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Dung matters: An experimental study into the effectiveness of using dung from hay-fed livestock to reconstruct local vegetation

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This paper explores the relationship between standing vegetation and dung from hay-fed cattle and sheep. In an experimental study, hay is retrieved from a known hay field, surrounded by a semi-open landscape of hedgerows, forests and heather fields. The hay is fed to cattle and sheep, after which the dung is collected and from which the botanical remains are analysed, according to archaeobotanical standards. The results from the macro-remains are compared to vegetation relevés from the hay field. The pollen analysis is compared to both the hay field and the surrounding vegetation. Results from the plant macro remains provide an excellent representation of the vegetation in the field itself on the presence/absence level. Pollen analysis reflects the regional vegetation very well and are comparable with 'surface samples'.

Keywords: Dung, Vegetation reconstruction, Palynology, Hay field, Macro remains, Experimental study

Introduction

In archaeobotany, and more particularly in the study of macroscopic plant remains (hereafter referred to generically as seeds in running text, unless the context necessitates a more specific term), the dung of herbivores has long since been regarded as a fruitful source of data for reconstructing past animal husbandry, be that grazing and fodder regimes or past vegetation (e.g. Körber-Grohne 1967; Brinkkemper 1993; Hall and Kenward 1998). The reason for this is obvious: dung from various animal species often holds a concentration of plant remains – in particular, endozoochorous diaspores (Stiles 1980; Janzen 1984; Cosyns and Hoffmann 2005; Stroh *et al.* 2012). Endozoochory is the dispersal of seeds through an animal's digestive system (as opposed to epizoochory, which is the dispersal of seeds by adhesion to an animal, for example by sticking to fur [Sorensen 1986; Couvreur *et al.* 2005; Mouissie *et al.* 2005a]). Studying dung will often result in a large number of seeds from a considerable number of taxa. Moreover, in wetland environments, dung is also an excellent sampling context for pollen analysis. Palynology may not only add information on the broader environment, it may also be a good alternative when too little dung is available to allow for macro-botanical analysis. This is especially relevant when multiple thin dung layers

alternate with other sediments, allowing for a study of change over time (e.g. Woldring and Kleine 2008).

In this study, we attempt to shed some light on how variable the botanical composition of cattle and sheep dung is on both the qualitative and the quantitative levels. By this means, we intend to contribute to our understanding of the local and regional vegetation in a landscape where typical pollen contexts in the form of long peat sequences are lacking, but where dung is abundant – specifically, the Dutch terps area. Terps are man-made dwelling mounds erected in a salt marsh landscape (see Schepers *et al.* 2013).

In our experiment, hay from a modern-day grassland was cut and subsequently fed to both sheep and cattle to determine to what extent seeds and pollen in the dung of animals represent the vegetation in the hay meadows. In addition, we also investigated to what extent the data from the dung can be used to reconstruct the vegetation pattern outside the meadows proper, namely, the surrounding, more regional vegetation. This signal is expected to be mainly represented by pollen, but also by wind-dispersed seeds that may be blown in from outside the grassland itself. When these seeds do not fall to the ground but instead stick to standing vegetation, they may also end up in hay and, ultimately, in animal dung (Cappers 2006).

A large number of studies deal with the relationship between vegetation and dung. These studies can be separated into two main categories. The first category encompasses ecological studies that focus on the

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relationship among grazing, endozoochorous dispersal and the ability of diaspores to germinate in a different area than their source area (e.g. Mouissie *et al.* 2005b; Wells and Lauenroth 2007; Bakker *et al.* 2008). The second category encompasses archaeobotanical studies, where germination experiments are unhelpful, since most seeds will have long ago lost their viability due to charring, waterlogging, or mineralisation. Exceptions to this rule only occur under very specific and extremely rare conditions (e.g. Sallon *et al.* 2008; Yashina *et al.* 2012). Archaeobotanists are often not primarily interested in the germination potential of seeds that have gone through an animal's digestive system. As long as a seed can still be identified to a low taxonomic level, it has fulfilled its primary role in the possible reconstruction of vegetation. This means that fragments of seeds or other small plant parts still identifiable to an ecologically relevant taxonomic level (mostly to species), such as cereal rachis fragments, moss leaves, or fern apices, are equally important and are also taken into account when reconstructing vegetation.

