-term perspective. Provenza et al. (2003) suggested that higher grazing pressure reduces selectivity, whereby providing support for both palatable and unpalatable species. Further, recently it has been shown that herbivores passively reduce selectivity due to high complexity of spatial neighbourhood between palatable and unpalatable plants (Wang et al. 2010a). Summing up, we propose fine-grained swards may be grazed under low grazing pressure because these plant communities compel herbivores to reduce selectivity, whereas coarse-grained swards should be utilized by less selective animals under high grazing intensity in order to preclude expansion of well defended plants on account of palatable ones. Coexistence of palatable and unpalatable plants is a prerequisite for sustainable utilization of grasslands ecosystems by herbivores, i.e. long-term maintenance of livestock production.

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CHAPTER VI

Grassland response to long-term management and amounts of nutrients in standing biomass

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Abstract

On a large scale of grasslands it was recognized that community-weighted leaf dry matter content (community LDMC) is negatively related to grassland productivity and N, P and K concentrations in biomass. Hence, higher total amounts of nutrients in above-ground standing biomass should be linked to lower community LDMC. However, current research provided evidence that community LDMC is substantially modified by defoliation regime. We asked whether management supporting vegetation with the lowest community LDMC also provides the highest amount of standing biomass and highest total amounts of N, P and K. We used three long-term management experiments (sites) with four management treatments (grazing with spring burning, grazing, mowing in mid-July and fallow) which were set up in *Bromion erecti, Cynosurion cristati* and *Violion caninae* grasslands in the White Carpathian Mountains (Czech Republic) in 2004. At each site 20 management plots (each 5 m × 5 m in size) were arranged in five blocks. During 2010 the first growth biomass was sampled at the end of May, in mid-June and mid-July, each time from one randomly allocated subplot 1 m^2 within each plot. The total amounts of N, P and K in a sample were calculated from dry matter standing biomass and laboratory analyses of nutrient concentrations. Community LDMC was calculated from sample proportions of species biomass and LEDA database values. All analyses were done with linear mixed-effect models (REML method), where management was treated as fixed effect while site and date as random effects. Variation in community LDMC was in 80% explained by site; in contrast variation in standing biomass and total amounts of N, P and K were explained by site only up to 25%. Filtering out the random effects all characteristics were significantly affected by management. We found, consistently with current studies, community LDMC was significantly the lowest under mowing, but unexpectedly, also total amounts of N, P and K were significantly the lowest under mowing. In summary, higher total amounts of N, P and K in standing biomass may not be expected for vegetation with lower LDMC when analyzing grasslands under different management regimes.

Key-words: Grazing; Fallow; Leaf dry matter content; Mowing; Standing biomass.

CHAPTER VII

Using phenological progression and phenological complementarity to reveal potential for late grassland harvest

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Abstract

Farmers often face the problem which grasslands enable harvest later in the season without a substantial decline in fodder quality. As decline is particularly driven by plant phenology, there arises a question which long-term management produces vegetation with a slower phenological progression and/or supports occurrence of later-developing species (i.e. phenological complementarity). We used an experiment in dry broad-leaved grassland in the White Carpathian Mts. (Czech Republic) with three treatments: sheep grazing, mowing in mid-July and fallow. Species cover and phenophase were recorded in permanent plots at the beginning of May, June and July during two seasons. Phenological complementarity appeared only in the grazed plots. Community-weighted means of plant traits revealed that grazed and mown plots were characterised by earlier flowering and lower leaf dry matter content than fallow plots. Consistently, community phenological progression was the fastest in the mown plots and the slowest in the fallow plots. Mown plots accelerated the development earlier than grazed plots which was apparent from a significantly higher cover proportion of non-sterile species in June. We concluded that long-term grazed swards offer a greater potential for a onetime late harvest than mown grasslands, as fodder quality is expected to decline slower.

Key-words: Asynchrony of growth; Fallow; Grazing; Late harvest; Mowing; Phenophase.

Introduction

Especially in mountainous and less-favoured areas farmers have to accommodate timing of grassland use to weather conditions or new agri-environmental schemes. Thus, they often face the problem which grasslands enable harvest later in the season without a substantial decline in fodder quality (Martin et al. 2009). As the fodder quality decline is particularly driven by the speed of species phenological progression (PP) (Duru et al. 2008); it is a challenging question which factors control the overall community PP. Grassland communities with higher community-weighted means (CWM) of leaf dry matter content (LDMC) flower later (Ansquer et al. 2009). However, no study has explicitly answered the question how community PP is modified by long-term management. The aim of our study was to test experimentally which long-term management supports a vegetation composition that produces slower community PP and/or enables later-developing species to coexist within a community. Both these processes may retard fodder quality decline and widen the ‘time window’ for harvesting (Martin et al. 2009; Mládek et al. 2011).

Materials and methods

During the 2009 and 2010, community PP and complementarity were investigated in plots of a long-term management experiment which was set up in 2004 in dry broad-leaved grassland. The site is located near the town of Brumov–Bylnice (49°05′58″ N, 18°01′59″ E; 370 m above sea level; mean annual temperature 7.9 °C, mean annual precipitation 760 mm) in the White Carpathians Mountains, Czech Republic. Three management treatments (rotational sheep grazing from April with two cycles per year, mowing in mid-July and fallow) were applied, each treatment in five 5 × 5 m experimental plots arranged in blocks (scheme in Mládek et al. 2011). We monitored a permanent subplot 1 m^2 in size within each experimental plot. The subplots in the grazed treatments were each year protected from grazing until all observations were completed and were then only grazed in autumn. In each plot, cover (in %) and phenophase of all species were recorded at the beginning of May, June and July. We distinguished five phenophases (*sensu* Martínková et al. 2005): sterile plant (1), plant with flower buds (2), flowering plant (3), plant with immature fruits (4), and plant with mature fruits (5). The phenophase for a species was assigned the highest of values attained by at least 30% of individuals in a subplot. Index of phenological complementarity (Stevens and Carson 2001) was used to describe the asynchrony of growth: if all species' peak cover occur at the same time, then the index value is << 0; if some dominant species display their peak cover in spring and other ones reach their peak cover in summer, then the value is > 0.

Results and discussion

Comparison of phenological complementarity (Fig. 1A) showed that in both years mown plots had the lowest index values, indicating the most synchronous community development. Indeed, the seven most abundant species in the mown plots reached their peak cover in May or June, whereas four out of seven species in the grazed plots peaked in May (grasses) and three species in July (dicotyledons) (data not shown). Later-developing species may substantially improve overall fodder digestibility due to positive effects of high nitrogen concentration tissues on the digestion process (Niderkorn and Baumont 2009). Remarkably, vegetation under the influence of long-term grazing displayed complementarity only in the first year of observation. This might be attributed to the protection of the monitored permanent plots from early spring grazing, enabling early developing species to gain competitive advantage and possibly suppressing the occurrence of later-developing species the next year.

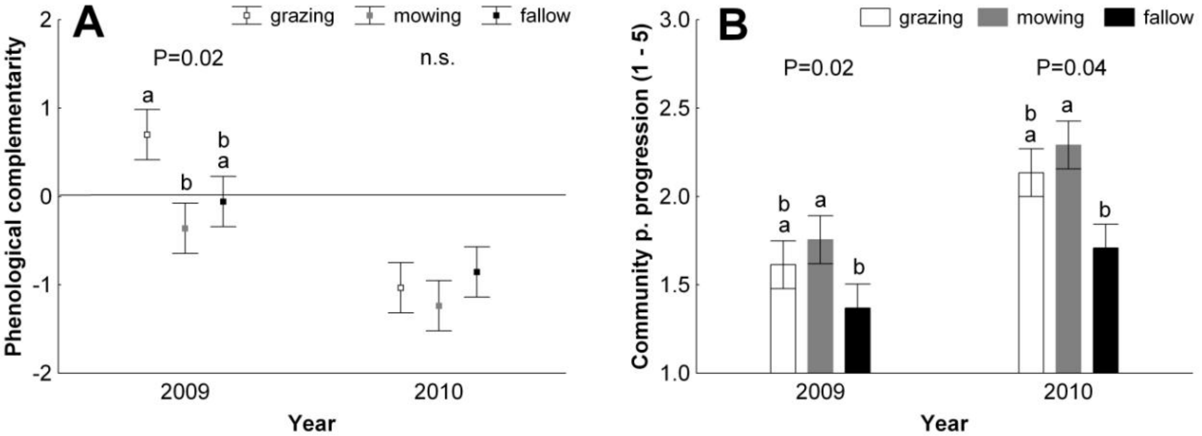

Fig. 1 Index of phenological complementarity (A), above zero values indicate high seasonal asynchrony of species peak cover. In community phenological progression (B) the cover weighted mean of species phenophases is presented (values from 1 - sterile plant until 5 - plant with mature fruits); it was averaged here over all three sampling dates. One-way ANOVA for each year separately; error bars represent SE; means with the same letter are not significantly different (Fisher's LSD test, $P < 0.05$).

