Cattle grazing on semi-natural pastures – animal behaviour and nutrition, vegetation characteristics and environmental aspects

by

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LICENTIATE THESIS

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Abstract

The knowledge of the grazing behaviour of cattle on Swedish semi-natural pastures and how this relates to the nutritional quality and quantity of the vegetation is low. In a situation where farming is being intensified both nationally and globally, it is important to gain more information about semi-natural pastures and how to utilise this resource properly. The aims of this thesis was to: (1) examine the grazing, resting and fouling behaviour of cattle on grazing areas mainly dominated by semi-natural vegetation which also includes portions of grassland affected by fertilisation; (2) determine the nutrient content and seasonal herbage production of different vegetation types within semi-natural pastures; (3) determine the *in vivo* digestibility of forages from different vegetation types in heterogeneous semi-natural grasslands; (4) study the division of nitrogen between faeces and urine and the enteric methane production from cattle fed these same forages.

One field and one indoor study were carried out. The field study covered three grazing seasons and included measurements of both cattle behaviour and of the nutritional properties of semi-natural pasture vegetation. Cattle preferred to graze, rest, urinate and defecate on previously fertilised areas. The vegetation in these areas was characterised by a high energy and crude protein content and a high seasonal herbage production. The indoor study measured *in vivo* digestibility, methane production and the division of nitrogen between urine and faeces of different forages from semi-natural grasslands fed to non-lactating cows and heifers. Forage digestibilities were lower than what is commonly reported for cultivated forages. Digestibilities did not differ between treatments, with the exception of a lower digestibility in the heifer group when fed of vegetation harvested on shore meadows compared with vegetation from naturalised cultivated grasslands. Methane production did not differ among forages. In conclusion, cattle prefer to graze in previously fertilised areas, but other vegetation types were also utilised by the animals. Furthermore, *in vivo* digestibility of semi-natural pasture vegetation was similar to *in vitro* values obtained with the standard Swedish method for estimating the energy value of forages.

Keywords: Semi-natural pasture, cattle, behaviour, digestibility, methane production, nitrogen balance, nutrient transport

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I love deadlines. I like the wooshing sound they make as they fly by.
Douglas Adams

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Pelve, M.E., Glimskär, A., Olsson, I. & Spörndly, E. 2010. The relationship between the grazing behaviour of cattle and vegetation quality and quantity on heterogeneous semi-natural pastures. (manuscript)

II Pelve, M.E., Olsson, I., Spörndly, E & Eriksson, T. 2010. Heterogeneous semi-natural pastures: forage digestibility, methane production and nitrogen balance among non-lactating cows and heifers. (manuscript)

Licentiate degree

The licentiate degree, which requires two years of full-time postgraduate study, is intended to guarantee, by means of course work and the completion of a dissertation, that the recipient

- has demonstrated an ability to investigate and to solve problems scientifically;
- is conversant with general scientific methodology and is familiar with the more important research methods within his or her subject area;
- is knowledgeable within his or her area of expertise and has contributed to the development of this area through his or her own research;
- is able to utilise the scientific literature within the subject area and relate it to his or her research results;
- has in the planning and execution of research, as well as in the analysis of results, worked both independently and in cooperation with others;
- has experience in presenting and discussing research results, both orally and in writing, e.g., before a board of examiners at a final public seminar.

Abbreviations and definitions

ADG	average daily gain
BW	body weight
CH_4	methane
CP	crude protein
DM	dry matter
DMI	dry matter intake
DOMI	digestible organic matter intake
GHG	greenhouse gas
IVOMD	*in vitro* organic matter digestibility
ME	metabolisable energy
N	nitrogen
NDF	neutral detergent fiber
OM	organic matter
SF_6	sulphur hexafluoride
VOS	96-h *in vitro* digestible organic matter

RP	Relative preference is the ratio between percent recordings of a certain behaviour in a vegetation type and the percent of the area within the study site that is covered by the vegetation type. In this thesis, $RP < 0.9$ means that the vegetation type is avoided, $RP \approx 1$ (0.9 – 1.1) means that the vegetation type is visited in proportion to its area, i.e. neither avoided nor preferred, and $RP > 1.1$ means that the vegetation type is preferred.
D	Dry vegetation. Can be found mainly on well-drained or nutrient-poor soil, on ridges or hills. Characterised by high biodiversity with mainly thin-leaved grasses and a large amount of forbs, some very drought-resistant (e.g. *Crassulaceae*).

M	Mesic vegetation. Can be found on moderately wet to moderately dry mesotrophic soils. Both broad- and thin-leaved grasses are common, along with many forbs and clovers.
W	Wet and moist vegetation. Can be found in depressions in the ground, along riverbanks and ponds or on any un-drained soil. Strongly characterized by broad-leaved grasses, larger forbs and very often by rushes and sedges.
S	Shaded vegetation. Can be found in shaded or sparsely to moderately forested areas. The vegetation is patchy and includes some grasses and forbs, but also low shrubs, mosses and lichens.
F	Previously fertilised vegetation. Can be found in previously cultivated or fertilised areas, such as old fields, meadows or naturalised cultivated grasslands. Fertilisation may have occurred long ago (i.e. over 50 years) but the vegetation is still characterised by it. Low biodiversity, mainly broad-leaved grasses and a limited amount of forbs.
WET	forage harvested from a temporarily inundated ("wet") shore meadow.
NL	forage harvested from a naturalised cultivated grassland.
SNL	forage harvested from a species-rich naturalised cultivated grassland.

1 Introduction

1.1 The state of semi-natural pastures in Sweden and Europe

Semi-natural pastures are ecotypes that exist all over the world. As opposed to natural grasslands, semi-natural pastures are permanent grasslands that are kept open through the actions of humans. They have been used as grazing areas for livestock and neither fertilised, nor ploughed for a long time. They are often characterised by plant species typical for permanent grasslands (Austrheim *et al.*, 1999). During the last 50-100 years, there has been a rapid decline in semi-natural grasslands all over Europe, mainly due to the industrialisation of farming. In 2009, there was approximately 436 000 ha of permanent grassland in Sweden, including previously cultivated, semi-natural and natural pastures as well as a small number of meadows (Swedish Board of Agriculture, 2010). Exactly how much of the pasture areas is semi-natural is uncertain; although, according to inventories made between 2002 and 2004, there were at least 230 000 ha (Swedish Board of Agriculture, 2005). This should be compared to the approximately 2 million ha of semi-natural pastures that were in use in the late 19th century (Mattson, 1985). Traditionally, in some countries and regions (such as Sweden, Norway, Finland, the Alps and Ireland), close to 100 % of cattle have been kept on pasture during at least a portion of the year. At the same time, in some Mediterranean countries, zero-grazing has been more common. Currently, the proportions of cattle that graze are declining in most European countries, with the exception of Slovenia, where they are instead increasing (Van den Pool-van Dasselaar, personal communication 2010).