Recently, a number of publications dealing with the taphonomy and interpretation of dung have appeared, the most prominent being the monograph *Manure Matters* (Jones 2012) and a special issue of *Environmental Archaeology*, edited by Marinova *et al.* (2013).

Shahack-Gross (2011, 215) summarises the multiple ways in which plant material might end up in dung. Although her observations also pertain to palaeoenvironmental reconstruction, they primarily pertain to identifying past animal husbandry. She rightly emphasises that fodder regimes and seasonality will have a considerable effect on the composition of dung and, thus, on the vegetation to be constructed.

In the special issue of *Environmental Archaeology*, the experiment presented by Wallace and Charles (2013) and, to a lesser extent, the study by Linseele *et al.* (2013) show considerable overlap with the issues addressed here. We refer to the study by Wallace and Charles (2013) for a concise recent overview of dung-related experiments in archaeobotany.

The experiments performed by Wallace and Charles (2013) show the discrepancy in composition between seeds that were fed to animals and those present in the dung these animals produce. Their study has the advantage that the authors knew exactly how many seeds of each taxon were consumed by the test animals in the experiment.

The focus in this paper is on the relationship between dung and vegetation, as opposed to the exact number of seeds consumed (Fig. 1). In this experiment, we deal with dung from hay-fed animals. Dung from animals that were fed hay that was harvested from the same area will have a different

Figure 1 Flow chart for the subject of this paper. The term seeds here refers to all plant macro-remains.

composition than dung from animals that were allowed to graze in a landscape, because in the former scenario, the ability of animals to avoid less-preferred plant taxa or dried-out specimens is reduced considerably.

In wetland sites, deposits of exceptionally well-preserved dung are frequently encountered and selected for palaeobotanical analysis, often with the aim of reconstructing the local vegetation (e.g. Van Zeist 1989; Cappars 1995, 2008; Kühn *et al.* 2013).

The interpretation of dung in archaeology is complicated by archaeologists' ability to recognise dung in the field (Körber-Grohne 1991, 11). Both Körber-Grohne (1967, 73) and Behre (1976, 25) conclude that what is generally labelled as 'dung' in excavation reports is likely to be typical byre mixture of dung, unconsumed hay, and straw. In terms, these dung labelled samples generally represent a mixture from a variety of vegetation types and appear to be surprisingly similar in botanical composition to the secondary fill of creeks and ditches on the presence/absence level (Schepers *et al.* 2013). This study was initiated to improve our interpretation of the frequent finds of dung layers in dwelling mounds in the northern Netherlands.

As Dieffenbacher-Krall (2007) points out, plant macro-remains may have the benefit of a deep taxonomic resolution, but because of their dispersal characteristics, they are less suited than pollen for estimating past abundances of identified taxa: 'They are not systematically (linearly or unimodally) related to the variable (proportion of a species within a vegetational community) of interest' (pp. 2367–2368). Dieffenbacher-Krall's formula to translate seed numbers into vegetation (which he explicitly states

that it does *not* hold true) does not take into account that vegetation is generally not described in terms of number of individuals, but rather in terms of percentage of coverage by area. This is relevant because some taxa may cover a large surface while producing relatively few seeds, whereas other taxa, in contrast, may produce numerous seeds even though they cover only a relatively small area.

As stated above, numerous ecological studies deal with seed content in dung, but because ecologists studying present vegetation have no need to reconstruct vegetation, their focus is predominantly on seed dispersal. The non-zoological natural dispersal of seeds and the relationship to vegetation have been addressed in both palaeolimnological studies (Gaillard and Birks 2013) and in ecological studies dealing with water dispersal (Wolters and Bakker 2002; Boedeltje *et al.* 2003).

Far more studies have dealt with the relationship between pollen and vegetation than have dealt with seeds and vegetation (Overpeck *et al.* 1985; Berglund *et al.* 1986; Groenman-van Waateringe 1986; Caseldine and Pardoe 1994; Broström *et al.* 1998; Bunting 2003; Court-Picon *et al.* 2005). The long-distance dispersal of pollen allows for the interpretation of the vegetation composition at a greater distance from the actual sampling area – in most cases long organic sequences of peat or lake sediments. A key concept here is the ‘relevant source area of pollen’ (RSAP) (Sugita 1994), defined as the distance beyond which the correlation between pollen deposited at a site and the surrounding vegetation no longer improves (see also Broström 2002, 12). This means that reliable conclusions about the vegetation around a sampling site can only be drawn within the limits of the RSAP. Also, the size of the RSAP depends on the size of the basin in which the pollen is preserved (e.g. small hollows, ponds or lakes). The RSAP for surface samples (this study) is 400 m (radius around sampling site).

