Habitat use by Scottisch Highland cattle in a lakeshore wetland

Autor(en): **Gander, Antoine / Rockmann, Alke / Strehler, Catherine**

Objekttyp: **Article**

Zeitschrift: **Bulletin of the Geobotanical Institute ETH**

Band (Jahr): **69 (2003)**

PDF erstellt am: **20.05.2024**

Persistenter Link: https://doi.org/10.5169/seals-377852

Habitat use by Scottish Highland cattle in a lakeshore wetland

ANTOINE GANDER[1]*, ALKE ROCKMANN[1], CATHERINE STREHLER[1] & SABINE GÜSEWELL[2]

[1] *Groupe d'Etude et de Gestion, Grande Cariçaie, Champ-Pittet, CH-1400 Yverdon, Switzerland;*
[2] *Geobotanisches Institut ETH Zürich, Zürichbergstrasse 38, Ch-8044 Zürich, Switzerland;*
**corresponding author: a.gander@grande-caricaie.ch*

Summary

1 Wetlands in Central European lowlands are mostly managed to prevent their succession towards forest and to maintain open, species-rich wetland plant communities. While this was mostly done by mowing in the past, wetland managers increasingly consider grazing as an alternative form of management. Grazing by three Scottish Highland cattle has been practised since 2000 on an area of 2.7 ha in the lakeshore wetland Grande Cariçaie, Switzerland. This study investigates how the cattle use their grazing area and how this changes in the course of the grazing season (May-September).

2 On 15 days from early June 2002 to late August 2002 the positions and activities of the three cattle were observed every minute from dawn till dusk. Activities were classified as grazing; resting and ruminating; other. The distribution of dung pats was recorded along transects in September 2002. The resulting maps of cattle and dung distribution were used to calculate the percentage use of the ten vegetation types occurring in the grazing area.

3 Over the whole season, grazing was most intensive in eutrophic marsh vegetation dominated by *Phalaris arundinacea* or *Carex acutiformis* and least intensive in patches of *Cladium mariscus;* tall-sedge fens were also grazed little in comparison to their large area. Cattle mainly rested in small areas under trees and more generally in the drier parts of the study site. These parts therefore also received the largest fraction of cattle dung.

4 Habitat use for grazing shifted in the course of the season: cattle successively focused on vegetation dominated by *Phalaris arundinacea* – *Carex riparia* – *C. elata* – *C. hostiana* – *P. arundinacea.* The first part of the sequence probably corresponds to decreasing feeding value, whereas the focus on *P. arundinacea* at the end of the grazing season may indicate that the food quality of the other vegetation types had decreased below the minimum acceptable level.

5 The spatial segregation of grazing and defecation means that nutrients are transferred from the vegetation types that are mainly grazed to those where cattle mainly stay to rest. In the long term, large parts of the pasture may become impoverished while small parts become heavily enriched, unless nutrients are redistributed when the site is flooded in winter.

Résumé

1 La plupart des bas-marais d'Europe centrale font l'objet d'une gestion des prairies axée sur la prévention des successions vers les stades boisés, favorisant ainsi des milieux riches en espèces et en associations végétales. Bien que le fauchage reste la méthode d'entretien la plus courante, une proportion croissante de gestionnaires prennent en considération le pâturage comme forme alternative d'entretien. Un essai de pacage est entrepris depuis l'an 2000 sur une surface de 2.7 ha dans la Grande Cariçaie, sur la rive sud du lac de Neuchâtel. Cette étude examine comment les vaches utilisent la parcelle au cours de la saison de pâture.

2 Pendant 15 jours répartis entre début juin et fin août 2002, la position et le type d'activité (pâture, repos, rumination ou 'autre') des trois vaches furent notés chaque minute de l'aube au crépuscule. La distribution spatiale des fèces fut relevée par transects en septembre 2002. Les cartes qui en résultent furent utilisées pour calculer le pourcentage d'utilisation de chacun des dix types de végétation de la parcelle.

3 Sur l'ensemble de la saison, la végétation dominée par *Phalaris arundinacea* ou par *Carex acutiformis* est préférée aux autres pour le pâturage, alors que les Cladaies sont dédaignées; les prairies à grandes laiches sont pâturées peu intensivement en comparaison avec leur grande surface. Les zones de repos correspondent à des surfaces restreintes à l'ombre des arbres et dans les parties les plus sèches de la parcelle. Elles correspondent aussi aux zones qui reçoivent la plus large fraction de fèces

4 Le régime de pâture change au cours de la saison selon la séquence suivante : les prairies de *Phalaris arundinacea* – *Carex riparia* – *C. elata* – *C. hostiana* – *P. arundinacea.* La première partie de la séquence correspond probablement à une valeur nutritive décroissante intrinsèque au type de végétation. Le retour de fréquence élevée de pâture de la prairie à *Phalaris* en fin de saison peut indiquer que le seuil de qualité nutritive des autres types de végétation est descendu en dessous d'un minimum acceptable.

5 La discrimination spatiale de la pâture et de la défécation provoque un transfert de matière organique de la végétation pâturée aux zones de repos. Si ces transferts persistent, de larges surfaces de la parcelle peuvent être appauvries en nutriments alors que de petites surfaces sont enrichies, à moins que les nutriments ne soient redistribués en hiver quand la parcelle est inondée.

Keywords: conservation management, dung distribution, grazing, plant species richness, resource selection, seasonal patterns

Nomenclature: Lauber & Wagner (1996)

Bulletin of the Geobotanical Institute ETH (2003), **69**, 3–16

Introduction

Lowland wetlands in Central Europe are subject to a process of natural succession which eventually leads to the establishment of forest vegetation (Bakker *et al.* 1997; Jensen & Schrautzer 1999). To maintain a diversity of non-forested plant communities in wetland nature reserves, it is necessary to hold up the succession process either through management or though periodic re-creation of early successional stages (Dierssen & Schrautzer

1997). The favoured form of management has long been late-season mowing because the latter was assumed to cause only little damage to wetland soils and to let plants set seeds (Egloff 1984; Pfadenhauer 1988). However, various studies have suggested that large-scale mowing schemes may have negative impacts on overall biodiversity by creating a more uniform vegetation and by regularly destroying the vegetation structure needed by arthropods and birds for overwintering or reproduction (Klieber *et al.* 1995; Huemer 1996; Radlmair & Laußmann 1997). In addition, late-season mowing proved unable to prevent vegetation succession at sites with high invasion potential of woody species (Güsewell & Le Nédic 2003). These drawbacks of mowing have caused wetland managers to increasingly consider grazing by free-ranging cattle or horses as an alternative form of management (Gordon *et al.* 1990; Hasler 1996).