Further, analyses of variance for the CWM of functional traits according to database values (BiolFlor database: onset of flowering, $P = 0.04$; LEDA traitbase: LDMC, $P = 0.04$) and post-hoc Fisher's LSD test revealed that grazed and mown plots were similar, but contrary to fallow plots they were associated with communities with earlier flowering and lower LDMC. Therefore, according to the results of Ansquer et al. (2009), in grazed and mown plots a parallel community PP may be expected, which should be faster than in fallow plots. In fact, community PP averaged over all three sampling dates was in both years the fastest in the mown plots and the slowest in the fallow plots (Fig. 1B). Community PP of grazed plots was in both years slower than that of mown plots, but not significantly. In addition, we analysed the seasonal development of the cover proportions of non-sterile species (Fig. 2A, 2B). Notably, the vegetation of the mown plots accelerated the development earlier (in June) than that of grazed plots (in July).

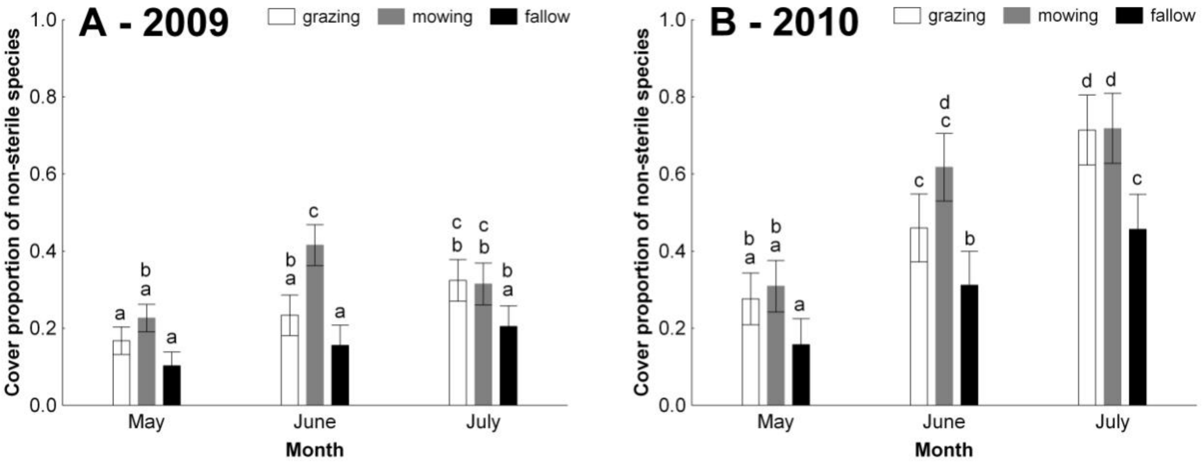

Fig. 2 Seasonal development of cover proportions of non-sterile species (from 2 – plant with flower buds until 5 – plant with mature fruits). Repeated measures ANOVA; error bars represent SE; means with the same letter are not significantly different (Fisher’s LSD test, $P < 0.05$).

Conclusion

We showed, consistently with Ansquer et al. (2009), that community PP is slower in grassland with a higher LDMC (here fallow plots). However, in case of a similar LDMC late harvest should be less unprofitable in long-term grazed than in mown grassland, because the former manifests a slower community PP and supports later-developing species.

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CHAPTER VIII

Community seasonal development enables late defoliation without loss of forage quality in low productive semi-natural grasslands

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Abstract

Agri-environmental measures often require postponing of grassland defoliation until summer months. We investigated how this affects agronomic characteristics, i.e. biomass production and forage quality, in species-rich grasslands in the White Carpathian Mountains, Czech Republic. Three distinct grasslands (vegetation alliances *Bromion erecti*, *Cynosurion cristati*, *Violion caninae*) were selected for biomass sampling in three dates: mid-May, early June and end of June. Proportions of individual species from total biomass, biomass production, crude fibre concentration, organic matter digestibility and community functional properties (forage value, leaf dry matter content, specific leaf area) were determined. Dry matter standing biomass at the end of June was highest in *Bromion* with 3.5 t ha^{-1}, followed by *Violion* with 2.7 t ha^{-1} and *Cynosurion* with 2.3 t ha^{-1}. A steep decline in forage quality (increase in crude fibre and decrease in organic matter digestibility) during accumulation of aboveground biomass was recorded in formerly unmanaged *Bromion* grassland but remarkably not in formerly grazed *Cynosurion* and *Violion* grasslands where early spring dominants were partly replaced by later-developing species, *Agrostis capillaris* and *Trifolium* spp. Abundance-weighted community functional properties were consistent with results obtained by biomass chemical analyses, thus the 'trait approach' can be used as a suitable surrogate of costly and labour-intensive laboratory procedures. Finally, we assume that the high degree of community seasonal development in *Cynosurion* and *Violion*, indicated here by a new community seasonal development index and by development in community specific leaf area, was accountable for the stabilization of forage quality later in the vegetation season.

Key-words: Biomass production; Community functional properties; Community seasonal development index; Legumes; Organic matter digestibility; Species-rich grasslands.

Introduction

Vast areas of species-rich grasslands throughout Europe are incorporated into agri-environmental schemes which compensate farmers for any loss associated with measures that aim to benefit the environment or biodiversity (Kleijn and Sutherland 2003). Grassland extensification schemes usually postpone defoliation activities to June - July in order to assure diaspore production of endangered plant species and reproduction of insects and ground nesting birds (Albrecht et al. 2007). One question that has not yet received sufficient study is, how does postponed defoliation affect biomass production and forage quality in different vegetation types and, therefore, profitability of livestock production systems.

For a long time, agronomists have focused on intensive grassland management, especially on agronomic characteristics (biomass production and forage quality) in productive sown grasslands (Frame 1994), whereas ecologists have tackled the issues of vanishing biodiversity (Bakker 1989). For these reasons, research of agronomic characteristics of semi-natural species-rich grasslands has received little attention, although such information is vital for the planning of grazing or cutting management in agri-environmental measures (Bokdam and Wallis DeVries 1992). Biomass production of particular vegetation units has been seldom investigated (Oomes and Mooi 1981; Schino et al. 2003; Hrevušová et al. 2009; Heinsoo et al. 2010), and forage quality in semi-natural grasslands obtained from late harvesting has also received little attention (Bruinenberg et al. 2003; Fiems et al. 2004; Bovolenta et al. 2008; Hessle et al.2008; Čop et al. 2009). The studies that were conducted generally concluded that forage quality was low and only suitable for low-performing animals.

Regarding the seasonal development of forage quality in intensive grasslands, crude fibre concentration increases, mean nitrogen and phosphorus concentrations in forage dry matter decrease with increasing standing biomass (dilution effect), with decreasing leaf:steam ratio and biomass senescence (Duru and Ducrocq 1997; Duru et al. 2008; Gibson 2009). Therefore, organic matter digestibility (OMD) during season usually quickly decreases and livestock performance is notably reduced (Frame 1994). However, semi-natural species-rich grasslands may host a great variety of dicotyledons that differ from the main forage grasses by, in most cases, having late-seasonal growth (Mitchley 1988; Martínková et al. 2002) and by higher OMD of stems, and particularly in leaves maintaining almost constant OMD over the growing season (Duru 1997). In spring, the proportion of leaves in the aboveground dry matter decreases faster in nutrient-rich than in nutrient-poor plots (Duru and Ducrocq 1997) or plant communities (Calvière and Duru 1999). A faster decline of OMD in highly productive compared with low productive plant communities may be therefore expected. Several recent studies (e.g. Garnier et al. 2004; Ansquer et al. 2009; Duru et al. 2009; Fortunel et al. 2009) provided evidence that grassland properties (including primary productivity, OMD) are well correlated with plant functional traits. Indeed, OMD for a wide range of grass species from semi-natural grasslands correlates negatively with leaf dry matter content (LDMC) and positively with specific leaf area (SLA) (Al Haj Khaled et al. 2006; Pontes et al. 2007).

The defoliation regime is one of the key factors determining phenological patterns in a grassland community (Mitchley 1988; Smith and Jones 1991; Bergfur et al. 2004). In productive fallow stands and summer mown meadows, the main factor driving species growth is competition for light; consequently dominant species are synchronous in their development (Martínková et al. 2002). However, productive stands exposed to repeated defoliation permit the coexistence of slower-developing species with dominants and thus support high functional diversity (*sensu* plant height, flowering time, LDMC) in plant communities (Al Mufti et al. 1977; Adler et al. 2001; Questad and Bryan 2008). Functionally diverse communities show less variation of standing biomass around the peak (Ansquer et al. 2009), and enable extending the cutting/grazing dates without a large effect on the amount of harvested forage. However, no studies have tested which plant communities enable postponing defoliation until summer months without a significant decline in forage quality. Several metrics appropriate for the evaluation of community temporal changes have recently been recommended (e.g. Frost et al. 1995; Collins et al. 2008), but all these metrics are designed for the description of temporal changes in permanent plots and are not suitable for destructively sampled biomass data. Therefore, we introduced a new measure of community seasonal development which appears from 'Canberra Metric Similarity Measure' by Lance and Williams (1967).