The Swedish agrarian landscape is generally patchy and heterogeneous. Semi-natural pastures are often isolated from one another by forest or farmland (Lindborg *et al.*, 2008). They are also usually quite small: the mean size of semi-natural pastures inventoried between 2002 and 2004 in Sweden was 5.15 ha (Blom, 2009). They often contain boulders, bare rock and patches of trees and shrubs that complicate the use of modern machinery (Pärt & Söderström, 1999). Semi-natural pastures of this size, as well as their inherent biological values, are endangered in the long term by fragmentation, which leads to species loss, and by abandonment, which leads to shrub encroachment and eventual forestation (Kiviniemi & Eriksson, 2002; Cousins & Eriksson, 2001; Hansson & Fogelfors, 2000). Many semi-natural pastures have previously either been used as meadows, or have been grazing land for hundreds of years. The long-term use of practices such as late harvest, little or no fertilisation and moderate grazing have contributed to shaping these pastures into unique areas that represent considerable biological, recreational and cultural values (Dahlström *et al.*, 2008; Emanuelsson, 2008).

1.2 Scandinavian semi-natural pastures – state of research

One of the first problems that researchers interested in semi-natural pastures meet is one of definitions. What is a semi-natural pasture? Is it possible to compare research made on semi-natural pastures in two countries? Part of the problem is that the definitions of semi-natural, natural or cultivated pastures are partly dependent on management: most definitions would agree that if it is largely unfertilised, unploughed and grazed and has been so for a considerable amount of time, it is a semi-natural pasture. Note that ecotype, vegetation types and specific species do not automatically enter into this definition and that a wide range of biological communities might fall under the name semi-natural pasture, a fact that greatly complicates the comparison of studies. Terms such as "permanent pasture" or "extensively managed or low-input pasture" are often used when trying to define or quantify these types of grazed areas. Unfortunately, these terms include both old, natural pastures as well as sown and fertilised pastures. In the case that natural or semi-natural pasture is seen as something worthy of conservation, it is more common to define them according to the species they harbour. The problem with this kind of definition is that it is hard to include all possible species worthy of protection – the kind of pasture that is ideal for one particular species of bird, for instance, may not be that interesting from a botanical point of view (Emanuelsson, 2009). In the end, these definition problems make it necessary for researchers to describe the pasture they have been working with in more detail. It is therefore a great help to other researchers to list the species occurring in the pasture and to describe the main features of the pasture where the research has been performed.

Grazing behaviour of cattle is a well-researched subject (for a contemporary review, see Soder *et al.*, 2009). However, there are still questions left unanswered, such as dietary choice in complex (multi-species) situations, which is exactly the situation in semi-natural pastures. There is also ample research into the chemical composition, nutrient content and digestibility of vegetation from semi-natural pastures (Bruinenberg *et al.*, 2004; Fiems *et al.*, 2004; Bruinenberg *et al.*, 2003; Berry *et al.*, 2002; Bruinenberg *et al.*, 2002; Tallowin & Jefferson, 1999). These studies are made under European conditions. Due to the aforementioned differences in definitions, one cannot assume that they are applicable to Scandinavian pasture vegetation. Some Scandinavian studies have been made (Hessle *et al.*, 2008a; Hessle *et al.*, 2008b; Pelve, 2007; Spörndly & Widén, 2007; Steen, 1972). There have also been studies made on individual pasture plants such as *Deschampsia caespitosa* and species of *Carex* and on specific vegetation types, e.g. wet vegetation (Spörndly *et al.*, 2005; Lifvendahl, 2004; Andersson, 1999).

The connection between global greenhouse gas emissions (GHG) and grazing cattle was brought to the public eye through the FAO report "Livestock's Long Shadow" (Steinfeld *et al.*, 2006) and has been thoroughly discussed since. Accordingly, there has been a large increase in research in this area, mainly with methods that can be used in the field, such as tracer gas techniques (Johnson *et al.*, 1994). Even though some recent studies with the tracer gas technique have been performed, Swedish researchers have mainly used an empirical model based on an extensive literature review to estimate methane production (Lindgren, 1980). Most estimations of methane production have been performed on cattle feeding on forage from cultivated land. Therefore, there is a lack of information about the methane production of cattle feeding on forage from semi-natural pastures. Lately, these environmental aspects have been discussed in relation to the biodiversity benefits of grazing semi-natural pastures. It is important to study the GHG emissions from cattle feeding on this type of vegetation to be able to present facts for further discussions.

1.3 Maintaining semi-natural pastures – a possible strategy

One possible strategy that has been proposed for conserving semi-natural pastures in Sweden is to combine a number of smaller pastures into a larger area, thereby rationalising their management (Kumm, 2004). The combined area would create larger, more management-efficient units that could support more animals at a time and need less fencing. In the end, the rationalisation would lead to lower costs for the farmer. However, since it is rare that semi-natural pastures lie close to each other, the farmer may need to include previously fertilised areas (such as cultivated pasture, naturalised previously fertilised pastures or meadows), thickets or sparsely wooded areas in the new enlarged pastures. This means that in the case of joining the semi-natural pasture with a previously fertilised area, the farmer would be joining pastures with high biodiversity and low soil fertility (semi-natural parts) to pastures with low biodiversity and high soil fertility (previously fertilised parts).

This proposed strategy has led to discussion among nature conservationists concerning a potential transport of nutrients from previously fertilised parts to the nutrient poor parts. There has, to the author's knowledge, not been any scientific research done to support this hypothesis, although the theory has been put forward several times in reports concerning the state of Swedish semi-natural pastures (Kumm, 2007; Lindborg *et al.*, 2006). In short, the fear is that the animals would mainly graze the previously fertilised parts and then rest on the semi-natural parts, which are often drier and have a higher elevation – conditions that have been shown to attract cattle during resting periods (Redbo *et al.*, 2001). Since the majority of the animals defecate and urinate after a longer period of rest (Aland *et al.*, 2002) they would place a disproportionally large nutrient load on the semi-natural parts. This continuous increase in nutrient availability would, in time, be detrimental to the flora. Previous research has shown that a large addition of inorganic nutrients (such as commercial fertilisers) can reduce the floral diversity as well as the total species richness on semi-natural pastures in that competitive species, such as *Lolium* spp., *Alopecurus pratensis*, or *Taraxacum* spp., take advantage of the surge in nutrients and take over at the expense of slower growing species (Tallowin, 1996; Smith, 1994). Also, the addition of organic nutrients in the form of dung pats reduces the herb portion of the flora around the dung pat (Norman & Green, 1958). In conclusion, scientific studies are needed to investigate whether or not this proposed nutrient redistribution between vegetation types actually takes place.