Compared to mowing the effects of grazing on vegetation and soils are more heterogeneous for several reasons. Firstly, free-ranging ungulates often use their habitat selectively: some areas are grazed, others are used as latrines, and still others avoided (Edwards & Hollis 1982). This selection can be based on site topography, vegetation structure, food quality, or features such as buildings, fences or water points (Haynes & Williams 1999; Jewell 2002), and it is also subject to diurnal and seasonal variation (Pratt *et al.* 1986; Putman *et al.* 1987). Secondly, even within grazed areas some plant species are consumed selectively and trampled so that they are reduced (e.g. van Deursen & Drost 1990; Erzinger 1996; Grant *et al.* 1996), while others are avoided and therefore favoured (Hickman & Hartnett 2002; Kleijn & Steinger 2002). Thirdly, grazing can either increase the productivity of the vegetation by stimulating nutrient mineralisation (Harrison 1985; de Mazancourt *et al.* 1998; Frank *et al.* 2000) or decrease the productivity by causing mechanical damage to plants, by increasing nutrient leaching from the soil, or by promoting unpalatable species with refractory litter (van Deursen & Drost 1990; Kooijman & Smit 2001). In addition, if pastures are used heterogeneously, some parts may become enriched with nutrients while others are depleted (Haynes & Williams 1999; Jewell 2002). Finally, grazing can either increase or decrease the diversity of the vegetation through effects on survival, reproduction and interspecific competition (e.g. Proulx & Mazumder 1998; Austrheim & Eriksson 2001; Hart 2001; Olofsson *et al.* 2002).

The specific effects of ungulate grazing on wetland vegetation have been rather little investigated. Given the great variety of wetland types it is currently not possible to *a priori* determine an 'optimal grazing regime' for a specific wetland nature reserve. Whenever grazing is implemented for conservation purposes, it is important to monitor the effects carefully to ensure that the aims will be reached. In addition, detailed research on the use of wetland pastures by grazing animals (e.g. Bassett 1980; Menard *et al.* 2002) and on the implications for plant and soil processes (e.g. Vinther 1983; Jutila 1999) could progressively lead to the development of guidelines on the appropriate grazing management for wetland sites.

This paper presents preliminary results from a long-term experiment aimed at assessing the effects of grazing on the vegetation and soil of the "Grande Cariçaie", a lakeshore wetland in western Switzerland. Grazing by Scottish Highland cattle was introduced at two sites in 2000 and 2001, respectively, mainly to test whether browsing and trampling by the cattle would prevent the encroachment of woody species and contribute to maintain a non-forested, diverse vegetation. Changes in plant species composition and vegetation structure are monitored every year in grazed and ungrazed areas. More detailed investigations were undertaken in 2002 in one of the two grazed areas to better understand how the cattle use their habitat, what factors determine this habitat use, and what nutrient transfers are caused by the cattle. In this paper we focus on the first of these three points, i.e. habitat use by the cattle. We describe the spatial and temporal patterns of cattle activity during a whole grazing season, and we analyse the data so as to determine which types of vegetation are used most intensively for feeding.

Methods

STUDY AREA

The "Grande Cariçaie" is situated on the southern shore of Lake Neuchâtel, at an elevation of 430 m, with a mean annual temperature 10.4 °C and a mean annual precipitation of 900 mm. The level of lake Neuchâtel was lowered by about 3 m in the late 19th and early 20th century, which exposed the former lake bottom and allowed the development of a diverse calcareous wetland vegetation. The plant communities currently found in the area form a characteristic hydrosere, with aquatic communities and reed stands in the wettest places, and sedge meadows or alluvial forests in the drier places (Buttler *et al.* 1985; Buttler 1987; Buttler & Gallandat 1990). Since 1984, approximately one quarter of the area has been mown in a large-scale rotational scheme where individual lots are mown every second or third year in winter (October-March).

The experimental site is a fen area of 2.7 ha near the village of Gletterens (46°54'N and 6°56'E). It is bordered by alluvial forest on the land side and by reed stands on the lake side. Soils are all neutral to alkaline (pH 7–8.5) gleysols over sandy or clayey lake sediments. The topsoil has a thickness of 5 to 20 cm; its organic matter ranges from 20% in drier places (Anmoor) to over 90% in permanently wet places. A variety of fen communities occurs within the site. Until 1999 the site was mown in winter every third year. In 2000, it was grazed by three heifers (the equivalent of 0.6 beef cattle units, BCU), and in 2001 by one adult and two heifers (0.7 BCU). In 2002, the site was grazed by one ox and two heifers from 16 May to 7 September (0.5 BCU). The animals were confined within the grazing area by an electric fence powered by a solar module (10 kV). They were supplied with water through a tank placed near the fence on the forest side.

FIELD METHODS

The vegetation of the grazed area was mapped using an aerial photograph as visual aid and a floristic key established previously for all plant communities in the Grande Cariçaie (C. Clerc, unpublished report). Nine vegetation types, which essentially correspond to associations of the phytosociological classification, were distinguished in the area (cf. Table 2). They are named according to the dominant plant species (> 25 % of total vegetation cover). To describe the vegetation types, we surveyed three randomly selected quadrats of 1 m^2 in each of them at each of three dates (22 May, 2 July and 9 September 2002), so as to sample a total of 9 m^2 per vegetation type in the course of the grazing season. We estimated the cover of all vascular plant species (Braun-Blanquet scale) and recorded the mean height of the upper and lower canopy strata. If there was standing water within a quadrat, the water level was measured. Five soil cores (5 cm diameter, 20 cm length) were taken in each vegetation type in July 2002 in order to roughly determine the soil type (sand, loam or peat).