In this paper, grasslands in the White Carpathian Mountains were investigated because of their extraordinary species richness, up to 103 vascular plant species per 24 m^2 (Jongepierová et al. 2007), which has been predetermined by a long history of low input management and by the biogeographical position situated between the Subatlantic, Montane Carpathian and Pannonian regions. Three types of the most widespread grassland communities in the region (Škodová et al. 2008) were selected for detailed analysis: *Bromion erecti* Koch 1926 (henceforth *Bromion*), *Cynosurion cristati* Tüxen 1947 (*Cynosurion*) and *Violion caninae* Schwickerath 1944 (*Violion*), i.e. three distinct vegetation alliances as described in Chytrý (2007). These grasslands possess high conservation values in central Europe; moreover, *Bromion* and *Violion* are included in the list of Natura 2000 priority habitats (Chytrý et al. 2001).

The aim of this study was to answer following questions: (a) Do selected grasslands differ in biomass production? (b) How is biomass production and forage quality affected by postponed defoliation? (b) Do selected grasslands differ in seasonal development of plant species composition? (c) Is it possible to explain seasonal development of forage quality determined by chemical analyses of biomass by means of seasonal change in community forage value, community LDMC and community SLA in selected grasslands?

Materials and Methods

Study sites

The study was carried out in the White Carpathians Mountains situated in the borderland between the Czech Republic and Slovakia. The soils in all sites are haplic cambisols, developed on tertiary flysch sediments which consist of alternating sandstone and rock clay layers of variable thickness. Three sites were selected where distinct communities have developed under different management histories on soils with highly contrasting properties (see Table 1).

Table 1 Description of investigated sites. Abbreviations used: MAT - mean annual temperature; MAP - mean annual precipitation; contents of P, K, Ca and Mg in soil determined with Mehlich III

Site		***Bromion***	***Cynosurion***	***Violion***
Altitude	m a.s.l.	370	720	450
MAT	°C	7.9	6.0	8.0
MAP	mm	760	850	669
Species richness	per 1 m^2	32	33	30
Clay	%	28	10	9
Silt	%	66	69	35
Sand	%	6	23	56
pH ($CaCl_2$)	units	5.4	5.0	4.6
P	mg kg^{-1}	7.4	7.8	9.0
K	mg kg^{-1}	342	245	99
Ca	mg kg^{-1}	3539	1963	1102
Mg	mg kg^{-1}	218	204	67

Bromion (49°05´58´´N, 18°01´59´´E) had been unmanaged for 13 years prior to the start of the study, formerly managed by cattle grazing; *Cynosurion* (48°56´20´´N, 17°48´00´´E) had been rotationally grazed by cattle from early spring for more than 25 years prior to the start of the study; *Violion* (48°53´47´´N, 17°34´44´´E) was old, eroded and continuously grazed pasture on a hilltop with a history of more than 50 years of sheep grazing beginning each year in early spring.

Sampling design, biomass production and forage quality analyses

In 2004, 15 permanent 5 m × 5 m plots were established in each investigated grasslands (45 permanent plots in all three sites together). In each 5 m × 5 m plot, three 1 m × 1 m sub-plots were randomly selected for data collection on three sampling dates, i.e. one sub-plot was cut in each sampling date only (Fig. 1). Such a systematic sampling design enabled the bias in temporal development of biomass characteristics caused by spatial heterogeneity in species composition to be minimized. All plots were fenced off before data collection to prevent them from any unwanted defoliation. Because of the complex analyses of agronomic characteristics and plant species composition, selection of more sites with the same plant community was not feasible. Furthermore, only two sampling dates in *Cynosurion* and *Violion* were used because of technical problems.

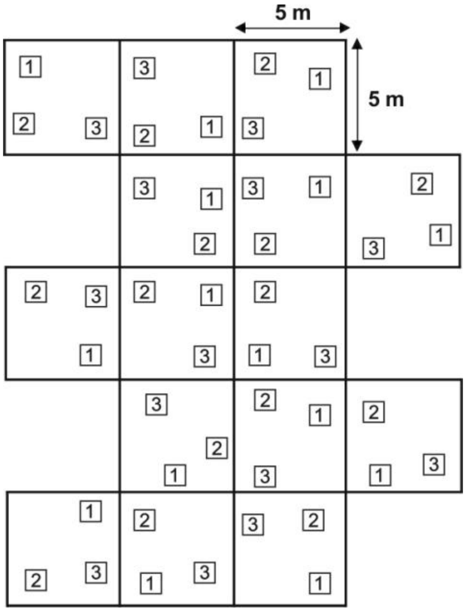

Fig. 1 Scheme of biomass sampling in grasslands, three subplots within each 5 m × 5 m permanent plot present sampling dates 1) 19th May, 2) 7th June, 3) 30th June. Arrangement of plots is not strictly contiguous because these established plots were, after this baseline data collection, used for management experiment with grazing plots at the edges

Sampling dates were 19th May, 7th June, and 30th June. Cutting in mid-May has been recommended as the best time for hay production on two cut meadows in central Europe as it offers the best compromise between forage yield and its quality (Buchgraber and Gindl 2004). On the other hand, the 30th June was recognized as the first possible day of harvest enabling generative reproduction of endangered plant species in the investigated grasslands (Háková et al. 2004). Sub-plots had been neither grazed nor cut since start of the vegetation season, and thus they always provided first-growth biomass in all sampling dates. Biomass from each sub-plot was harvested 3 cm above ground, weighed and taken to the laboratory and dried at 55 °C until total desiccation was reached. Dry matter content was determined and dry matter standing biomass was calculated for each sub-plot.

Weende analysis was used to determine crude fibre (AOAC 1984) and in vitro OMD was analysed according to Tilley and Terry (1963). Both parameters of forage quality were analysed from each biomass sample.

Plant species composition and community seasonal development

Species biomass in a sample was estimated by calibrated weight-estimate method (Tadmor et al. 1975). In several training plots visual estimates of species biomass were calibrated by clipping and weighing, and when consistent estimates were attained, estimations of species biomass in studied sub-plots were undertaken. Further, proportion of each species from the total sample biomass was calculated. The sum of proportions of all species present within the sub-plot was 100%. As seasonal development of community plant species composition was evaluated from destructive biomass sampling undertaken in each term in the new sub-plots, proportions of species from all 15 sub-plots were averaged and species ranked in declining order. Subsequently, species whose cumulated biomass reached 80% of community standing biomass (taken as an average from two or three sampling terms) were analysed for temporal development; in our case 14 of the most abundant species were taken in all three grasslands. Analysing species accounting for 80% of the total biomass has been recognized to be sufficient for the capture of community properties (Garnier et al. 2004; Fortunel et al. 2009).

For quantification of community temporal turnover, the community seasonal development index (CSDI) was proposed (Equation 1). It is derived from the ‘Canberra Metric Similarity Measure’ (Lance and Williams 1967) which so far has been used by ecologists for the evaluation of species abundance similarity between two samples. Our modification quantifies a temporal change of the proportions of the most abundant species in a community.

$$CSDI_n = \frac{1}{n}\sum_{i=1}^{n}\frac{|x_i - y_i|}{x_i + y_i} \qquad (1)$$

where x_i is an average proportion of species i from all sub-plots at the locality on the initial (spring) sampling date and y_i is an average proportion of species i from all sub-plots at the locality on subsequent (summer) sampling date and n is the number of the most abundant species with a cumulated biomass proportion reaching approximately 80% (taken as an average from both sampling terms).

The index has a range of 0–1 and following desirable characteristics: the minimum value 0 is applied if there has been no change from initial (spring) proportions of all species, and the maximum value 1 is only reached when all initial (spring) species have been completely replaced by other species appearing first in the subsequent (summer) sampling term. The index is symmetrical (interchanging x_i and y_i gives same result) but nonlinear, i.e. a unit change in $|x - y|$ does not have the same effect at all values of x. This means that it is sensitive to proportional rather than absolute differences, for example, CSDI gives a value ten times higher to species change from a proportion of 0.01 to 0.1 than from a proportion of 0.51 to 0.60. This seems to us to be a biologically sensible transformation, since later-developing species (e.g. legumes) bring young digestible tissues into the community biomass. Although minor, these tissues often synergistically improve the OMD of the community biomass as a whole due to associative effects of high nitrogen concentration plants on the digestion process of biomass with a poor forage quality (Niderkorn and Baumont 2009). Conversely, initial dominants increase their proportions mainly with structural material, which is hardly digestible, therefore dominant change (is often higher in absolute values) is deliberately not emphasized. The index is vulnerable to sampling errors for rare species, therefore only the most abundant species with cumulated biomass proportions reaching 80% should be taken into consideration.