2 Aims of the thesis

The aim of this thesis was to provide basic knowledge of cattle behaviour on heterogeneous semi-natural pastures, especially pastures that had been combined with previously fertilised areas. The thesis also aimed to produce reliable results for the quantity and nutritional quality of vegetation from semi-natural grasslands and to describe how animals utilise this vegetation.

Specific questions were:

- Where do cattle graze when given free choice on a heterogeneous semi-natural pasture?
- On which vegetation types within a heterogeneous semi-natural pasture do cattle deposit faeces and urine?
- How much vegetation is produced per season on different types of vegetation from heterogeneous semi-natural pastures?
- What is the nutrient content of different types of vegetation from heterogeneous semi-natural grasslands?
- What is the digestibility in cattle of different types of vegetation from heterogeneous semi-natural grasslands?
- How much methane is produced by cattle fed different types of vegetation from heterogeneous semi-natural grasslands?
- What is the division of nitrogen between faeces and urine in low-producing cattle fed different types of vegetation from semi-natural grasslands?

In addition, the aim was to discuss the transport of nitrogen between vegetation types within the pasture, and the probable implications of the results found in the studies on such a transport.

3 Material and methods

3.1 Paper I

3.1.1 Experimental design

The first paper involved a two-part behavioural study combined with a three-year vegetation sampling study. Behavioural studies were performed during 2007 and 2008. In 2007, two study sites and three observation periods per site (June, July and August) were used to include possible seasonal effects. In 2008, there was only one observation period per site, but nine sites (including the two sites used in 2007) were used to include possible location effects. This year, the study was performed between June 3rd and August 19th. Vegetation sampling was performed three times per season on two sites in 2006 and 2007 and once per season in nine sites in 2008, in connection with the behavioural studies.

3.1.2 Vegetation types

Five vegetation types found in heterogeneous semi-natural pastures in Scandinavia were identified and used as the basis for the behavioural study and vegetation sampling. The types were "dry", "mesic", "wet" and "shaded", along with a fifth vegetation type defined as "previously fertilised", that mainly consisted of former arable fields or cultivated pasture (shortened to D, M, W, S and F, respectively). For a detailed description of the vegetation types, see Table 1 of paper I.

3.1.3 Study sites

A total of nine sites were used during the three years; all were situated on farms in the Uppsala region of eastern central Sweden. The study sites varied in size: the smallest being 5.5 ha and the largest 28 ha. Water and minerals were available *ad libitum* in at least one location on each site. The sites all had to contain at least two semi-natural vegetation types (D, M, S or W) and an area of previously fertilised vegetation.

The sites were grazed by commercial herds of either non-lactating dairy cows or suckler cows with calves. The dairy cows were of the breeds Swedish Red, Swedish Holstein, or Swedish Jersey. The suckler cows were Charolais, pure Hereford or different Hereford crossbreeds. Some of the herds had a bull accompanying them; however, neither the bulls nor the calves were subject to observation.

3.1.4 Behavioural studies

Behavioural observations were performed in 2007 and 2008 on three randomly selected adult females in each herd (focal animals). Each observation period consisted of a total of 24 hours, divided into sessions of at least six hours each. Three kinds of behaviour were registered during the observations: "grazing", "resting" and "other", which was any behaviour that did not fall into the first two categories (such as vocalising, walking, fighting, etc.). The behaviour was recorded every five minutes. If the cow was grazing, the vegetation type being grazed was recorded and a vegetation sample in the immediate vicinity was collected. Samples were continually pooled together to represent the type of herbage consumed during the entire 24 hour period for each focal animal. Besides the observations taken every five minutes, continuous observations were performed with regard to defecation and urination and each time a focal animal defecated or urinated during observation periods, the time and place was recorded. Urination and defecation patterns were referred to as "fouling" when analysed or discussed together.

3.1.5 Sampling and laboratory analyses

Vegetation was sampled during all three years, and the same procedure was used all years. Each time a 24-h behaviour observation period was completed in a site, all of the vegetation types present were sampled for a chemical analysis of sward nutritional content and available herbage mass (in 2006, a pilot study of the vegetation characteristics was made, but no behavioural study). Three 1 x 1 m sampling plots were placed randomly in each vegetation type. All grasses and forbs (broad-leaved herbs) in the plot were cut using household scissors to the height of 1 cm. The samples were analysed for DM, ash, NDF, CP and VOS.

Furthermore, the total herbage production over the entire season in different vegetation types was estimated on the two study sites used in 2007. Three wire mesh cages (0.5 x 0.5 x 0.28 m) were randomly placed in each vegetation type and the vegetation inside the cages were cut six times per season between May 19th and October 3rd. The cutting frequency followed the vegetation growth curve, in that the first three cuts (during the time of season with highest productivity) were taken with approximately two-week intervals, and the three last cuts were taken with one-month intervals.

Botanical inventories were made for seven of the nine pastures. The presence or absence of approximately 340 plant species (including trees, bushes, grasses, herbs, ferns, horsetails, clubmosses and mosses) were noted by a skilled observer in 1 x 1 m plots.

3.1.6 Statistical analyses

Statistical analysis was performed in SAS 9.1 for Windows. Data from the chemical analysis of vegetation were analysed using the GLM procedure. Behavioural data, i.e. grazing, resting, urination and defecation, was converted into relative preference (RP) of the cattle for different vegetation types. RP was calculated using the method described by van Dyne and Heady (1965) (see Definitions). Behavioural data were natural logarithm transformed to obtain normal distribution and then analysed using the MIXED procedure. Main effects and interactions were considered significant at $P < 0.05$. If an effect was significant, pair-wise comparisons were made and considered significant at $P < 0.05$. Pearson correlation coefficients for RP values of all behaviours were calculated using the CORR procedure and considered significant at $P < 0.05$.

3.2 Paper II

3.2.1 Experimental design

The second paper involved a change-over digestibility trial using three forages from semi-natural pastures. The trial consisted of three periods of 21 days each. The first 11 days of each period served as an adaption period, while the remaining 10 days were used for sampling methane and the last five days for sampling urine and faeces.

3.2.2 Animals and feeds

In total, twelve animals of the Swedish Red breed were used in the experiment from two categories: non-lactating cows and heifers. They were housed in a stanchion barn at Kungsängen Research Centre in Uppsala, Sweden. All the animals were weighed prior to the experiment as well as before and after each sampling week. At the start of the experiment the cows and heifers weighed on average 563 ± 46 kg and 309 ± 34 kg, respectively (body weight ± SD).