Habitat use by the cattle was observed during the whole grazing season 2002 on one day per week from dawn till dusk (15 days in total). During this period, the position and activity of the three cattle were observed every minute for 30 min per hour (the other 30 min serving as break). To locate positions, a grid with 94 cells of approximately 10 m by 30 m (Fig. 1b,c) was established by planting long sticks with coloured marks every 10 m along the fence on both sides of the area. Cells were identified by codes; their size and shape reflected the accuracy with which cattle positions could be determined visually. Every minute, the main activity of each cow (lasting for more than 30 s) was attributed to one of three categories (1, grazing; 2, resting or ruminating; 3, moving, drinking, social contact, scratching etc.) and was recorded together with the corresponding cell code. Cattle were observed from a stand built in one corner of the site with the help of a binocular to minimise any influence on their behaviour. Only if they moved out of sight or too far away to determine their exact position, they were followed outside the fence.

Dung distribution was mapped on 10 July and 2 September 2002 by walking along transects across the area and by counting the number of dung pats seen within 1 m on both sides of the line (using a stick to check the distance). The number of pats was noted every 5 m along the transect. Neighbouring transects were 10 m apart so that 20 % of the area were surveyed. In July it proved difficult to distinguish between previous-year and present-year dung pats, and since the site was partly flooded, some dung pats were probably overlooked. Therefore, only the results from September, which seemed more reliable, were used to establish a distribution map showing the number of dung pats per cell of 2 m by 5 m.

DATA ANALYSIS

To describe the various vegetation types present in the area, we combined the relevés from the nine 1-m^2 quadrats into a pooled species list and calculated for each vegetation type the species richness (total number of species in the pooled list), species density (mean number of species per 1 m^2), as well as weighted average ecological indicator values for nutrient availability and soil moisture. The latter were based on Landolt's (1977) indicator values for plant species in Switzerland, which range from 1 = low to 5 = high (cf. Table 1), and on the pooled species lists per vegetation type. Species received a simple weight if their frequency and dominance was coded as '+' in Table 1, double weight if their code was '++', and triple weight if their code was 'DD', 'D+' or '+D'.

To visualise how cattle used their habitat, distribution maps of cattle activity and dung were constructed by overlaying maps of the grazing area with the cell grid and representing the number of observations per cell through different patterns.

To determine which vegetation types were mainly grazed and how this changed in the course of the grazing season, we converted the number of observations of grazing cattle per cell and per observation date into the percentage of a day's grazing observations made in each cell, and then into the percentage of a day's grazing observations made in each vegetation type. The second conversion was done through an iterative stepwise procedure because many cells included more than one vegetation type (cf. Fig. 1). In the first step we assumed that within each cell, vegetation types were grazed approximately in propor-

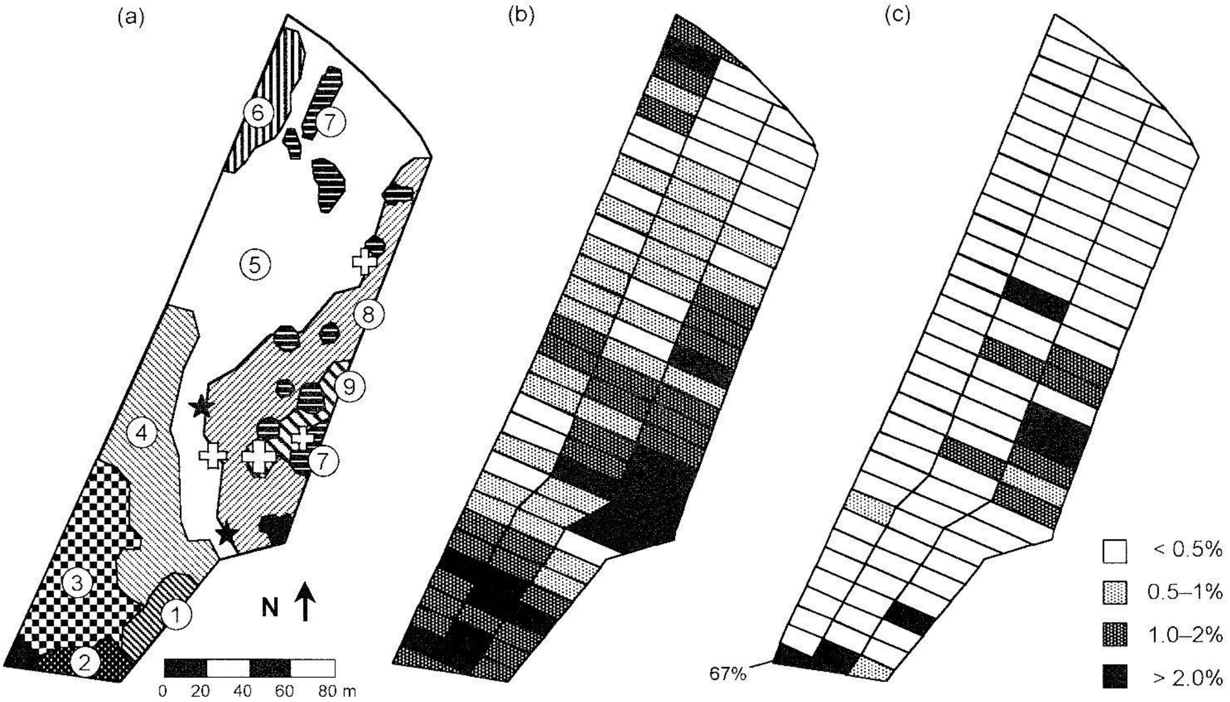

Fig. 1. *Distribution of (a) vegetation types, (b) grazing cattle and (c) resting/ruminating cattle over the grazing area (2.7 ha). In (a), numbers refer to the vegetation types (cf. Table 2); black colour depicts unvegetated areas, black stars represent trees, and white crosses stand for shrubs. In (b) and (c) cell patterns indicate the percentage of observations made in each cell, based on the pooled records from 15 days between June and August 2002. The legend in (c) is also valid for (b). As there were 94 cells, those with > 1% of observations were used overproportionally, and those with < 1% of observations, underproportionally.*