For a clear visualization of the index characteristics, contours of the CSDI were plotted for all combinations of *x* (spring proportion, range 0–1) and *y* (summer proportion, range 0–1) in the case of two species in a sample (Fig. 2). Since CSDI had to be expressed as a function of two variables for graph construction, Equation 1, for two species:

$$CSDI_2 = \ \left|x_1 - y_1\right| / \ \ x_1 + y_1 \ \ + \left|x_2 - y_2\right| / \ \ x_2 + y_2 \ \ \ /\, 2 \qquad (2)$$

was modified by substituting the proportions of the second species from their definition by

$$x_2 = 1 - x_1 \qquad (3)$$

and

$$y_2 = 1 - y_1 \qquad (4)$$

After substitution, Equation 2 for graph construction may be rewritten as follows:

$$CSDI_2 = \ \left|x_1 - y_1\right| / \ \ x_1 + y_1 \ \ + \left|x_1 - y_1\right| / \ \ 2 - x_1 - y_1 \ \ \ /\, 2 \qquad (5)$$

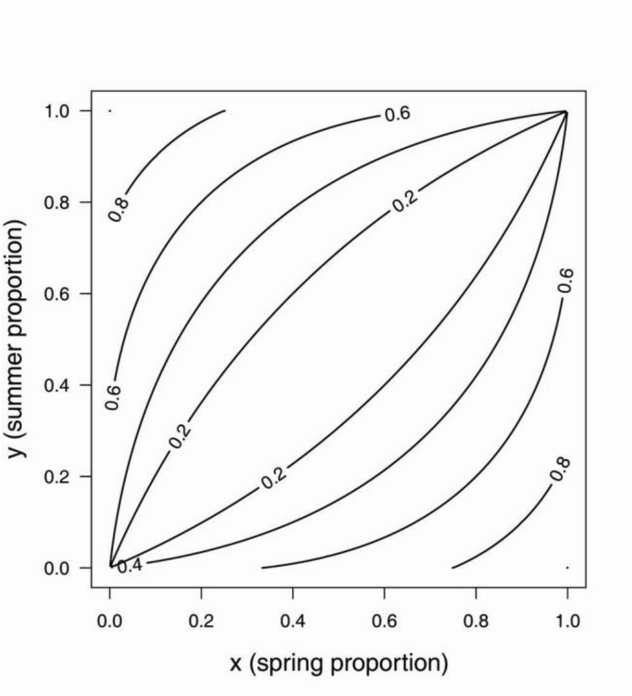

Fig. 2 The values of a community seasonal development index (CSDI) as a function of spring (x) and summer (y) proportions when two species are available

Community functional properties

Based on the assumption of the ‘biomass ratio hypothesis’ (Grime 1998), functional parameters at the community level were calculated by weighing the trait value of species with their relative contributions to the sample biomass (Fortunel et al. 2009). The community forage value, community LDMC and community SLA were calculated for each sub-plot.

To calculate the community forage value, forage indicator values of individual species were taken from the BiolFlor database (Klotz et al. 2002). Forage indicator values ranged from 1 (lowest) to 9 (highest). Out of a total of 89 recorded species, nine lacked forage indicator values in the BiolFlor database which is why missing values were supplemented from the database by Jurko (1990) and adapted to the BiolFlor scale. The tabular LDMC (average of aggregated records) and tabular SLA (average of aggregated records) of individual species were taken from the LEDA trait-base (Kleyer et al. 2008). Community LDMC and community SLA were calculated using 78 and 85 species, respectively, as data for 11 and 4 species (fortunately rare in samples) were not available.

Data analysis

Plotting values of CSDI in a model example of two species in a sample was performed with R 2.10.1 software (R Development Core Team 2010). Further analyses were performed using the statistical package SYSTAT 13 (www.systat.com). Prior analyses data were checked for normality and homogeneity of variances and when necessary they were log-transformed. In the statistical analyses of standing biomass, crude fibre, OMD and community functional properties (response variables), site (*Bromion*, *Cynosurion*, *Violion*) and date (19th May, 7th June, 30th June) were in ANOVA considered as fixed factors (explanatory variables). Technical problems caused that there were no observations for some cells in a standard two-way ANOVA, such data were difficult to analyze. Therefore, simpler means model was used that treats the analysis as a large single factor ANOVA comparing all cells with tests for main effects and interactions. Contrasts based on cell means were used for the tests of sensible hypotheses according to recommendations of Quinn and Keough (2002, p 244–247). The null hypotheses were as follows: Site: *Bromion* vs. *Violion* for the first and the last sampling date ($\mu_{\mathrm{Bromion\_19\ May}} + \mu_{\mathrm{Bromion\_30\ June}} = \mu_{\mathrm{Violion\_19\ May}} + \mu_{\mathrm{Violion\_30\ June}}$), *Bromion* vs. *Cynosurion* for the second and the last sampling date ($\mu_{\mathrm{Bromion\_7\ June}} + \mu_{\mathrm{Bromion\_30\ June}} = \mu_{\mathrm{Cynosurion\_7\ June}} + \mu_{\mathrm{Cynosurion\_30\ June}}$), and *Cynosurion* vs. *Violion* for the last sampling date ($\mu_{\mathrm{Cynosurion\_30\ June}} = \mu_{\mathrm{Violion\_30\ June}}$); Date: the first vs. the last date for *Bromion* and *Violion* ($\mu_{\mathrm{Bromion\_19\ May}} + \mu_{\mathrm{Violion\_19\ May}} = \mu_{\mathrm{Bromion\_30\ June}} + \mu_{\mathrm{Violion\_30\ June}}$), the second vs. the last date for *Bromion* and *Cynosurion* ($\mu_{\mathrm{Bromion\_7\ June}} + \mu_{\mathrm{Cynosurion\_7\ June}} = \mu_{\mathrm{Bromion\_30\ June}} + \mu_{\mathrm{Cynosurion\_30\ June}}$); Site × date: *Bromion* vs. *Violion* at the first vs. the last date ($\mu_{\mathrm{Bromion\_19\ May}} - \mu_{\mathrm{Violion\_19\ May}} - \mu_{\mathrm{Bromion\_30\ June}} + \mu_{\mathrm{Violion\_30\ June}} = 0$), *Bromion* vs. *Cynosurion* at the second vs. the last date ($\mu_{\mathrm{Bromion\_7\ June}} - \mu_{\mathrm{Cynosurion\_7\ June}} - \mu_{\mathrm{Bromion\_30\ June}} + \mu_{\mathrm{Cynosurion\_30\ June}} = 0$). Post hoc comparisons on the least squares means were conducted using Fisher's LSD as recommended by Milliken and Johnson (1984). Further, seasonal development of each of 14 the most abundant species within each site was compared by one-way ANOVA and Tukey’s HSD post-hoc test was applied to evaluate differences between sampling dates after obtaining significant ANOVA result.

Results

Biomass production and forage quality

The amount of dry matter standing biomass ranged from 0.8 to 3.2 t ha^{-1} over all of the sites and sampling dates (Fig. 3a). The standing biomass was greater in *Bromion* than in other sites over whole season (site: $F = 43.22$, $P < 0.001$) and increased during season at all sites except for *Bromion* where it stagnated in the last two sampling dates (date: $F = 45.56$; site × date: $F = 9.69$, all $P < 0.001$).

Regarding forage quality, crude fibre concentrations ranged from 24.6 to 28.9 % over all of the sites and sampling dates (Fig. 3b). It significantly differed among sites ($F = 13.33$, $P < 0.001$) and dates ($F = 3.83$, $P = 0.05$). There was also significant effect of site × date interaction ($F = 10.50$, $P < 0.001$). *Cynosurion* had significantly lower crude fibre concentration than other sites. During season, a significant increase in crude fibre concentration was recorded in *Bromion* but no significant changes were observed in other sites. OMD ranged from 59.4 to 70.5 % over all of the sites and sampling dates (Fig. 3c). It significantly increased in the direction *Bromion* →*Violion* → *Cynosurion* (F = 15.96, P < 0.001) but except for its decrease from the first to the second sampling date in *Bromion* and increase from the second to the third sampling date in *Cynosurion*, no changes over season were observed (date: F = 2.99, P = 0.057; site × date: F = 10.50, P < 0.001).