The forages were harvested from three different semi-natural grasslands close to the cities of Sala, Flen and Uppsala in eastern central Sweden: a periodically inundated shore meadow (WET), a species-rich naturalised cultivated grassland (SNL) and a naturalised cultivated grassland (NL). The heifers were fed 20 g DM/kg BW and day to allow for a daily weight gain of 400-500 g/day, while the cows were fed 15 g DM/kg BW and day, based on the latest weighing. The animals were fed manually three times per day (at 08.00, 12.00 and 16.00 h).

3.2.3 Sampling and laboratory analyses

The offered and leftover feeds were weighed daily. More detailed feed, leftover, faeces and urine measurements were taken during the last five days of the sampling period. Feed samples were taken daily (at 16.00 h) for DM, ash, NDF, CP and VOS analysis. Leftover feed was collected for DM analysis. All of the faeces produced by the 12 animals were collected in plastic containers, one for each animal. Representative samples were taken daily and later mixed into one period sample for DM, ash, NDF and CP analysis. Urine was collected as spot samples on spontaneous urination from all 12 animals. The collection continued until 20 urine samples were taken from each animal. The samples were analysed for Kjeldahl-N, urea-N and creatinine. CH_4 levels in exhalation air were measured from the six cows during the entire sampling period, i.e. 10 days, using the SF_6 tracer gas technique developed by Johnson *et al.* (1994) and the collection apparatus developed by Iwaasa *et al.* (2005). CH_4 and SF_6 analysis was performed using gas chromatography.

3.2.4 Statistical analyses

The experiment was designed as an orthogonal 3 x 3 Latin square with three treatments and three periods. A total of 12 animals in two animal categories (6 cows and 6 heifers) were used, using two randomised blocks within each category. All 12 animals participated in the digestibility trial, but estimations of methane production were only performed on the six cows. Statistical analysis of data was performed using procedures MIXED and CORR in SAS 9.1 and 9.2 for Windows. Main effects and interactions were considered significant at $P < 0.05$. If an effect was significant, pair-wise comparisons were made and considered significant at $P < 0.05$.

4 Results

4.1 Characteristics of semi-natural pasture vegetation (paper I and II)

4.1.1 Botanical composition

Paper I

The seven pastures that were inventoried contained, on average, 100 identified species and genera per pasture (range 79 to 135). 27 of these species occurred in at least 66 % of the inventoried squares in a pasture, and of those 27, 11 occurred in at least 66 % of inventoried squares in more than one pasture. These 11 species or genera were *Achillea millefolium*, *Agrostis capillaris*, *Fragaria* spp., *Galium boreale*, Ranunculus spp., *Rumex acetosa*, Stellaria graminea, Taraxacum spp., Trifolium pratense, *Trifolium repens* and *Veronica chamaedrys*. The average amount of identified species or genera per vegetation type was 36 in D, 37 in M, 25 in W, 30 in S and 19 in F. For species typical to each vegetation type, see Table 1.

Paper II

In the shore meadow where the WET forage was harvested, 37 different species were identified. In the species-rich naturalised cultivated grassland where the SNL forage was harvested, 22 species were identified, while the naturalised cultivated grassland where the NL forage was harvested only contained 13 identified species. Of the species identified in NL and SNL, eight occurred in both: *Achillea millefolium*, *Alopecurus pratensis*, *Anthriscus sylvestris*, *Dactylis glomerata*, *Deschampsia cespitosa*, *Galium album*, *Poa pratensis* and *Ranunculus acris*. Of these, only *Deschampsia cespitosa* occurred in the

WET pasture. For a list of all the species identified in the pastures see Table 1, paper II.

4.1.2 Chemical composition and nutrient content

Paper I

In 2006 and 2007, when two sites and three months were studied, OM, ME, CP and NDF concentrations in the DM differed between vegetation types ($P < 0.0001$) and between months ($P < 0.05$). Previously fertilised vegetation had the highest ME and CP contents and the lowest OM and NDF contents. The overall ME and OM contents decreased and NDF content increased during the season. CP content decreased from June to July and increased again in August.

In 2008, when nine sites were used once, ME and NDF contents differed between vegetation types but CP and OM contents did not. Previously fertilised vegetation had the highest ME content and the lowest NDF content (Table 3, paper I; summary in Table 1).

Paper II

The DM, OM, CP and ME contents differed between the three forages ($P < 0.05$), but NDF content did not. The WET forage had the highest DM, OM and CP contents, but the lowest ME content. The mineral analysis showed a higher content of magnesium (Mg) and sulphur (S) and a lower content of potassium (K) in the WET forage than in the other two forages (Table 2, paper II; summary in Table 1).

4.1.3 Seasonal yield

Wet and previously fertilised vegetation types were the most productive with seasonal yields of around 5000 kg/ha. Mesic vegetation had an intermediate yield, around 2500 kg/ha and season, while dry and shaded vegetation had the lowest yields, around 1000 kg/ha and season. There was no difference in production between the two sites (Figure 3, paper I; Table 1).

Table 1. *Content of metabolisable energy (ME, MJ/kg dry matter), crude protein (CP, g/kg dry matter) and neutral detergent fiber (NDF, g/kg dry matter), seasonal production (kg dry matter/ha) and common species of the five vegetation types used in paper I and the three forages used in paper II. W and WET vegetation correspond in nutrient content and botanical composition, while SNL and NL most closely correspond to F in botanical composition, but not in nutrient content.*

Name[1]	ME	CP	NDF	Seasonal production	Common species
D	9.3	110	489	1134	*Festuca ovina*, *Hieracium pilosella*, *Galium verum*, *Lychnis viscaria* and species of the family *Crassulaceae*.
M	9.6	129	470	2575	*Agrostis capillaris*, *Alchemilla spp.*, *Rumex acetosa*, *Primula veris*, and *Trifolium spp.*
W	8.2	127	564	5039	*Deschampsia cespitosa*, many species of *Carex* and *Juncus*, *Filipendula ulmaria*, *Geum rivale* and *Caltha palustris*.
WET	8.1	118	600	-	
S	9.2	108	552	927	*Anthriscus sylvestris*, *Convallaria majalis*, *Calamagrostis arundinacea*, *Geranium sylvaticum*, *Pteridium aquilinum*, *Vaccinium myrtillus* and *Vaccinium vitis-idaea*.
F	10.0	160	434	4880	*Rumex*, *Taraxacum* and *Trifolium spp.*, *Achillea millefolium*, *Plantago major* and *Festuca rubra*.
SNL	9.1	80	566	-	
NL	8.5	76	597	-	

[1]D = dry; M = mesic; W = wet; S = shaded; F = previously fertilised; WET = periodically inundated shore meadow, NL = naturalised cultivated grassland, SNL = species-rich naturalised cultivated grassland.

4.1.4 Composition of selected vegetation

The vegetation selected by the cattle in 2007 differed from month to month ($P < 0.01$) for OM, ME and NDF contents, but not for CP content. The ME content decreased over the season, while the NDF content increased. The OM content decreased successively between June and August. Since the cattle were only observed once per pasture in 2008, there was no statistical analysis made for that year (Table 3, paper I).