Table 1 *(next page). Description of the vegetation types occurring within the grazing area, with the height of the upper stratum of the canopy, the soil type (L, loam; S, sand; LS, loamy sand), the water level in May in cm above soil surface, the average Landolt (1977) indicator values for soil moisture (1=dry, 5=flooded) and nutrients (1=extremely poor, 5 = extremely rich), the species richness (number of species in nine 1-m² quadrats), the species density (mean number of species per 1-m² quadrat), and the species list (pooled from nine 1-m² quadrats), with the frequency and dominance of the species indicated as follows: DD, dominant with cover >25% throughout the season; D+, D-, +D, dominant in the first or second part of the grazing season, present or absent in the other part; ++ , frequent, present in >40% of the quadrats but with cover < 25%; +, infrequent, present in <40% of the quadrats. Vegetation types 8 and 9 were not distinguished in this survey..*

Vegetation type	1	2	3	4	5	6	7	8+9
Vegetation height May (cm)	70	90	123	73	80	200	60	40
Vegetation height Sept (cm)	28	22	87	70	87	273	63	12
Soil type	LS	L	L	L	LS	S	LS	LS
Water level May (cm)	-	-	-	1	3	20	-	-
Moisture indicator value	4.3	4.1	4.4	4.6	4.8	4.8	4.3	4.3
Nutrient indicator value	3.2	3.6	3.5	2.9	2.7	3	2.6	2.5
Species richness	15	14	23	8	10	8	9	17
Species density (m^{-2})	4.8	5.8	7.0	4.4	4.0	2.9	3.1	8.7
Phragmites australis	D+	D+	DD	+	+	DD	+	++
Carex acutiformis	DD	+	+	.	.	.	.	.
Phalaris arundinacea	+	D+	+D	.	.	.	.	.
Poa pratensis	+	+D	+	.	.	.	.	.
Ranunculus ficaria	.	D-	+	.	.	.	.	.
Galium palustre s.l.	+	+	+D	++	++		+	+
Carex riparia	+	.	+	DD	+	+	.	.
Carex elata	.	.	+	.	DD	+	.	+
Cladium mariscus	.	.	.	.	.	.	DD	.
Carex hostiana	.	.	.	.	.	.	.	DD
Carex panicea	.	.	.	.	.	.	+	DD
Molinia litoralis	+	.	.	.	.	.	.	.
Circaea lutetiana	+	++	+	.	.	.	.	.
Epilobium parviflorum	++	+	+	.	.	.	+	.
Juncus effusus	+	+	.	.	.	.	.	.
Solidago virgaurea	+	.	+	.	.	.	.	.
Alnus glutinosa	+	.	+	.	.	.	.	.
Urtica dioica	.	+	+	.	.	.	.	.
Veronica beccabunga	.	+	+	.	.	.	.	.
Geum rivale	.	+	.	.	.	.	.	.
Rorippa palustris	.	+	+	+	.	.	.	.
Myosotis scorpioides	.	.	+	.	.	.	.	.
Rorippa amphibia	.	.	+	.	.	.	.	.
Scrophularia umbrosa	.	.	+	.	.	.	.	.
Symphytum officinale	.	.	+	.	.	.	.	.
Cardamine amara	.	.	+	+	.	+	.	.
Nasturtium officinale	.	.	+	.	.	+	.	.
Lysimachia vulgaris	.	.	.	+	+	.	+	++
Mentha aquatica	.	.	+	+	+	.	.	+
Scutellaria galericulata	+	.	+	+	+	.	.	+
Peucedanum palustre	.	.	.	.	+	.	.	.
Thalictrum flavum	.	.	.	.	+	.	.	.
Utricularia minor	.	.	.	.	+	+	.	.
Myriophyllum verticillatum	.	.	.	.	.	++	.	.
Quercus robur	.	.	.	.	.	+	.	.
Cirsium arvense	.	.	.	.	.	.	+	+
Eleocharis palustris s.l.	.	.	.	.	.	.	.	++
Epilobium palustre	.	.	.	.	.	.	.	++
Galium aparine	.	.	.	.	.	.	.	+
Hydrocotyle vulgaris	+	.	.	.	.	.	++	++
Juncus articulatus	+	+	.	.	.	.	.	++
Molinia caerulea	.	.	.	.	.	.	.	++
Calamagrostis epigeios	.	.	.	.	.	.	.	+
Schoenus nigricans	.	.	.	.	.	.	+	+

tion to their area and calculated an approximate utilisation coefficient for each vegetation type on this basis (Appendix 1). In the second step, these coefficients were used to distribute the observations per cell among vegetation types more accurately. We now assumed that vegetation types within a cell were grazed in proportion to their area and to their approximate utilisation coefficients, and on this basis recalculated more precise utilisation coefficients. We repeated these two steps three times and used the final utilisation coefficients to calculate the percentage of a day's grazing observations made in each vegetation type (Appendix 1). These percentages were plotted against time, and as there were substantial day-to-day fluctuations, the curves were smoothened through running averaging: each date's value was replaced by the mean of the preceding, current and following values, so that the general temporal trend would become more apparent.

The overall utilisation of each vegetation type by the cattle (in %) was derived from the pooled observations of all dates. The number of observations per cell and per activity (grazing, resting, other) was converted into the percentages of observations per cell, and then into percentages of observations per vegetation type, as described above. Dung distribution among cells was converted into dung distribution among vegetation types by attributing each cell to the vegetation type covering most of the cell's area. This simplified procedure appeared legitimate as the cells were much smaller than those for cattle observations.