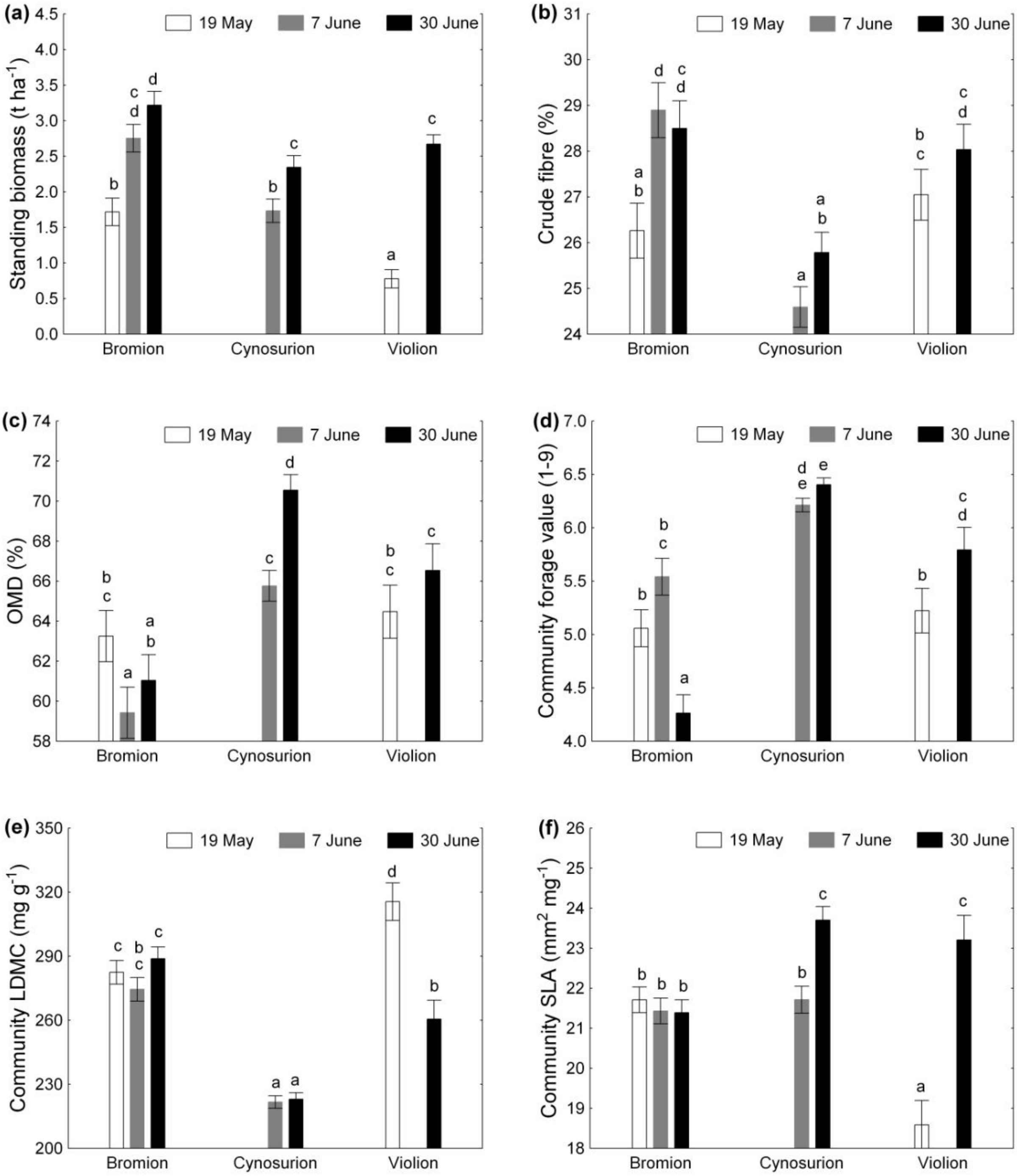

Fig. 3 Seasonal development of (a) dry matter standing biomass, (b) crude fibre concentration, (c) *in vitro* organic matter digestibility (OMD), (d) community forage value, (e) community leaf dry matter content (LDMC) and (f) community specific leaf area (SLA); error bars represent SE; means with the same letter are not significantly different (Fisher's LSD test, P < 0.05)

Community functional properties

Community forage value ranged from 4.3 to 6.4 over all of the sites and sampling dates (Fig. 3d); it was the highest in *Cynosurion*, followed by *Violion* and the lowest in *Bromion* (site: F = 28.78, P < 0.001). Seasonal development of community forage value was site-specific (date: F = 4.43, P < 0.001; site × date: F = 12.29, P < 0.001). While significantly decreased in the last sampling date in *Bromion*, it was stable in *Cynosurion* and increased in *Violion*. Community LDMC (Fig. 3e) was stable in *Bromion* (high values) and *Cynosurion* (low values) while strongly changed in *Violion* from high to middle values over season (site: F = 28.21, P < 0.001; date: F = 6.54, P = 0.005; site × date: F = 10.97, P < 0.001). Community SLA (Fig. 3f) was stable in *Bromion* (middle values) while strongly changed from low or middle to high values over season in *Violion* and *Cynosurion*, respectively (site: F = 2.94, P = 0.037; date: F = 11.05, P < 0.001; site × date: F = 16.17, P < 0.001).

Plant species composition

In *Bromion*, four out of 14 of the most abundant species exhibited significant seasonal development. The proportion of the dominant *Brachypodium pinnatum* had increased substantially while proportions of *Poa pratensis* and *Dactylis glomerata* had significantly decreased by the last sampling date (Fig. 4a). In *Cynosurion*, two out of 14 of the most abundant species exhibited significant seasonal development. The proportion of *Agrostis capillaris* had substantially increased whilst that of *Knautia kitaibelii* had significantly decreased (Fig. 4b). In *Violion*, seven out of 14 of the most abundant species exhibited significant seasonal development (Fig. 4c). Proportions of *Festuca rubra, Agrostis capillaris, Trifolium repens* and *T. pratense* had significantly increased while proportions of *Bromus erectus*, *Festuca rupicola* and *Poa pratensis* had significantly decreased by the last sampling date in comparison to the first sampling date.

In *Bromion*, CSDI calculated with biomass proportions of 14 of the most abundant species was 0.30 for community change from 19th May to 7th June and 0.39 for change from 7th June to 30th June, and 0.39 was also reached for change from 19th May to 30th June. In *Cynosurion*, CSDI was 0.38 for community change from 7th June to 30th June and in *Violion*, CSDI was 0.54 for community change from 19th May to 30th June.

Discussion

Biomass production

As expected from soil properties of the sites (Table 1, *Bromion* had substantially higher pH, K, Ca and Mg contents than other two sites), dry matter standing biomass was the highest in *Bromion* and the peak standing biomass of 3.2 t ha^{-1} was comparable to the maximum levels measured in *Bromion erecti* grasslands throughout Europe (Ryser et al. 1995; Schino et al. 2003; Smits et al. 2008). Grasslands dominated by *Brachypodium pinnatum* or *Bromus erectus*, common grasses exhibiting resource conservation strategies (Duru et al. 2009), seem to have ceiling standing biomass at around 4 t ha^{-1}. In *Violion*, the peak standing biomass of 2.7 t ha^{-1} was consistent with amounts measured for various *Nardus* grasslands similar to *Violion caninae* (Bakker et al. 2002; Schino et al. 2003; Hejcman et al. 2006; Hejcman et al. 2007). The maximal standing biomass of grasslands with *Nardus stricta* seems to be around 3 t ha^{-1}. In *Violion caninae* and *Bromion erecti* grasslands, the increase in biomass production above maximal limits is connected with the expansion of highly productive species from different alliances and therefore occurs with changes in grassland communities. This is clearly visible from long-term fertilizer experiments where increase in nutrient availability eliminated species typical for *Violion caninae* in favour of more productive species typical for *Arrhenatherion elatioris* alliance (Hejcman et al. 2010a).