Pollen derived from dung found in archaeological contexts may be a valuable contribution to the interpretation of past landscapes if they are found to reflect vegetation in a comparable way to pollen from modern surface samples. In this study, we follow the figures defined by Groenman-van Waateringe (1986, 197) to evaluate the degree of openness of a landscape. From her experimental studies in the Netherlands, she concluded that arboreal pollen (AP) percentages of less than 25% in surface samples indicate an open landscape. Between 25 and 55% AP indicates open woodland, forest edge, or shrub, while over 55% AP indicates woodland. Pollen analysis on dung has frequently been used in archaeological research to reconstruct past vegetation (Akeret *et al.* 1999 and references therein; Carrión *et al.* 2000;

Nieuwhof and Woldring 2008). Carrión *et al.* (2000), interestingly, present modern cow dung pollen samples to support their interpretation. In another study, dealing with grazing animals, Carrión suggests that samples from dung contain a combination of both local and regional flora, because each leaf eaten by a herbivore may contain pollen rain (Carrión 2002, 230). Although that study deals with dung from free-ranging animals, this pollen rain is also likely to be present on dung from hay-fed livestock.

In this study, we attempt to shed some light on how variable the botanical composition of cattle and sheep dung is on both the qualitative and the quantitative levels. The main research question is to what extent dung represents the local (seeds and pollen) and regional (pollen) vegetation. For plant macroremains, following Dieffenbacher-Krall (2007), we expect the null-hypothesis of no relationship between sample composition and vegetation to hold on the quantitative level. We expect the alternative hypothesis of a clear relationship between sample composition and vegetation to be true on the qualitative level.

Methods

Choice of Hay Field Location

Because the dwelling mounds are situated in a salt marsh landscape, the initial intention was to obtain hay from a salt marsh area. Unfortunately, a wet summer in combination with the relatively modest size of the present marshes in comparison to the historic situation made this impossible. We considered inland grasslands used for grazing in commercial farming to be an unfit alternative because they are characterised by *Lolium perenne*-dominated, species-poor swards. Instead, we chose hay fields located in a heritage landscape national park containing a stream called the Drentsche Aa (Figs. 2 and 3).

The general area is dominated by the stream itself and consists of a mosaic of forest, riparian vegetation along the stream and hay fields – the type of vegetation that is suitable for answering our questions related to the diversity of plant taxa in dung as compared to that in the standing vegetation. The selection of the specific study area was based, first, on the taxonomic diversity of the meadows proper. The hay fields that we selected, mostly former cultivated areas that were abandoned several decades ago, have a great diversity of plant taxa, and this diversity makes them suitable for an experiment that includes seed analysis. The expected diversity of species in the hay makes this area a better source for comparison with the former salt marsh area than most present-day commercial grasslands. The second criterion was high variation in the surrounding vegetation; this makes a comparison with the pollen samples more complicated, but also more interesting. We can assess whether or not

Figure 2 The Drentsche Aa valley near Oudemolen, province of Drenthe, the Netherlands. The numbered dots indicate the locations of the vegetation relevés 1–12. The hay originated from both the field with the relevé plots and the fields directly south to this. All three fields have a similar vegetation.

Figure 3 Overview of the relevé hay field before mowing, looking northeast from relevé 1.

all vegetation units in the area are represented in accordance with their relative coverage in the pollen samples. The final selection criterion was accessibility; the hay from this area could be relatively easily obtained.

Collecting Hay (2011)

The hay fields near the village of Oudemolen are subject to normal seasonal variety in moisture, but, in contrast to the grasslands in the riparian zone, will not flood in wetter periods. The hay grasslands

are mown in mid-summer, when many grassland species are in their fruiting stage. The plant material is left to dry on the field for several days. The drying process is stimulated by repetitive turning, thus resulting in both mixing of plant remains and declining diaspore density as diaspores fall onto the ground and become incorporated into the local seed bank, rather than being removed with the hay. Finally, the hay is packed in rolls approximately 1 m high and 1.5 m in diameter. In the summer of 2011, we obtained five of these rolls for the experiments.