Selection ratios for grazing, resting and defecation were obtained by dividing the percentage utilisation of each vegetation type by its percentage area (Manly *et al.* 2002). Given the temporal changes in habitat use (cf. Fig. 2), these selection ratios did not directly reflect the preference or avoidance of certain vegetation types by the cattle but the overall intensity of use resulting from both tendencies over the 15 observation dates. Thus, a selection ratio of 100 % means that the vegetation type was on average used for grazing, resting or dung in relation to its area; values

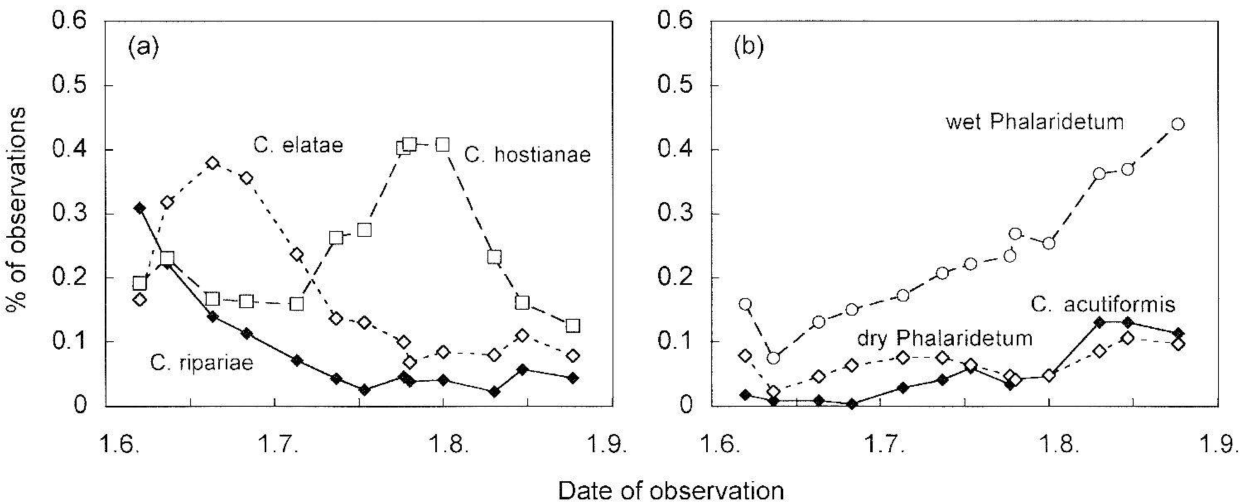

Fig. 2. Seasonal changes in the utilisation of various vegetation types for grazing (a, sedge meadows; b eutrophic wet meadows). For each observation date, the time spent grazing in each vegetation type was expressed as percentage of all grazing observations. The curves were smoothened by replacing each date's value by the mean of the preceding, current and following values to show the general trend more clearly. Vegetation types that were hardly grazed are not represented. See Appendix 2 for the original values from all vegetation types.

Table 2. Utilisation of the vegetation types as calculated from the vegetation map and cattle distribution maps (cf. Fig. 1). Cattle activity was expressed as percentage of all daytime observations during the whole grazing season, and dung density as the percentage of all dung pats recorded at the end of the grazing period. The selection ratio is the percentage utilisation of a vegetation type (in % of the total per category) relative to its percentage area; 100% means that the vegetation type was used in proportion to its area.

Vegetation type	Area	Cattle activity (% of daytime)				Dung	Selection ratio (%)		
	(%)	Grazing	Resting	Other	Total	(%)	Grazing	Resting	Dung
1 *Caricetum acutiformis*	2.2	2.4	0.4	0.6	2.3	5.2	208	48	235
2 Dry *Phalaridetum*	2.5	3.5	1.9	0.4	5.3	6.1	281	183	246
3 Wet *Phalaridetum*	9.7	12.1	0.9	0.6	14.5	20.0	252	23	207
4 *Caricetum ripariae*	15.3	5.3	0.3	0.5	5.2	7.6	70	4	50
5 *Caricetum elatae*	39.5	8.1	1.3	0.7	14.7	10.7	41	8	27
6 *Phragmitetum*	3.6	3.1	0.0	0.0	1.5	0.2	175	0	6
7 *Cladietum marisci*	5.6	1.3	2.3	0.7	3.9	6.1	46	99	110
8 *Caricetum hostianae*	16.6	11.5	1.4	1.6	13.8	20.8	140	20	125
9 *Schoenetum*	3.5	2.3	2.0	1.6	4.3	8.0	132	139	229
10 Unvegetated	1.5	0.0	30.8	3.8	34.6	15.3	0	1466	300
Total per category	100.0	49.3	41.2	10.5	100.0	100.0	–	–	–

below 100 % indicate underproportional use, and values above 100 %, overproportional use.

Results

Ten distinct vegetation types were encountered on the study site (Table 1, Fig. 1a). Their distribution reflects a gradient with increasing moisture and decreasing soil fertility from the southern to the northern part of the site (cf. Fig. 1a and Table 1). The largest part of the area is a tall-sedge fen on a sandy loam soil with either *Carex riparia* (community type 4) or *Carex elata* (type 5) as dominant species. The south-western part is a eutrophic terrestrial reed stand dominated by *Phragmites australis* and *Phalaris arundinacea,* on a loam soil. The vegetation close to the forest border supports several nitrophilous forest edge species (type 2), whereas the wetter part includes eutrophic fen species (type 3). The south-eastern part is relatively dry with a sandy loam soil; plant communities are dominated by *Carex panicea* and *C. hostiana* (type 8), *Schoenus nigricans* (type 9) or *Carex acutiformis* (type 1). In the northern part, a dense aquatic stand of *Phragmites australis* grows on sand in a permanently flooded area (type 6). Patches of *Cladium mariscus* are scattered throughout the northern half of the site (type 7). Differences in water level and in soil type are also reflected by the average moisture and nutrient indicator values of the vegetation (Table 1). The four drier plant communities were more species-rich than the five wetter ones, both for species richness (14–23 in the drier communities, 8–10 in the wetter ones) and for species density (4.5–8 species m^{-2} vs. 3–4.5 species m^{-2}).

Cattle spent approximately half of the daytime grazing and 40 % resting and/or ruminating (Table 2). The vegetation types were used differently by the cattle. Grazing focused on the vegetation types dominated by *Phalaris, Carex elata* and *Carex hostiana* (Fig. 1b).

The *Phragmites* stand showed a high average use (Fig. 1b), which resulted from two very hot days in mid-summer, with 14.5 % and 44.5 % of the observations, respectively, whereas the stand was hardly used otherwise. Cattle mostly rested in the unvegetated southwestern corner (as much as 67 % of observations), followed by the communities dominated by *Phalaris, Schoenus* or *Cladium* (Fig. 1c). The distribution of dung pats reflected fairly well the total distribution of cattle activity, except that more dung pats than expected were found in the *Caricetum hostianae* and fewer in the unvegetated areas (Table 2).