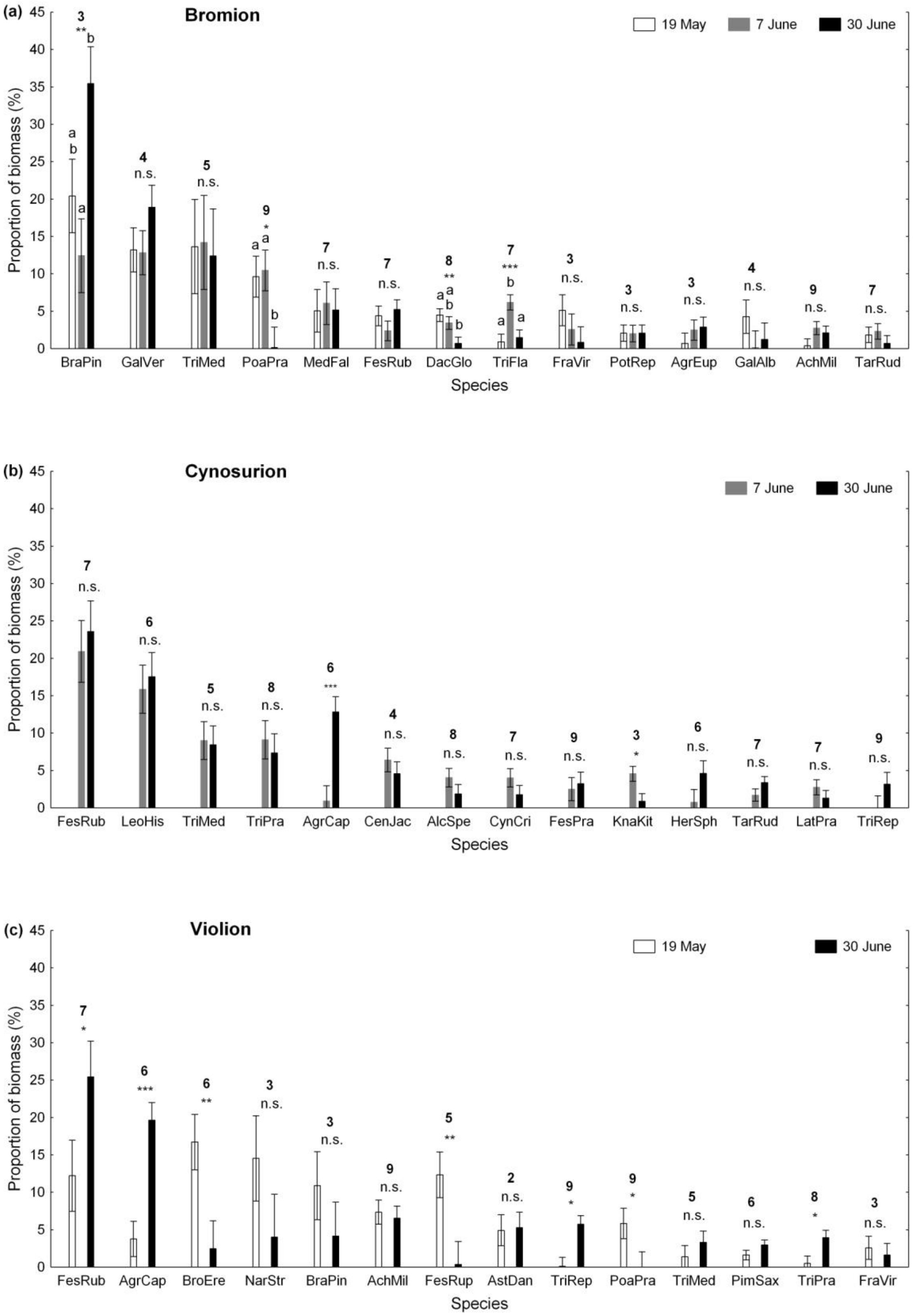

Fig. 4 Seasonal development of 14 of the most abundant species in (a) *Bromion*, (b) *Cynosurion* and (c) *Violion*; error bars represent SE

n.s., not significant result of one-way ANOVA; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; sampling dates within each species with the same letter in *Bromion* are not significantly different (Tukey's LSD test, $P < 0.05$); number above bar for individual species is its tabular forage value (according to BiolFlor database; see Methods)

Species abbreviations in Fig. 4: AchMill - *Achillea millefolium*, AgrCap - *Agrostis capillaris*, AgrEup - *Agrimonia euaptoria*, AlcSpe - *Alchemilla* sp., AstDan - *Astragalus danicus*, BraPin - *Brachypodium pinnatum*, BroEre - *Bromus erectus*, CenJac - *Centaurea jacea*, CynCri - *Cynosurus cristatus*, DacGlo - *Dactylis glomerata*, FesPra - *Festuca pratensis*, FesRub - *Festuca rubra*, FesRup - *Festuca rupicola*, FraVir - *Fragaria viridis*, GalAlb - *Galium album*, GalVer - *Galium verum*, HerSph - *Heracleum sphondylium*, KnaKit - *Knautia kitaibelii*, LatPra - *Lathyrus pratensis*, LeoHis - *Leontodon hispidus*, MedFal - *Medicago falcata*, NarStr - *Nardus stricta*, PimSax - *Pimpinella saxifraga*, PoaPra - *Poa pratensis*, PotRep - *Potentilla reptans*, TriFla - *Trisetum flavescens*, TriMed - *Trifolium medium*, TriPra - *Trifolium pratense*, TriRep - *Trifolium repens*

Although *Cynosurion* possessed intermediate soil properties, the standing biomass here was not different from *Violion* on 30th June. The recorded standing biomass of 2.3 t ha^{-1} contrasted with that of 5–7 t ha^{-1} reported for *Cynosurion cristati* grasslands by other studies (Pavlů et al. 2003; Schino et al. 2003; Hejcman et al. 2010b). Lower standing biomass found in *Cynosurion* can be partly explained by the delayed growth due to higher altitude and by the adaptability of the sward to frequent defoliation which supports short species able to easily regenerate after defoliation. A maximal yield can probably be obtained in this grassland by frequent defoliation, not by the postponing of the first defoliation to the end of June.
Furthermore, in contrast to *Violion caninae* and *Bromion erecti* communities with clear upper biomass production limits, *Cynosurion cristati* grasslands can be highly variable in standing biomass as its characteristic species are adapted to frequent defoliation under a wide range of nutrient availabilities (Jurko 1969). This is the reason why the upper biomass production limit in *Cynosurion cristati* grasslands can hardly be estimated.

Forage quality

The seasonal patterns of forage quality development in the selected sites differed greatly. From middle May to the end of June, tall sward *Bromion* exhibited slight decline in OMD and significant increase in crude fibre concentration (and significant declines of N, P and K biomass concentrations, unpublished data), whereas the short sward communities *Cynosurion* and *Violion* displayed unexpected increase or stability of OMD and stability of crude fibre concentration (the same pattern was detected for N, P, K, Ca and Mg biomass concentrations, unpublished data). Such patterns might be attributed to the fact that the higher nutrient supply (indicated by soil properties, Table 1) in *Bromion* produced a ‘dilution effect’ (Duru and Ducrocq 1997) through growth of long stems with lower nutrient concentrations and lower OMD than leaves (Calvière and Duru 1999). Furthermore, an increase in dominance of *Brachypodium pinnatum*, with a high proportion of senescent leaves, was recorded in *Bromion* in the last sampling date. Stable forage quality in *Cynosurion* and *Violion* contrasted with frequently reported declines in forage quality in the case of postponed defoliation in species-poor intensive grasslands (Bruinenberg et al. 2002). *Cynosurion* and *Violion* could manifest such forage quality patterns due to their long grazing histories with early spring defoliation, which enabled the coexistence of slower developing species and also supported more digestible species occurring often in frequently defoliated sites (Louault et al. 2005; Čop et al. 2009). Differences in OMD between low altitude *Bromion* and upland *Cynosurion* could be partly explained by the fact that lignification of cell wall material increases at high temperatures and accumulation of digestible storage products is greater at low temperatures (Gibson 2009). Therefore, on the basis of our results it is not possible to declare that the described seasonal patterns of forage quality are typical for these vegetation units in general. But Hejcman et al. (2010c) recently reported from long-term fertilisation experiment that late cutting management decreases forage quality more in highly productive (*Arrhenatherion* *elatioris*) than in low productive (*Violion caninae*) plant communities and this is consistent with our results.

The OMD ranged from 59% to 71% and, as we expected, was lower than for the standard forage grass, *Lolium perenne* with an average digestibility of 80% (Bruinenberg et al. 2002). It can be concluded that the biomass from all of the investigated sites was of low quality and could not be used for highly intensive milk production systems. Instead, the biomass from the investigated grasslands could satisfy the lower nutritional requirements of low-performance beef cattle or sheep. This conclusion corresponds to the results by Bokdam and Wallis DeVries (1992) from semi-natural grasslands in the Netherlands.

Plant species composition and community functional properties

The development of community functional properties, derived from species composition, was well reflected in the divergent seasonal development of biomass quality parameters (crude fibre, OMD) in *Bromion* versus *Cynosurion* and *Violion*. No development in community LDMC and community SLA was recorded in *Bromion*, whereas community SLA sharply increased in *Cynosurion* and *Violion* and community LDMC decreased in *Violion*. Community values of SLA were at the end of June, in the case of the long-time grazed pastures of *Cynosurion* and *Violion*, higher than in the case of the abandoned *Bromion*. Community LDMC showed this pattern in reverse. These results are consistent with those of other studies (Louault et al. 2005; McIntyre 2008) where SLA was found to positively correlate with intensity of disturbance whereas LDMC was found to negatively correlate with intensity of disturbance.