Table 1 Composition of 13 relevés in the Drentsche Aa grasslands*

Relevé number	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Anthoxanthum odoratum</i>	1	1	1	1	1	1	1	1	1	1	1	r	+
<i>Holcus lanatus</i>	2a	1	2a	1	+	r	2a	1	2b	+	1	1	+
<i>Plantago lanceolata</i>	2a	3	2b	3	+	4	2b	3	2b	2a	4	3	
<i>Leontodon autumnalis</i>	2a	+	2a	+	r	+	2a		1	r	+	2a	
<i>Rumex acetosa</i>	+	2a	r	r	r		+		+	r	2a	r	
<i>Rhinanthus angustifolius</i>	2a			+	2a	1	+		+	+		2a	+
<i>Cirsium palustre</i>	r	r		r				r		1	r	r	
<i>Ranunculus acris</i>	2b	3			+			+	2a	r	2a		
<i>Cerastium fontanum</i>	r	2a	+				+				r	+	
<i>Cynosurus cristatus</i>	1	1		r	r		+						R
<i>Poa pratensis</i>	1	1			1		1			1	1		
<i>Ranunculus repens</i>			2a	3	+	2b		2b					
<i>Dactylorhiza majalis</i> subsp. <i>majalis</i>	+	+	r				r						
<i>Juncus effusus</i>		r			2a			2a		2b			4
<i>Cardamine pratensis</i>									r		r	r	
<i>Cirsium</i>		r				r	+						
<i>Galium palustre</i>			r						r				2b
<i>Hypochaeris radicata</i>										2b	r	2a	
<i>Trifolium pratense</i>		+		+								2a	
<i>Trifolium repens</i>	2b			+						r			
<i>Agrostis capillaris</i>										2b		r	
<i>Deschampsia cespitosa</i>	+	2a											
<i>Festuca pratensis</i>	1	+											
<i>Ranunculus</i>							2b						2a
<i>Bellis perennis</i>							+						
<i>Betula</i>											r		
<i>Carex ovalis</i>										r			
<i>Luzula campestris</i>										+			
<i>Phragmites australis</i>													+
<i>Quercus</i>										r			
<i>Quercus robur</i>											r		
<i>Ranunculus flammula</i>													2a
<i>Rubus fruticosus</i>										r			

*See Fig. 2 for the location of the relevés.

r, very few; +, few; 1, numerous; 2a, 5–12.5 coverage; 2b, 12.5–25 coverage; 3, 25–50% coverage; 4, 50–75% coverage. Species are ordered according to the number of relevés in which they occur and within that alphabetically.

Mapping the Vegetation (2013)

We were unable to map the vegetation in 2011, since the hay had already been cut by the time the area was selected. We therefore mapped the vegetation two years later. In this experiment, the goal is to find out whether the reconstruction of vegetation from the dung is similar to the vegetation that was present in the source area. It is therefore not essential that the relevés be taken on the actual vegetation that was to be fed to the animals. It is, nevertheless, acknowledged and emphasised that because the vegetation that was mapped was not the actual vegetation collected, the present study does not meet the ideal situation of an unbroken *chaîne opératoire*.

The Drentsche Aa grasslands are extensive and diverse. This diversity is already apparent on a very local level. One extensive field was selected to create 12 relevés (plots), laid out in a systematic pattern. Each of the relevés measures 2 × 2 m. Their position in the field was determined using a handheld Global Positioning System (GPS) device. In addition, a linear relevé measuring 2 × 10 m was created along a shallow ditch that runs straight through the grassland.

The vegetation mapping was carried out in 2013. The relative coverage of the species were estimated

using Braun–Blanquet scales for cover abundance, as available through the database system for vegetation data TURBOVEG (Hennekens and Schaminée 2001; see caption to Table 1). We scanned the grassland around the relevés to spot additional species that occurred rarely or only locally clustered in the field. In addition, we surveyed the vegetation pattern outside the grassland that lay within a 400 m radius measured from the centre of the grassland. The size of this area corresponds to the area that is generally regarded as the RSAP for samples that are taken from soil surfaces (see above). All trees surrounding the meadows were inspected, and the relative abundance of the different taxa was estimated. The heath fields to the west and south of the grassland were not inspected in detail but can be described as typical heathlands, dominated by *Calluna vulgaris* and *Erica tetralix*.