If the utilisation of the various vegetation types is related to the area covered by these vegetation types, it appears that the vegetation types dominated by *Phalaris* and *Carex acutiformis* were grazed most intensively, whereas the large areas covered by *Caricetum elatae* or *Caricetum ripariae* vegetation as well as the *Cladium* patches were avoided. Resting activity was even more heterogeneous, with most intensive use of the unvegetated area and slightly overproportional use of the *Phalaridetum* and *Schoenetum.* Dung pats were frequent in all drier communities (Table 2).

The distribution of grazing varied in the course of the grazing season (Fig. 2, Appendix 2). At the first observation date, cattle mainly grazed in the *Caricetum ripariae* (Fig. 2a) and the two *Phalaridetum* types (Fig. 2b), and their decreasing use between the first and subsequent observation suggest that these vegetation types were probably preferred in May, before observations started. As the season proceeded, grazing focused successively on the *Caricetum elatae,* the *Caricetum hostianae* (Fig. 2a), and increasingly on the *Phalaridetum* and the *Caricetum acutiformis* (Fig. 2b). The generally small percentage of observations in the *Caricetum acutiformis* and the dry *Phalaridetum* (Fig. 2b) is related to their small area. The other vegetation types were scarcely used, except for the aforementioned incidental use of the *Phragmites* stand on hot days (not shown in Fig. 2).

Discussion

The observations of cattle activity confirmed our expectation that the pasture would be used heterogeneously. The tendency of the cattle to focus their activity on certain areas of the pasture was far more pronounced when they rested and ruminated then when they grazed. The same type of behaviour was observed in other types of pastures (Jewell 2002) and with other livestock species (Haynes & Williams 1999). At our site, however, the difference was particularly pronounced. This may be related to the relatively small grazing area which forced the cattle to use a large part of the available herbage in the course of the season. In contrast, the sheltered areas close to the forest border, where the cattle preferred to rest, could be used throughout the season without need to shift towards other places.

The clear seasonal pattern of habitat use for grazing probably reflected differences in forage quality, i.e. presumably the cattle first used their preferred food sources and then moved towards other vegetation types as the former became depleted. We did not investigate food quality in this study but suppose that digestibility and nutrient concentrations of the dominant species determined the sequence of pasture use, as reported for horses in the Camargue (Duncan 1983) and in the New Forest (Putman *et al.* 1987), given that the nutrition of cattle and horses in wetlands is similar (Menard *et al.* 2002).

Nutrient-based food selection was also suggested by the order in which the vegetation types were used in our area. The first series of observations took place three weeks after the beginning of grazing. By that time, the *Phalaridetum* vegetation (type 1) had already been heavily grazed. This association typically colonises nutrient-rich riverine marshes (Müller *et al.* 1992; Rosenthal 1992; Ellenberg 1996) and only occurs at the most nutrient-rich sites within the Grande Cariçaie. The loamy soil on which it developed in our grazing area together with the high nutrient indicator values of the vegetation suggest that the *Phalaridetum* offered a nutritious herbage to the cattle. Once this valuable source of food was largely depleted (as shown by a very low sward), the cattle shifted towards the sedge-dominated communities which covered most of the grazing area; this shift was indicated by changes in habitat use at the very beginning of our observation period (Fig. 2). The sedge meadows were used in the sequence *Caricetum ripariae – C. elatae – C. hostianae.* This corresponds to a sequence of decreasing fertility according to the nutrient indicator values (Table 1) and previous studies in the Grande Cariçaie (Buttler 1987); lower nutrient concentrations (especially of phosphorus) were indeed found in biomass of *C. elata* than in biomass of *C. riparia* (Marti 1994).

At the end of the season, grazing focused on the *Phalaridetum* again, even though the amount of herbage was very low by that time (cf. vegetation height in Table 1). Probably the food quality of the other vegetation types had decreased below the acceptable level, so that they were refused even if their height and biomass might suggest that food was still available. The same type of behaviour was observed by Jewell (2002) with Scottish Highland cattle on an alpine pasture: they first grazed the nutrient-rich lawns surrounding the stables, and then the nutrient-poor *Nardus stricta*-dominated pastures, but at the end of the season, they focused on the nutrient-rich (though extremely short) lawns again, discarding the largely senesced *Nardus stricta* material.

The patterns of use of *Phragmites australis* can be explained by differences in food quality and water level. The pure *Phragmites* stand was heavily used on hot days in mid summer, probably because the standing water provided some refreshment. That this stand was hardly used otherwise contrasts with other studies showing highly selective use of *Phragmites* (Bassett 1980; van Deursen & Drost 1990; Rozé 1993; Jutila 1999). The reason may be that in our area, *Phragmites* was also abundant within the eutrophic *Phalaris* vegetation and in the tall-sedge stands (*C. elatae, C. ripariae*), where *Phragmites* shoots were grazed very selectively. Much of the early-season grazing in tall-sedge stands was actually grazing of *Phragmites.* The pure *Phragmites* stand was probably less attractive due to deep flooding in spring and the low food quality of tall, lignified *Phragmites* shoots in late summer (e.g. Güsewell & Klötzli 1997; Güsewell 1998) Thus, the attractiveness of *Phragmites* for grazing, as reported previously, was underestimated by vegetation type-based resource selection ratios in this study.

Vegetation dominated by *Cladium* is characteristic of nutrient-poor sites (Buttler 1987). Besides low nutrient concentrations (Pfadenhauer & Eska 1986), the hard and cutting nature of the leaves explains why these were an unattractive food even for cattle that are reputed for their ability to use low-quality herbage. However, the rough material was highly appreciated as litter on which to rest.