Moreover, *Bromion* showed a significant decrease in the community forage value whereas this value remained stable or even increased in *Cynosurion* and *Violion*, respectively. This was because of changes in plant species composition – spring dominants *Poa pratensis* and *Dactylis glomerata*, with high forage indicator values, significantly decreased while *Brachypodium pinnatum*, with little forage indicator value, substantially increased in *Bromion*. In contrast, *Knautia kitaibelii* with little forage indicator value significantly decreased and *Agrostis capillaris* and *Heracleum sphondylium* with intermediate forage indicator values and *Trifolium repens* (the latter two almost significantly), with high forage indicator value, increased in *Cynosurion*. Similarly, in *Violion*, spring dominants *Bromus erectus*, *Nardus stricta*, *Festuca rupicola* and *Brachypodium pinnatum*, with little forage indicator values, were replaced by *Agrostis capillaris* and *Festuca rubra* with intermediate forage indicator values and by *Trifolium pratense* and *T. repens* with high forage indicator values. Contrasting values of CSDI indicated different seasonal developments of plant species compositions in the investigated sites: *Violion* had substantially higher community seasonal development than *Bromion*.

We assume that the high degree of community seasonal development, which was indicated by high CSDI in *Violion* and by significant development in community SLA in both *Cynosurion* and *Violion*, together with high forage indicator values of later-developing species were accountable for the remarkable stabilization of forage quality later in the vegetation season in these sites. According to author’s knowledge, it has been for the first time described that seasonal decline in forage quality was deferred by seasonal development of plant species composition within the community. However, it was previously suggested that late-flowering species at an immature stage of reproductive development might moderate the seasonal decline in forage quality (Smith and Jones 1991; Duru 1997). Seasonal development of plant species composition is an intrinsic characteristic of many types of semi-natural grasslands, and the extent of such development is influenced by the diversity of plant functional types which is elevated by intensity of disturbance (Kleyer 1999; Louault et al. 2005). This is clear from the long-time unmanaged *Bromion*, where the early spring dominant

Brachypodium pinnatum quickly closed the canopy and even increased its dominance later in the season. Thus, forage quality decline at this site may be further explained by the plant ageing process which is connected to an increase in less digestible structural tissues (stems) on the account of metabolic tissues (leaves). Contrary to this, *Cynosurion* and *Violion* sites possess communities which have become established under long-lasting grazing pressures starting each season in May or even earlier. Each year, species with early spring growth are suppressed by defoliation and trampling, therefore species such as *Agrostis capillaris* and *Trifolium repens* requiring higher thermic sum (Bovolenta et al. 2008) are able to coexist and their young tissues become a significant part of the community biomass later in the season. In *Violion*, the increase in legumes (*Trifolium pratense, T. repens*) was particularly responsible for stabilization of forage quality, partly due to their high nitrogen concentrations (Ďurková and Jančovič 2003), partly due to positive effect of high nitrogen concentration tissues on digestion process (Niderkorn and Baumont 2009) and partly due to increasing growth and foliar nitrogen concentrations in neighbouring plants (Spehn et al. 2002).

Conclusions

The remarkably stable forage quality obtained by a late harvest of species-rich grasslands should be added to the list of important functional characteristics of semi-natural grasslands, which were lately synthesized by Sanderson et al. (2004). Future agri-environmental measures should take into consideration the fact that a late harvest without decreased forage quality could be expected in grasslands with high seasonal development of species proportions, at least in the first year after the shift from early spring to summer defoliation management.

As the design of this study did not enable the separation of effects of community type from grazing history, future research based on replicated experimental plots with different management types within each respective community is needed. Also, the use of CSDI as a tool for the prediction of seasonal development of forage quality should be further tested and confronted with seasonal developments of crude fibre and OMD of biomass samples.

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CHAPTER X

General conclusions

In order to encourage farmers and their advisors to promote using species-rich grasslands, the agronomic services they can provide should be demonstrated. Reviewing literature on diet selection of livestock (**Chapter III**), we may conclude that domesticated ruminants perform better for having available a variety of food types. Species-rich grasslands offer a wide variety of food types, in which livestock can meet their demands for energy and intake of nutrients, and regulate their intake of toxins better than when constrained to a single food, even if the food is nutritionally balanced. In this way livestock also experience the benefits of ingesting small amounts of compounds with medicinal effects and they learn to prefer plant species containing such compounds. This is the case for sheep preferentially grazing highly toxic White hellebore (*Veratrum album*) or even Meadow saffron (*Colchicum autumnale*) in species-rich pastures in the Czech Republic. Grazing herbivores seldom consume enough toxins to result in poisoning because they regulate their intake through post-ingestive feedback and quickly learn to eat mixtures of plants that mitigate toxicity. For instance, tannins contained in many wild plants may interact in rumen with highly toxic alkaloids from other plants, thus neutralising their negative effects. Such experiences enable animals to adapt to local diets and stressors. Particularly low grazing intensity allowing animals to manifest their feeding preferences increases animal welfare and also production per animal. This agronomic service of species-rich grasslands, i.e. welfare of grazing livestock, has not yet been sufficiently highlighted.

By investigating causes and consequences of heterogeneous grazing we should detect livestock grazing preferences. However, absolute feeding preferences for plant species, which can be obtained from feeding trials, may not be applicable to species-rich pastures. On pastures, a herbivore's diet selection is substantially modified by species availability, spatial distribution and neighbourhood effects. The pattern of selection is largely determined by the herbivore's body-size; small herbivores as sheep and goats are generally more selective than large ones such as cattle. Larger herbivores are forced to select lower-quality forage in order to maintain a certain level of intake. However, both small and large animals adopt relatively selective strategies if available food resources exceed their needs. We tested whether sheep adopt different foraging strategies in productive mesic (*Arrhenatherion*) vs. low-productive dry (*Bromion*) species-rich grasslands dominated by resource-acquisitive vs. resource-conservative species, respectively (**Chapter IV**). Indeed, we found that in mesic grasslands, where forage was abundant and which offered a choice of highly nutritious species, the strategy of maximising forage quality was the most pronounced. On the contrary, in less productive dry grasslands, where the sward consisted mainly of species with low forage value, the strategy of maximising forage quantity was preferred. This new result provided a better understanding of various effects of grazing under different environmental conditions. Maximisation of forage quantity in dry grasslands was detected consistently at several scales. Sheep selected plots with higher community-weighted canopy height as well as plant species with greater canopy height. This finding helped to elucidate the decrease in community-weighted canopy height and suppression of grasses under the grazing regime in the long-term management experiments within broad-leaved dry grasslands (**Chapter V**). This pattern might not be expected, because the dominant Tor-grass (*Brachypodium pinnatum*) belonging to the tallest species in the community is reported to be a highly unpalatable plant, having one of the lowest forage indicator values within the community. Presumably forage quality in early spring does not differ as much as is indicated in databases, therefore at the beginning of May *Brachypodium* biomass possessed a sufficient digestibility for sheep. Thus, sheep were not yet forced to select less productive dicotyledons (**Chapter IV**) exhibiting generally higher forage values throughout the season.

Semi-natural species-rich grasslands may be less productive than agriculturally improved ones, they could however have other advantages such as late-season or slower growth providing flexibility in grassland harvest. We examined which species-rich grasslands have a potential for late harvest without significant loss of forage quality, and how this agronomic service is related to functional vegetation properties. We revealed that for vegetation under long-time grazing pressure starting each year in early spring seasonal alterations in plant species proportions are typical. These can be uncovered in permanent plots with the help of the index of phenological complementarity or with the community seasonal development index, newly proposed by us for destructively sampled biomass data. Later-developing species seem to be partially accountable (together with a high proportion of species with persistent leaves – **Chapter VIII and IX**) for stabilisation of forage quality later in the season, which was demonstrated analysing the development of organic matter digestibility. In another study (**Chapter VII**), plots under long-time grazing comprised also more later-developing species and featured slower community-weighted phenological progression than vegetation in plots under mowing. Thus, within two independent studies we evidenced that in vegetation under long-time grazing pressure postponing of defoliation until summer produced the lowest decrease in forage quality. Therefore, permanent pastures render the greatest potential for flexibility in grassland harvest; this feature constitutes the agronomic service of species-rich grasslands, which may be utilised by farmers when the regular harvest (grazing) date has to be shifted due to bad weather conditions. Furthermore, one-year application of late harvest could be established as a low-cost agri-environmental measure. Nature conservation interest, i.e. reproduction of insects and ground-nesting birds, would be attained, while forage quality and subsequent profitability of livestock production would not be strongly diminished.