4.2 Choice of vegetation type for various behaviours (paper I)

In 2007, the cattle divided their time as follows (the average observed time over three focal animals and both sites): June: 31 % grazing, 59 % rest, 10 % other; July: 29 % grazing, 62 % rest, 9 % other; August: 38 % grazing, 53 % rest, 9 % other. In 2008, the average over three focal animals and nine sites was 34 % grazing, 43 % rest and 23 % other. The average percentage of time spent grazing was similar both over the season and over many sites. However, data from the nine sites studied in 2008 showed that there was a fairly large variation between sites in the observed animal time budgets. Grazing varied between 23 and 50 % of the observed time, rest varied between 31 and 51 %, and other activity varied between 12 and 32 %. It is not possible to explain this variation by differences in breed or in animal category (heifers/dry cows/suckler cows) or by pasture availability.

4.2.1 Grazing

The RP values for grazing differed between vegetation types ($P < 0.0001$) for both years. The choice of vegetation type for grazing was similar during both 2007 and 2008. Seen across sites, the only vegetation type that was clearly preferred was F with RP values above or around 2.0, while M was grazed in proportion to its area. Both S and D were avoided both years, while W was grazed in proportion to its area in 2007 and avoided in 2008 (Table 2, Figure 1 and 2, paper I).

4.2.2 Resting

The RP values for resting were different between vegetation types ($P < 0.0001$) both years. Resting behaviour varied between pastures and was largely influenced by where the cattle chose to rest during the night, as this was the longest resting bout. Overall, F and D were most popular for resting with RP values above 1.5 both years, while S was avoided both years. The other vegetation types varied between years. W was preferred one year and avoided the next, while M was avoided one year and visited in proportion to its area the next (Table 2, paper I).

4.2.3 Urination and defecation

The RP values for both urination and defecation differed between vegetation types ($P < 0.0001$) both years. In most cases, RP for urinating or defecating in an area was similar to RP for grazing in that area. However, the cattle avoided both urinating and defecating on W vegetation in 2007, but grazed it in proportion to its area that year. Additionally, cattle neither avoided nor preferred to urinate on D in 2008, while both grazing and defecation in the same areas were clearly avoided that year. Urination on M was avoided in 2008, while both grazing and defecating were in proportion to the area (Table 2, Figure 1 and 2, paper I).

4.2.4 Correlations between behaviours

In 2007, there was a correlation between RP for vegetation types for grazing and the behaviours urination and defecation (r = 0.36 and P = 0.0004; r = 0.54 and $P < 0.0001$, respectively). There was no correlation between grazing and resting or between resting and urination/defecation that year. In 2008, there was again a correlation between grazing and urination/defecation (r = 0.40 and $P < 0.0001$; r = 0.51 and $P < 0.0001$, respectively). There was also a correlation between resting and urination/defecation (r = 0.51 and $P < 0.0001$; r = 0.59 and $P < 0.0001$, respectively), but no correlation between grazing and resting.

4.3 The utilisation of semi-natural pasture vegetation by cattle (paper II)

4.3.1 Digestibilities

There were overall differences between the forages ($P < 0.05$) and between animal categories ($P < 0.05$) in DM, OM and CP digestibilities and a tendency for a difference between forages ($P = 0.05$) and animal categories ($P = 0.09$) in NDF digestibility. There was, however, an interaction between forage and animal category ($P < 0.05$) for DM, OM and CP digestibility. For cows, there were no differences in OM and NDF digestibilities for any of the forages. The DM digestibility in SNL was higher than in WET, and CP digestibility was higher in WET than in both other forages. For heifers, DM, OM and NDF digestibilities were lower in WET than in the other forages, but there was no difference in CP digestibility between the forages (Table 4, paper II).

4.3.2 N allocation in urine and faeces and urinary volume

Excretion of total faecal and urinary N differed between forage treatments ($P < 0.0001$). The WET forage treatment had the highest amounts of both faecal and urinary N excretion for both cows and heifers. Urea excretion was also highest in the WET forage treatment. Urine volume was calculated from creatinine excretion. It did not differ between animal categories, but was lower for the WET forage treatment than for the other forage treatments (Table 4, paper II).

4.3.3 Enteric methane production

There were no significant differences between the forage treatments with respect to CH_4 production, regardless if it was regarded as g/day, g/kg DMI, or as g/kg DOMI (Table 5, paper II).

5 General discussion

5.1 Choice of vegetation type

Cattle clearly preferred to graze previously fertilised vegetation when it was available to them (paper I). The main reason for this is most probably that this vegetation type had the highest digestibility and nutrient contents as well as a fairly high production level in terms of kg DM per ha. The animals could, in other words, maximise their nutrient intake with each bite (Ganskopp & Bohnert, 2009; Senft *et al.*, 1985a). Grazing behaviour and urination and defecation (fouling) generally follow each other, which can also be seen in the correlation between grazing and fouling both years. Therefore, it is natural that previously fertilised vegetation should be preferred areas for fouling as well (Jewell *et al.*, 2007; White *et al.*, 2001). Resting behaviour does not seem to be as clearly linked to grazing as either defecating or urinating do, which has also been observed previously (Senft *et al.*, 1985b). Cattle choose resting places according to topography and microclimates rather than vegetation properties. Slope, elevation, ground insulation and dryness all affect their choice, as does macroclimate (ambient temperature, wind, rainfall etc.). Resting behaviour also varies between night-time and day-time (Redbo *et al.*, 2001; Yasue *et al.*, 1997; Senft *et al.*, 1985b). In this study it was noted that cattle often spent their night rest in specific areas, while daytime rest was much more haphazard.

It is possible that the method in which RP was measured may have resulted in misleading values for resting behaviour. The cattle's behaviour on one specific site influenced the mean RP value for resting on areas with dry vegetation both years. There was only one dry area on this site, which represented only 4 % of the total pasture area. Since the cattle on this site often spent their entire night's rest in this dry area, the large number of observations there resulted in RP values between 11.2 and 18.5 for that site, driving the mean RP for resting in dry areas to a value over 2.5 both years. If this site was excluded from analyses, the mean RP value for resting on dry vegetation was 0.6 in 2007 and 0.4 in 2008. Despite the shortcomings of the RP method, it should not be ignored that the animals did choose to rest on dry areas in some pastures.