The overall distribution of cattle activity and the distribution of dung pats basically corresponded to each other, in agreement with the observation that cattle drop their dung haphazardly during the day (White *et al.*

2001). That relatively more dung was found in the *Caricetum hostianae* than in unvegetated places and in the *Phalaridetum* must be due to the intensive trampling of the cattle in the most intensively used areas, causing part of the dung pats to become unrecognisable before the September survey. It is therefore likely that the concentration of defecation in a very small fraction of the pasture was even more pronounced than indicated by our dung map. Similarly, Highland cattle on an Alpine pasture deposited a large part of their dung on only 1% of the area (Jewell 2002).

The pronounced spatial and temporal patterns of habitat use observed in this study have implications for the long-term effects of this management on the vegetation. Our survey indicates that a transfer of nutrients is taking place from the vegetation types that are mainly grazed, to the unvegetated places used for resting. This will probably cause a decrease in productivity in about half of the grazing area. As our observations of cattle behaviour suggest that the availability of acceptable herbage was already below the needs of three cattle during the four-months grazing season in 2002, a further decrease in food quantity and quality would imply that the stocking density, duration of grazing or frequency of grazing will have to be reduced in the future. On the other hand, the areas receiving high loads of dung and urine are likely to act as sources of nutrients when the grazing area is flooded, causing the nutrients to be either re-distributed towards the rest of the grazing area (which would be desirable) or washed away towards the lake (not desirable). The productivity and food quality of the vegetation, the rates of nutrient transfers caused by the cattle, their importance relative to other nutrient pools and fluxes, and the fate of nutrients concentrated in camp areas will be assessed in further studies. This information will be used to assess the possible environmental implications of the current grazing scheme and to adapt the latter accordingly.

Acknowledgements

We thank F. Bolle and R. Bonzi for assistance with field work, and J. Kollmann, P. Müller, H. Wagner and an anonymous referee for useful comments on a draft of the manuscript.

References

Austrheim, G. & Eriksson, O. (2001) Plant species diversity and grazing in the Scandinavian mountains – patterns and processes at different spatial scales. *Ecography,* **24**, 683–695.

Bakker, S.A., Jasperse, C. & Verhoeven, J.T.A. (1997) Accumulation rates of organic matter associated with different successional stages from open water to carr forest in former turbaries. *Plant Ecology,* **129**, 113–120.

Bassett, P.A. (1980) Some effects of grazing on vegetation dynamics in the Camargue, France. *Vegetatio,* **43**, 173–184.

Buttler, A. (1987) *Etude écosystématique des marais non boisés de la rive Sud du lac de Neuchâtel* (Suisse). Ph.D. thesis, Institut de Botanique, Université de Neuchâtel.

Buttler, A., Buche, M., Cornali, P. & Gobat, J.-M. (1985) Historischer und ökologischer Überblick über das Südostufer des Neuenburger Sees. *Telma,* **15**, 31–42.

Buttler, A. & Gallandat, J.-D. (1990) Phytosociologie des prairies humides de la Rive Sud du lac de Neuchâtel (Suisse) et modèle de succession autogène. *Phytocoenologia,* **18**, 129–158.

de Mazancourt, C., Loreau, M. & Abbadie, L. (1998) Grazing optimization and nutrient cycling: when do herbivores enhance plant production? *Ecology,* **79**, 2242–2252.

Dierssen, K. & Schrautzer, J. (1997) Wie sinnvoll ist ein Rückzug der Landwirtschaft aus der Fläche? Aspekte des Naturschutzes sowie der Landnutzung in intensiv bewirtschafteten agrarischen Räumen. *Laufener Seminarbeiträge,* **1/97**, 93–104.

Duncan, P. (1983) Determinants of the use of habitat by horses in a Mediterranean wetland. *Journal of Animal Ecology,* **52**, 93–109.

Edwards, P.J. & Hollis, S. (1982) The distribution of excreta on New Forest grassland used by cattle, ponies and deer. *Journal of Applied Ecology*, **19**, 953–964.

Egloff, T. (1984) *Richtlinien zur Bewirtschaftung und Pflege von Riedern und Mooren im Sinne des Naturschutzes.* SBN, Basel.

Ellenberg, H. (1996) *Vegetation Mitteleuropas mit den Alpen* 5. Aufl. Eugen Ulmer, Stuttgart.

Erzinger, S. (1996) Einfluss von Schottischen Hochlandrindern auf eine montane Weide im oberen Tösstal. *Bulletin of the Geobotanical Institute ETH*, **62**, 47–60.

Frank, D.A., Groffman, P.M., Evans, R.D. & Tracy, B.F. (2000) Ungulate stimulation of nitrogen cycling and retention in Yellowstone Park grasslands. *Oecologia*, **123**, 116–121.

Gordon, I.J., Duncan, P., Grillas, P. & Lecomte, T. (1990) The use of domestic herbivores in the conservation of the biological richness of European wetlands. *Bulletin d'Ecologie*, **21**, 49–60.

Grant, S.A., Torvell, L., Common, T.G., Sim, E.M. & Small, J.L. (1996) Controlled grazing studies on *Molinia* grassland: effects of different seasonal patterns and levels of defoliation on *Molinia* growth and response of swards to controlled grazing by cattle. *Journal of Applied Ecology*, **33**, 1267–1280.

Güsewell, S. (1998) Does mowing in summer reduce the abundance of *Phragmites australis* in fen meadows? *Bulletin of the Geobotanical Institute ETH*, **64**, 23–35.

Güsewell, S. & Klötzli, F. (1997) Measuring the abundance of *Phragmites communis* Trin. in wet meadows: A methodological investigation. *Bulletin of the Geobotanical Institute ETH*, **63**, 11–24.

Güsewell, S. & Le Nédic, C. (2003) Effects of winter mowing on vegetation succession in a lakeshore fen. *Applied Vegetation Science*, in press.

Harrison, A.F. (1985) Effects of environment and management on phosphorus cycling in terrestrial ecosystems. *Journal of Environmental Management*, **20**, 163–179.

Hart, R.H. (2001) Plant biodiversity on shortgrass steppe after 55 years of zero, light, moderate or heavy cattle grazing. *Plant Ecology*, **155**, 111–118.

Hasler, A. (1996) Mit Rindern gegen Büsche und Schilf. *Ornis*, **4/96**, 14–15.

Haynes, R.J. & Williams, P.H. (1999) Influence of stock camping behaviour on the soil microbiological and biochemical properties of grazed pastoral soils. *Biology and Fertility of Soils*, **28**, 253–258.