The Two-year Gap Between Dung Collection and Vegetation Survey

As stated above, the fact that the vegetation survey was carried out two years after the dung collection is a major flaw in the experimental set-up that we would have preferred to have avoided. How do we know that the vegetation composition of the grassland was

similar (enough) to not render the whole study invalid? However, tempting it might be to point to the good general match between the dung composition and the vegetation, this would obviously constitute circular reasoning. A more convincing argument comes from the vegetation surveys in the area, which show very similar vegetation composition more than 20 years ago (Everts and De Vries 1991). Year-to-year variability in the vegetation is influenced by multiple factors, such as rainfall, temperature and other weather conditions. Taking the total rainfall in June as a reference point, the values reported for the north of the province of Drenthe, where the sampled Drentsche Aa grasslands are situated, are very similar in 2011 (69.4 mm; KNMI 2011, 5) and 2013 (68.6 mm; KNMI 2013, 5). The average temperatures reported for June in both years show that it was slightly colder in 2011 (14.5°C; KNMI 2011, 4) than in 2013 (15.6°C, KNMI 2013, 4). The weather conditions not only influence the vegetation directly, but also determine the moment of hay-cutting. For these reasons (and additional factors that complicate these counts, as discussed below), the seed counts in particular should not be used for a direct comparison between dung samples and standing vegetation. But on a presence/absence level, we expect the differences between the two years to have been negligible.

Choice of Animals As Well As Stabling and Feeding Regime

Most dung studied from the Dutch terps consists of cattle dung. Although many sheep bones have been identified, no sheep pellets have been recognised in this region. Given the excellent preservation of the organic material, this is noteworthy. Pellets have, for example, been recognised in sites with comparable preservation conditions along the Dutch west coast (Brinkkemper 1993, 84) and in numerous archaeological sites outside the Netherlands (Akeret *et al.* 1999 and references therein). The emphasis in this experiment therefore lies on cattle, but sheep were included as well, in order to establish whether or not their dung will show profound differences in botanical composition compared with cattle. A discussion of prehistoric animals' digestive systems and their effects on the preservation of plant materials in dung compared to modern animals' is beyond the scope of this paper.

We used three cows and three sheep from the test facilities at Wageningen University, the Netherlands. The animals were fed *ad libitum*, meaning plenty of hay was available for them at all times, theoretically allowing them to 'select' their food. To make sure no remains of previous feeding regimes could contaminate the dung samples, the animals underwent a three-week adaptation period (November 29–December 19) prior to the sampling period

(December 20–23). We acknowledge that it is possible that, once the hay was placed in the feeding troughs at the Wageningen test centre, ambient local pollen, which would be very different in composition from the pollen in the study area, may have joined the study area pollen that was already present on the hay. But because the feeding experiments were carried out in December, that is, at a time when airborne pollen are only minimally present, little pollen contamination from pollen in the air at the feeding location is expected. As an extra safeguard, all animals were kept inside during the experiment, thus also making sure they had no access to food other than the hay intended for the experiment.

The cattle were kept separated from each other. They were tied to a bar running the length of the barn in order to allow for easy gathering of dung after defecation. Within several hours, the hay that had been presented to the cattle as fodder became sorted into coarse and finer material by the animals. It became moist with saliva. Hay was removed and replaced with fresh material when the animals appeared to have lost interest in the remaining hay.

The sheep were kept separated from each other during daytime only. A bucket of hay a day per sheep proved to be sufficient for the sheep to feed on. At night, the sheep were reunited and allowed to feed on the same kind of hay from a communal trough.

Sampling the Dung

A total of 24 wet samples were secured – 12 for cattle and 12 for sheep.

Throughout the day (8.45 AM–6.30 PM) all cattle dung was collected manually, directly following defecation. The night production was collected first thing in the morning. Both day and night production were weighed and subsequently mixed. Two 850-ml samples were taken from the mixture for each of the three animals. For each animal, one of these two samples was dried in a hot air drying chamber at 65°C for 24 hours, thus producing a 'dung cake'. By weighing this dung cake, we were able to determine the original relative proportion of moisture in the dung; this proportion was then used to calculate the absolute amount of dry matter in the wet sample.