In spite of the previously fertilised vegetation being most popular, the cattle did not entirely avoid the other vegetation types. Mesic vegetation was generally grazed in proportion to its area, and was preferred in some pastures. The three least grazed vegetation types have their own reasons to be attractive at certain times. It has been shown that when stocking rates are high, cattle tend to choose more according to quantity than quality (Dumont *et al.*, 2007). Wet vegetation has a very high production rate, which means that the animals always have at least one source of feed, even in shortage situations. Another reason to graze in areas that are perpetually wet or moist, such as riverbanks may be that they can provide a measure of coolness during warm summer months (Senft *et al.*, 1985b). This behaviour was observed in one of the pastures, which was situated by a stream. The heifers grazing this area waded in the shallows on hot days while eating from stands of Glyceria maxima. Dry vegetation may in itself provide very little for the animal both in quantity and quality. Instead, they may choose to visit such areas for other reasons. Dry vegetation often grows in places with good runoff and high elevation, which are places that cattle have been shown to choose to spend their rest (Redbo, 2001; Senft *et al.*, 1985b). When they rest in dry areas, cattle also graze for short times before and after resting. As with the dry vegetation, shaded vegetation does not offer much in the way of nutrients or production, but the shade and shelter given by trees and shrubs may reduce heat stress and give a reason for grazing there (Tucker *et al.*, 2008; Bailey *et al.*, 1996).

5.2 Semi-natural pasture vegetation

5.2.1 Properties of the vegetation

There is a marked difference between the vegetation types defined and used in paper I. For the farmer it is good to be aware of these differences to optimise animal production when grazing the vegetation. For clarity, it is possible to rank the types according to chemical composition, production and nutrient content. When it comes to chemical composition and nutrient content, it is attractive for the vegetation to have high CP and ME contents and a low NDF content. Another aspect is the botanical diversity (in this case, measured as relative species richness), which is perhaps more important from a conservation point of view. However, this also has an importance for the farmer as the increased subsidies for semi-natural pastures are, in part, based on their flora (Swedish Board of Agriculture, 2010).

The properties of the vegetation types can be summarised from the inventories made in the first study and from Figure 3 and Table 3 in paper I. Dry vegetation has a high botanical species richness but low production, medium to low energy content, medium NDF content and low protein content. Mesic vegetation has a high to medium botanical species richness, medium production, medium to high energy and protein contents and medium to low NDF content. Wet vegetation has a low to medium botanical species richness, high production, low energy content, medium protein content and high NDF content. Shaded vegetation has a medium botanical species richness, low production, medium energy content, low protein content and high NDF content. Previously fertilised vegetation has a low botanical species richness but high production, medium to high energy content, high protein content and low NDF content.

In short, the vegetation types rank approximately in the following way: from low to high quantity: D/S, M, W/F; from low to high nutrient quality: W, S, D, M, F; and from low to high species richness: F, W, S, M, D. Vegetation from wet or moist areas can present a problem because of the high productivity. If this vegetation type is not grazed early, it tends to become over-grown and the energy content decreases rapidly (Andersson *et al.*, 2000; Lifvendahl, 2004).

5.2.2 The utilisation of vegetation by cattle

The digestibility values obtained from the study in paper II are in line with values from previous studies of vegetation from extensively managed or semi-natural pastures (Tallowin & Jefferson, 1999; Bruinenberg *et al.*, 2002; Bruinenberg *et al.*, 2003). DM and OM digestibilities for both cows and heifers are generally around 60 %, and NDF digestibility is slightly higher. The large difference between cows and heifers fed WET forage is hard to explain. One possibility is that there are differences in digestive function between young and old cattle. Varel and Kreikemeier (1999) saw differences in ruminal NDF digestion between ruminally and duodenally cannulated heifers and cows fed *ad libitum* amounts of alfalfa hay and mature brome hay. In their study, ruminal NDF digestibility, but not total tract digestibility, was lower in heifers. However, the heifers used in that study were younger than the ones used in this study. CP digestibility among heifers fed WET forage should have been higher than for the other forages, as it was among cows, since CP digestibility is expected to be related to the CP content of the feed. This suggests that the low digestibilities are an artefact, although neither forage fibre bound protein, nor excretion of endogenous protein were monitored in the experiment, so this cannot be confirmed.

In Sweden, metabolisable energy is estimated from the 96-h *in vitro* digestible organic matter (VOS) method developed by Lindgren (1979). Since this method was developed using forages from cultivated leys fed to sheep on maintenance levels, one could doubt its accuracy for forages from semi-natural pastures eaten by cattle. The main reasons for doubt is that digestibilities in semi-natural vegetation are generally below those used in the range of calibration data, and that the calibration forages and semi-natural forages contain entirely different species. To address this concern, OM digestibility was estimated from both the *in vitro* VOS method and from *in vivo* measurements (Table 4, paper II). The overall OM digestibility mean was 0.60 and 0.61 for *in vivo* and *in vitro* based values, respectively. In addition, Bruinenberg *et al.* (2003) used the Tilley and Terry (1963) method, which is similar to the Lindgren method, on forages harvested from semi-natural pastures and arrived at OM digestibilities similar to the *in vivo* values they obtained with lactating cows. This suggests that the *in vitro* method can be used with acceptable accuracy for semi-natural forages. Since the problems inherent in making larger digestibility trials on semi-natural pastures (see below) creates a need for a "quick and easy" way of estimating digestibility, it is very useful that the *in vitro* estimate from VOS is close enough to provide researcher with a general idea. Since a VOS analysis is quite easy for Swedish farmers to obtain, this also means that they can have access to more information about their forages.

5.3 Transport of N between vegetation types within the pasture

As stated in the Introduction there is a fear that nutrients, N in particular, can be transported from previously fertilised to semi-natural parts of a pasture, thereby changing the conditions for plant communities and jeopardising botanical diversity. This kind of transport or nutrient redistribution is hard to study. It depends on a number of things: the grazing behaviour of the animals, which also affects their fouling behaviour; the distribution of dung pats and urine patches; the production and N content of removed vegetation; and on the N content and N dynamics of faeces and urine (Saarijärvi & Virkajärvi, 2009; Jewell *et al.*, 2007; Kohler *et al.*, 2006; White *et al.*, 2001; Haynes & Williams, 1993; Marsh & Campling, 1970). Also, an in-depth study of the nutrient redistribution would have to be made over a longer period of time to accurately assess any changes to the botanical composition. Such a lengthy and detailed study on even one pasture requires vast amounts of time and money. Even the longest journey begins with a small step and the studies in this thesis aim to provide that step. By combining the results from paper I and II and by making certain assumptions, it is possible to roughly estimate the redistribution of nitrogen in the studied pastures.