Hickman, K.R. & Hartnett, D.C. (2002) Effects of grazing intensity in growth, reproduction, and abundance of three palatable forbs in Kansas tallgrass prairies. *Plant Ecology*, **159**, 23–33.

Huemer, P. (1996) Frühzeitige Mahd, ein bedeutender Gefährdungsfaktor für Schmetterlinge der Streuwiesen (NSG Rheindelta, Vorarlberg, Österreich). *Vorarlberger Naturschau*, Dornbirn, 1, 265–300.

Jensen, K. & Schrautzer, K. (1999) Consequences of abandonment for a regional fen flora and mechanisms of successional change. *Applied Vegetation Science*, **2**, 79–88.

Jewell, P. (2002) *Impact of cattle grazing upon the vegetation of an Alpine pasture.* Ph.D. thesis. Swiss Federal Institute of Technology (ETH), Zürich, Switzerland.

Jutila, H. (1999) Effect of grazing on the vegetation of shore meadows along the Bothnian Sea, Finland. *Plant Ecology*, **140**, 77–88.

Kleijn, D. & Steinger, T. (2002) Contrasting effects of grazing and hay cutting on the spatial and genetic population structure of *Veratrum album*, an unpalatable, long-lived, clonal plant species. *Journal of Ecology*, **90**, 360–370.

Klieber, A., Schröder, U. & Irmler, U. (1995) Der Einfluss der Mahd auf die Arthropoden des Feuchtgrünlandes. *Zeitschrift für Ökologie und Naturschutz*, **4**, 227–237.

Kooijman, A.M. & Smit, A. (2001) Grazing as a measure to reduce nutrient availability and plant productivity in acid dune grasslands and pine forests in The Netherlands. *Ecological Engineering*, **17**, 63–77.

Landolt, E. (1977) Ökologische Zeigerwerte zur Schweizer Flora. *Veröffentlichungen des Geobotanischen Instituts ETH, Stiftung Rübel, Zürich*, **64**, 1–208.

Lauber, K. & Wagner, G. (1996) *Flora Helvetica.* Paul Haupt, Bern.

Manly, B.F.J., McDonald, I.L., Thomas, D.L., McDonals, T.L. & Erickson, W.P. (2002) *Resource Selection by Animals*, 2nd Ed. Kluwer, Dordrecht.

Marti, K. (1994) Zum Standort von *Magnocaricion*-Gesellschaften in der Schweiz. *Veröffentlichungen des Geobotanischen Instituts ETH, Stiftung Rübel, Zürich*, **120**, 1–97.

Menard, C., Duncan, P., Fleurance, G., Georges, J.-Y. & Lila, M. (2002) Comparative foraging and nutrition of horses and cattle in European wetlands. *Journal of Applied Ecology*, **39**, 120–133.

Müller, J., Rosenthal, G. & Uchtmann, H. (1992) Vegetationsveränderungen und Ökologie nordwestdeutscher Feuchtgrünlandbrachen. *Tuexenia*, **12**, 223–244.

Olofsson, J., Moen, J. & Oksanen, L. (2002) Effects of herbivory on competition intensity in two arctic-alpine tundra communities with different productivity. *Oikos*, **96**, 265–272.

Pfadenhauer, J. (1988) Pflege- und Entwicklungsmassnahmen in Mooren des Alpenvorlandes. *Natur und Landschaft*, **63**, 327–334.

Pfadenhauer, J. & Eska, U. (1986) Untersuchungen zum Nährstoffhaushalt eines Schneidried-Bestandes (*Cladietum marisci*). *Veröffentlichungen des Geobotanischen Instituts ETH, Stiftung Rübel, Zürich*, **87**, 309–327.

Pratt, R.M., Putman, R.J., Ekins, J.R. & Edwards, P.J. (1986) Use of habitat by free-ranging cattle and ponies in the New Forest, Southern England. *Journal of Applied Ecology*, **23**, 539–557.

Proulx, M. & Mazumder, A. (1998) Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology*, **79**, 2581–2592.

Putman, R.J., Pratt, R.M., Ekins, J.R. & Edwards, P.J. (1987) Food and feeding behaviour of cattle and ponies in the New Forest, Hampshire. *Journal of Applied Ecology*, **24**, 369–380.

Radlmair, S. & Laußmann, H. (1997) Auswirkungen extensiver Beweidung und Mahd von Moorstandorten in Süddeutschland auf die Heuschreckenfauna (Saltatoria). *Verhandlungen der Gesellschaft für Ökologie*, **27**, 199–205.

Rosenthal, G. (1992) Problempflanzen bei der Extensivierung von Feuchtwiesen. *NNA-Berichte*, **5**, 27–36.

Rozé, F. (1993) Successions végétales après pâturage extensif par des chevaux dans une roselière. *Bulletin d'Ecologie*, **24**, 203–209.

van Deursen, E.J.M. & Drost, H.J. (1990) Defoliation and treading by cattle of reed *Phragmites australis*. *Journal of Applied Ecology*, **27**, 284–297.

Vinther, E. (1983) Invasion of *Alnus glutinosa* (L.) Gaertn. in a former grazed meadow in relation to different grazing intensities. *Biological Conservation*, **25**, 75–89.

White, S.L., Sheffield, R.E., Washburn, S.P., King, L.D. & Green, J.T. (2001) Spatial and time distribution of dairy cattle excreta in an intensive pasture system. *Journal of Environmental Quality*, **30**, 2180–2187.

Received 11 March 2003
Revised version accepted 15 June 2003

Electronic Appendices

Appendix 1. Formula for the calculation of the percentages of cattle observations in each vegetation type

Appendix 2. Seasonal changes in the utilisation of the nine vegetation types for grazing (cf. Table 2; type 9 = *Schoenetum*). For each observation date, the time spent grazing in each vegetation type was expressed as percentage of total grazing time (see Appendix 1 for calculations).

Appendices can be downloaded as PDF files at
http://www.geobot.umnw.ethz.ch/publications/periodicals/bulletin.html
(select 'Electronic Appendices', App. 2003–1 and App. 2003–2).