Since financial resources for biodiversity-targeted management are limited, effects of long-term grassland management on the agronomic value of semi-natural grasslands within large protected landscape areas should receive more attention. In this light finding optimal low-cost management is one of the major tasks in the European agri-environmental policy. We investigated effects of four management treatments in 120 permanent plots established in formerly abandoned dry grasslands (**Chapter V**). Although mowing in mid-July decreased the performance of grasses and enhanced forbs most of all treatments, we cannot recommend it as an optimal low-cost management type for maintenance of broad-leaved dry grasslands. Long-term mid-July mowing produced vegetation with a high proportion of rosettes, whose biomass is mostly not accessible to mowing machines or grazing livestock. Thus, sparse upright herbage provides forage of low quantity. In addition, the high proportion of species relying on generative reproduction and on early flowering indicates that vegetation under a long-term mowing regime, contrary to grazing, yields forage of lower quality.

Simple diagnostic tools for assessment of forage quantity and quality are needed. However, relationships found for community functional traits and ecosystem properties (e.g. biomass production – predictor of forage quantity) often originate from large ecological gradients and may not be applicable at other scales. On the large scale of grasslands, community-weighted LDMC was acknowledged to be connected to high herbage productivity and high nutrient concentrations in biomass. Hence, higher total amounts of nutrients in above-ground standing biomass should be linked to lower community LDMC. We tested this hypothesis using a dataset from management experiments (**Chapter VI**). Community LDMC appeared to be significantly the lowest under mowing, but in this light unexpectedly also the total amounts of N, P and K were significantly the lowest under mowing. We concluded, taking into account grasslands under different management regimes, that community-weighted LDMC cannot be used as a suitable indicator of agronomic value. This may be explained by high proportion of rosettes under mowing (**Chapter V**) which made a large part of the above-ground biomass inaccessible to harvesting. Furthermore, community-weighted LDMC long considered as a trait responding to fertility also responds to intensity of disturbance (**Chapter V**), which is in line with other current studies. Summing up, the relationships between community-weighted LDMC and forage quantity and quality are scale dependent and according to new results of Michel Duru's research group (INRA, Toulouse) largely influenced by the proportion of dicotyledonous species. Hence they have newly proposed simple diagnostic tools based on LDMC of dominant grass species.

It can be concluded that community-weighted means of plant functional traits represent a powerful tool for analyses of causes and consequences of selective livestock grazing as well as for an evaluation of management-induced effects on ecosystem properties. Functional trait approach might also be helpful to assess forage quantity and quality obtained from species-rich grasslands and also for delimiting grassland types in which postponing of grassland harvest until summer at least diminishes the profitability of livestock production.

I hope that the presented complexity of grassland management incorporating views of nature conservationists and agronomists will help to trigger the much needed collaboration of scientists of biological and agricultural universities as well as administrative workers of the Ministry of the Environment and Ministry of Agriculture of the Czech Republic.

CHAPTER XI

Summary

Mládek J (2011) Selective livestock grazing and its consequences for functional vegetation properties and agronomic services of species-rich grasslands

Planning of agri-environmental measures requires knowledge of the effects of management regimes on the occurrence of endangered plant and animal species as well as of the effects on grassland agronomic services, i.e. forage quantity and quality and their seasonal development. Effects of management on agronomic services of species-rich grasslands were seldom examined. In the face of the renascence of grazing at the end of the 1990s we particularly assessed the causes of selective grazing by livestock and evaluated its consequences for the agronomic value of the extraordinarily species-rich grasslands in the White Carpathian Mts., Czech Republic. In order to understand feedbacks of grazing on vegetation properties, studies of diet selection were reviewed and sheep grazing patterns in productive mesic and low-productive dry species-rich grasslands were analysed. The effects of four management regimes (sheep grazing, sheep grazing including spring burning of litter every third year, mowing in mid-July, abandonment) were investigated in long-term experiments using community-weighted means of plant functional traits. In addition, as nature conservation frequently requires postponing of grassland harvest until summer, we were interested to know in which grassland types this measure does not substantially reduce forage quality.

Our results indicate that maximising forage quality and maximising forage quantity are alternative diet selection strategies of sheep to exploit food resources in mesic and dry grasslands, respectively. This provided insight into the effects of early-spring grazing in broad-leaved dry grasslands, where sheep grazing unexpectedly eliminated productive but unpalatable grasses. Although mid-July mowing decreased the performance of grasses and enhanced forbs most of all management treatments, a pattern desired by nature conservationists, it cannot be recommended as the optimal low-cost management for broad-leaved dry grasslands due to its adverse effects on forage quantity and quality. Community-weighted mean of leaf dry matter content was a good indicator of seasonal growth pattern and forage quality, but not a suitable predictor of forage quantity when grasslands under different management regimes were taken into account. In two independent studies we evidenced that later-developing species were best supported under long-time grazing pressure, and postponing of defoliation until summer produced the smallest decrease in forage quality in grasslands managed in this way. We propose to establish a one-year late harvest application in permanent pastures as a low-cost agri-environmental measure. Nature conservation interest, i.e. reproduction of insects and ground-nesting birds, would be attained, while forage quality and subsequent profitability of livestock production would not be strongly reduced.

It can be concluded that community-weighted means of plant functional traits represent a powerful tool to analyse causes and consequences of selective livestock grazing as well to evaluate management-induced effects on agronomic services of species-rich grasslands.

CHAPTER XII

Souhrn (Czech summary)

Mládek J (2011) Selektivní pastva dobytka a její důsledky na funkční vlastnosti a agronomické servisy druhově bohatých travních porostů

Plánování agro-environmentálních opatření vyžaduje znalosti vlivu managementu na výskyt ohrožených druhů rostlin a živočichů stejně jako vlivu na agronomické servisy travních porostů, tj. množství a kvalitu píce a jejich sezónní vývoj. Vliv různých typů managementu na agronomické servisy druhově bohatých porostů byl zřídka zkoumán. Vzhledem k renesanci pastvy na konci 90. let 20. století v mimořádně druhově bohatých travních porostech Bílých Karpat (Česká republika) bylo hlavním cílem této práce posoudit příčiny selektivní pastvy dobytka a vyhodnotit její dopady na agronomickou hodnotu. Aby bylo možno lépe porozumět zpětnému vlivu pastvy na vegetaci, byly nejdříve revidovány studie selektivity pastvy a následně analyzovány pastevní preference ovcí v produktivních (mezických) a nízkoproduktivních (suchých) druhově bohatých travních porostech. Byly také založeny dlouhodobé experimenty se čtyřmi typy managementu (pastva ovcí, pastva ovcí spojená s časně jarním vypalováním stařiny jednou za tři roky, sečení v polovině července, ponechání ladem), na základě kterých byl hodnocen vliv managementu na vegetaci pomocí vážených průměrů rostlinných znaků. Protože ochrana přírody často vyžaduje odložení sklizně travních porostů do letních měsíců, zajímalo nás také, ve kterých typech travních porostů toto opatření výrazně nesnižuje kvalitu píce.

Naše výsledky ukazují, že maximalizace kvality píce a maximalizace množství píce jsou alternativní pastevní strategie ovcí pro využití potravních zdrojů v mezických vs. suchých travních porostech. Toto zjištění významně pomohlo objasnit efekt časně jarní pastvy v širokolistých suchých trávnících, kde pastva neočekávaně eliminovala produktivní, ale nechutné trávy. I když sečení v polovině července nejvíce ze všech typů managementu snížilo dominanci trav a zvýšilo proporci bylin (tj. nejvíce podpořilo procesy požadované ochranou přírody), sečení v polovině července nelze doporučit jako optimální nízkonákladový management pro širokolisté suché trávníky z důvodu nepříznivých dopadů na množství a kvalitu dostupné píce. Na základě našich výsledků lze konstatovat, že vážený průměr obsahu sušiny v listech byl dobrým indikátorem sezónního vývoje společenstva i ukazatelem kvality píce, ale nebyl shledán jako vhodný prediktor množství dostupné píce v případě, když byly společně analyzovány travní porosty s různým obhospodařováním. Ve dvou nezávislých studiích jsme dále prokázali, že fenologicky pozdní druhy jsou nejvíce podporovány režimem dlouhodobé časně jarní pastvy, a odložení sklizně do letních měsíců způsobuje nejmenší pokles kvality píce v travních porostech obhospodařovaných dlouhodobě právě tímto způsobem. Navrhujeme tedy zavést jednorázovou pozdní sklizeň na dlouhobých pastvinách jako levné agro-environmentální opatření. Zájem ochrany přírody, tj. reprodukce hmyzu a na zemi hnízdících ptáků, by byl splněn, a zároveň kvalita píce a následně i výnosnost živočišné produkce by neměla být výrazně snížena.

Závěrem lze konstatovat, že vážené průměry funkčních znaků rostlin představují efektivní nástroj k analýze příčin a důsledků selektivní pastvy dobytka a také k vyhodnocení vlivu managementu na agronomické servisy druhově bohatých travních porostů.