A simple estimation can be made by comparing the grazing and fouling behaviour of cattle. The correlations from paper I suggest that the places that are grazed are also the places that receive faeces and urine. In other words, cattle urinate and defecate preferentially in the same vegetation types that they graze (Figures 1 and 2, paper I). Given the assumption that the amount of N deposited through faeces and urine is roughly the same as the amount removed by grazing, this would mean that no significant nutrient redistribution is taking place. However, one grazing observation on one vegetation type may not equal to one grazing observation on another vegetation type. If an animal grazes for 30 minutes on previously fertilised vegetation, it will most probably ingest more N that if it had grazed 30 minutes on dry vegetation, because of the higher N concentration and larger herbage mass of the previously fertilised vegetation (Table 3, paper I). If, at the same time, the composition of the urine and faeces deposited would not be very different between the two vegetation types, it would mean that even if the two types were grazed and fouled on with the same frequency, there would be a larger amount of N deposited on the dry vegetation than was removed, and *vice versa* for the previously fertilised vegetation.

The situation is made more complex by the composition of the vegetation, which varies with the vegetation type (Table 3, paper I; table 2, paper II). It is quite hard to estimate the exact amounts of N that are removed from the pasture, and calculating from the N content alone is not enough. One cannot assume an equal bite size on all vegetation types, since bite size declines with decreasing herbage mass (Barrett *et al.*, 2001; Gibb *et al.*, 1997) and herbage mass differs between vegetation types. Bite rate, bite size and intake are hard to assess at the best of times. In addition, one cannot assume that equal amounts of urine and faeces are deposited on each occasion. An urination event sometimes consists of several litres of urine and sometimes much less. The same is true for defecations. The situation is further complicated by the composition of the urine and faeces, which varies with the diet (Table 4, paper II). Nitrogen in urine, which is largely in the form of urea (Orskov & Macleod, 1982), is rapidly available to plants (Haynes & Williams, 1993). Nitrogen release from faeces is slower and large dung pats can suffocate the vegetation beneath it (Bastiman & Dijk, 1975). Animal response to fouled vegetation may also be a factor in nutrient redistribution. Vegetation in and around urine patches may initially be rejected by animals but only for a short time, as it may even be preferred later (Norman & Green, 1958). Vegetation around dung pats on the other hand is generally avoided, sometimes for over a year (Wilkins & Garwood, 1986; Marsh & Campling, 1970).

From the studies it is possible to conclude that the theory of nutrient redistribution does not hold from at least one point of view – the cattle do not specifically graze in previously fertilised areas and then deposit urine and faeces in semi-natural areas (Figure 1). But given the complexity of the situation it is hard to say whether this means that including nutrient-rich areas in semi-natural pastures is entirely risk-free, or not. It has been done before. There are semi-natural pastures that contain areas that have been cultivated as early as the Bronze Age. Some of the adverse effects of nutrient redistribution may be mitigated by bringing many small semi-natural pastures closer to each other, thereby allowing species dispersion between areas and by decreasing the problem of fragmentation that has a negative impact on biodiversity in these types of pastures (Cousins & Eriksson, 2001).

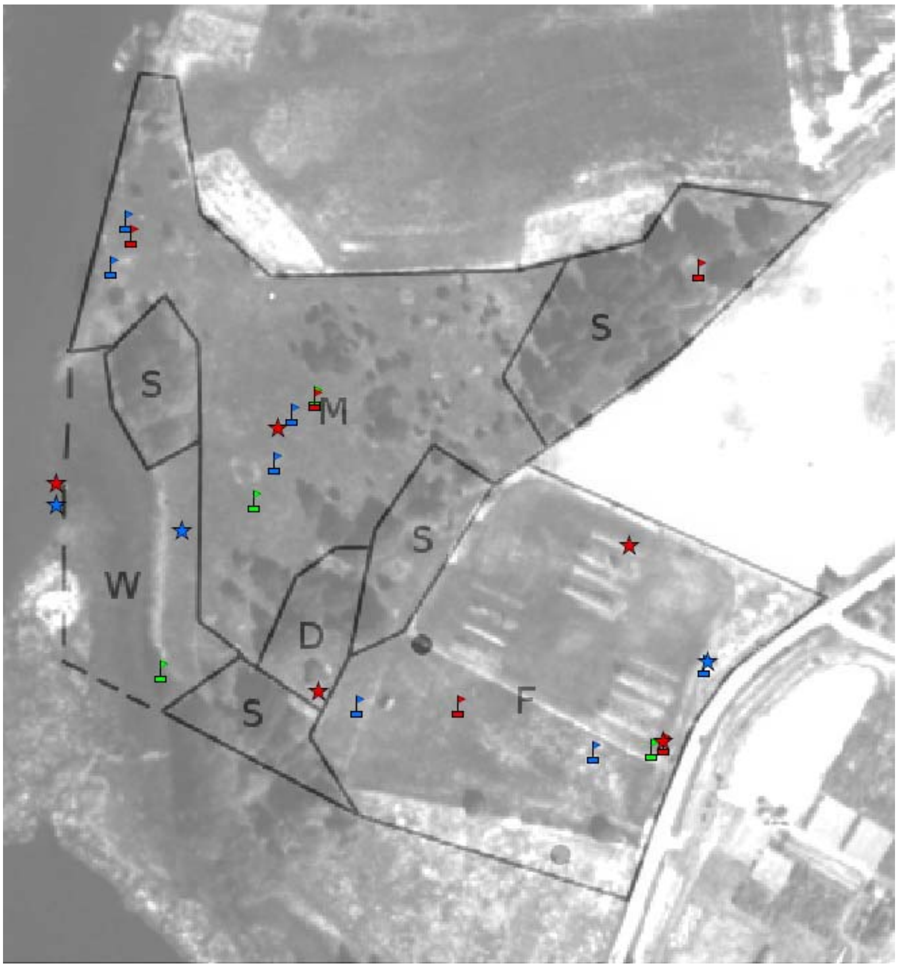

Figure 1. Example of one of the study sites used in paper I. Flags denote defecation events, stars denote urination events. Vegetation types are: D = dry; M = mesic; W = wet; S = shaded; F = previously fertilised. The mean relative preference for grazing on this site was: D = 0.0; M = 1.4; W = 0.9; S = 0.7 and F = 0.8.

5.4 The problem with management goals for semi-natural pastures

On semi-natural pastures, management practices for increased biodiversity sometimes involve the late onset of grazing to allow plants to reproduce. This approach is shown to be effective for promoting fruiting among vascular plants (Wissman, 2006). Unfortunately, research has shown that there is a rapid and considerable decline in vegetation quality on these pastures over the season, especially in the absence of grazing (Pelve, 2007; (Spörndly & Widén, 2007). In some species (e.g. Deschampsia caespitosa), this rapid decline is repeated during re-growth (Lifvendahl, 2004). Thus, late onset leads to lower quality, which in turn leads to lower animal weight gains (Spörndly & Widén, 2007). It is not uncommon for two goals (in this case diversity and animal production) to clash in this way in semi-natural pasture management.

Even when diversity goals are considered alone, problems may arise. One practice that increases one type of diversity may not be beneficial for another type. For instance, grassland bird diversity decreases dung beetle diversity (Vessby *et al.*, 2002). This clash of goals can also be seen on a global scale, if one considers the environmental impact of grazing animals worldwide. High-forage diets produce more CH_4 in g/day than low-forage diets (Beauchemin & McGinn, 2005; Harper *et al.*, 1999; Kurihara *et al.*, 1999; Johnson & Johnson, 1995). An obvious response to this would be to reduce the number of grazing ruminants and to feed high-grain diets to lower the methane emissions. However, such an action would be disastrous for the biological diversity of the Swedish landscape and result in the reforestation of pasture, since grazing animals are essential for keeping the landscape open and diverse. Such a strategy is also questionable from an animal welfare point of view, since cattle are not evolved for high-grain diets. In the end, we have to decide which goals are most important for us and for the environment, and to make compromises where they must be made.

5.5 Heterogeneous pastures – a research and management challenge

A heterogeneous semi-natural pasture is challenging both for the researcher wanting to study it and for the farmer wanting to manage it. Since semi-natural pastures are generally small and far apart (Lindborg *et al.*, 2008; Blom, 2009) it can be costly for the farmer to move the animals between pastures for rotational grazing or during vegetation shortage. Other costs include the transport of machinery (e.g. mowers) and fencing, which is higher for shorter fences (Riegel *et al.*, 2009). The farmer may also be unsure of the actual value of their land in terms of production potential. For the researcher, there are both methodological and practical challenges when studying the behaviour of grazing animals, or the properties of the grazed vegetation. In order to capture the wide range in forage quantity and quality, researchers need to increase the breadth and depth of their studies.

Breadth in the sense that many sites are needed to ensure that the pastures studied are representative and that many sites together show the variation. Depth in the sense that each site should be studied many times per season, as both behaviour and vegetation may change over the season. Such breadth and depth in one study requires a lot of work and, subsequently, a lot of funding. In this thesis, it was decided to first use only two sites but three times per season to see if the behaviour and vegetation properties changed over time. When it was concluded that there were no great differences in behaviour throughout the season (June-August), nine sites were used to include the variation between pastures to be able to draw more general conclusions.

In behavioural studies it is possible to lessen the work load by switching from direct observations to more indirect methods such as GPS collars, activity meters, accelerometers, IGER behaviour recorders, or radio surveillance (Guo *et al.*, 2009; Putfarken *et al.*, 2008; Rutter, 2000). These methods can be very useful when grazing and resting are the only behaviours of interest, but in the grazing study presented in paper I, we also wanted to study the pattern of urination and defecation. While defecation can, to a certain extent, be assessed by counting dung pats, urine disappears into the ground very quickly and requires, therefore, direct observation. Indirect methods also involve interacting with the animals, sometimes once a day or more, to change batteries and download recordings. Interactions disturb the animal's behaviour patterns and should be kept to a minimum to avoid influencing the results. In our study, most of the pastures were on commercial farms so it would have required assistance from the farmer to round up and handle the animals. The decision to only use direct observations put a large work load on the observer, but minimised animal disturbances and virtually eliminated straining the farmer; in turn, making it possible to perform the study in multiple pastures.

Some vegetation properties are easier to study than others. The only limitation to analysing chemical composition is the number of man-hours one can afford. Digestibility analyses are more complicated. The heterogeneity of Scandinavian semi-natural pastures makes it hard to harvest enough forage to perform a full-scale trial from some vegetation types, as it is rarely possible to use the kind of machinery needed. This limits the range of vegetation types that can be studied.

5.6 Reflections and ideas for further studies

This thesis aimed to answer many questions, and, in the end, these questions have at least begun to be answered. The results from the behavioural studies are applicable to a large range of Scandinavian semi-natural pastures; however, cattle grazing on pastures with completely different compositions from the ones studied here would likely behave differently. For instance, in a semi-natural pasture dominated by dry vegetation, the dry vegetation would by necessity be used to a higher degree. It is also possible that higher stocking rates would change the grazing patterns, compared with the moderate to low stocking rates used in this study. Higher stocking rates puts constrains on the amount of feed available to each animal, and thus limiting the scope for selection as the animals will eat whatever is available.

The results from the digestibility study are, unfortunately, somewhat limited in their usefulness, as two of the three forages were only partly representative of the vegetation types normally found on Scandinavian semi-natural pastures. To get more useful results, one of the forages from the naturalised cultivated grasslands should have been exchanged for forage from an actual semi-natural vegetation type, such as the mesic type identified in paper I. Despite this, the results can provide a starting point for future research. It is also very useful to know that *in vitro* OM digestibility can be used as an approximation of *in vivo* OM digestibility of vegetation from semi-natural pastures, as this reduces the need for large-scale digestibility trials in studies of semi-natural pasture vegetation.

Further studies could concentrate on the behavioural patterns towards the end of the season, i.e. October. Also, more samples collected in semi-natural pastures from other regions in Sweden would give a better idea of the production potential on a national level. One possibility would be to include vegetation sampling as a part of the national landscape survey project NILS (Nationell inventering av landskapet i Sverige; Ståhl *et al.*, 2010). Where there is an interest both from farmers and authorities, it would be beneficial to make a large-scale, long-term study of the botanical changes within semi-natural pastures that are combined with previously fertilised areas. Such changes could not be followed in this study, only guessed at. Since combining semi-natural pastures with other farmland might be a way to conserve pastures that would otherwise be abandoned, it is important to understand the positive and negative consequences of such management.

6 Conclusions

Performing research on Scandinavian semi-natural pastures is a challenge, and great care should be taken to include the variation that exists both within and between semi-natural pastures. Vegetation types on these pastures differ from each other in terms of nutrient content, production and botanical diversity. Nutrient content is also variable over the season, and the digestibility of vegetation from semi-natural pasture is generally lower than from cultivated pasture. In this study we could see that cattle grazing a heterogeneous semi-natural pasture that includes previously fertilised areas clearly preferred those previously fertilised areas. These areas had adequate energy and crude protein contents coupled with high seasonal production, which explained their popularity. Other vegetation types in the pasture were also grazed but to a lesser extent, but may also be visited for other reasons than their grazing value. Grazing behaviour was correlated to urination and defecation behaviour, but not with resting behaviour.

According to our data it is possible to estimate the digestibility of semi-natural pasture vegetation with sufficient accuracy from the *in vitro* method commonly used in Sweden, which is helpful to both researchers and farmers. We could find no evidence to support the theory that cattle graze in one area and urinate and defecate in another; however the mechanisms of nutrient redistribution depend not only on this, but on a number of other factors as well. Therefore, from this study it is not possible to definitely determine whether or not including previously fertilised areas in semi-natural pasture is a threat to the botanical diversity.

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