Sampling of the sheep pellets was carried out during daytime only (9.00 AM–6.00 PM). Droppings were gathered continuously, to prevent the sheep from trampling them or mixing them up with the hay. The whole day's worth of production per animal was taken as a sample.

Processing the Dung Samples

After being soaked in hot water for several days, both the cow and the sheep dung samples readily dissolved. For the pollen analysis, samples were taken from four

of the wet cattle samples and from two of the sheep samples. The samples were prepared following Faegri and Iversen (1989). For the seed analysis, all wet samples were sieved separately over a stack of sieves with mesh aperture sizes of 2.0, 1.0, and 0.5 mm. No mechanical force or manual pressure was applied during sieving.

All 12 cattle samples were sorted completely. The total seed count was corrected to an equal amount of dry matter, normed to the sample with the highest absolute amount of dry matter as a starting point. This correction was performed to allow for comparison of plant remains based on the density of seeds in the plant material only, irrespective of the moisture component (i.e. water).

Six of the sheep samples (those collected during the first two days) were analysed, but because of the low density and variety of seeds present, only about half of the 0.5 mm sieve residue was sorted. The relative proportion of the amount of residue in the samples was measured in ml. By measuring the unsorted residue of the 0.5 mm sieve as well, the seed counts in the residue could be corrected to the total sample.

Results

Vegetation Relevés

The results of the mapping of the standing vegetation in the relevé field are presented in Table 1. A number of species dominated the vegetation (Fig. 4). These were the grasses *Holcus lanatus* and *Anthoxanthum odoratum* and the common grassland herbs *Plantago*

Figure 5 Seedlings of birch (*Betula*, left) and oak (*Quercus*, right) in relevé 11.

lanceolata, *Leontodon autumnalis* and *Rumex acetosa*. Plants of wetter stands were represented by *Galium palustre*, *Phragmites australis* and *Ranunculus flammula*, the latter two being concentrated along the shallow ditch (relevé 13).

In relevés 10 and 11, seedlings of *Betula* and *Quercus* were present, emphasising the possible vegetation development in the area if mowing practices were to be abandoned (Fig. 5). Relevés 10 and 11 are located along the edge of the field, and included such species as *Anthriscus sylvestris*, *Urtica dioica* and *Dactylis glomerata*, pointing to more nitrogen-rich soils. A small concentration of *Juncus articulatus* was present in a less well-drained area not included in the relevés. All relevés except for number 13 can be identified as grasslands within the *Molinio-*

Figure 4 Variety in species composition in the studied hay field. Clockwise from top left: relevé 3, relevé 5, relevé 11 and relevé 12.

Figure 6 Relative proportion of dry matter for the cattle samples. The seed counts for the cattle samples were corrected to the highest absolute amount of dry matter based on these proportions.

Arrhenatheretea, in this case represented by semi-natural, wet to moist hay field (syntaxonomy follows Schaminée *et al.* 1996). These grasslands are common in the Drentsche Aa stream valley (Everts and De Vries 1991).

Vegetation Pattern Surrounding the Sampled Grassland Established Through the RSAP Survey

The landscape within a 400 m radius of the sampled grassland can be characterised in general as open to semi-open. To the west, north and south, the landscape consists mainly of grasslands dissected by hedgerows with trees and shrubs or grassy heathland vegetation. The sampled grassland itself is surrounded by a 5–10 m wide hedgerow, which as far as the trees and shrubs are concerned consist mainly of *Betula*, *Quercus*, *Betula* and *Prunus serotina/padus*. *Rubus fruticosus*, *Salix* spp, *Lonicera periclymenum*, *Sorbus aucuparia*, *Corylus avellana* and *Sambucus nigra* are also present. To the east of the sampled grassland lies a dense forest dominated by *Quercus* and *Fagus* (see Figs. 2 and 3). *Alnus* is present on wet locations along the Drentsche Aa stream.

Cattle Dung

The relative proportion of dry matter in the cattle dung samples is presented in Fig. 6. It proved, in general, rather easy to produce solid dung cakes fit to be stored from dung alone – that is, without using any admixture such as threshing remains (Fig. 7). A total of 3757 seeds were collected and identified from the wet samples. A large number of moss fragments (not counted) were also recovered from the dung. By correcting all values to the highest dry matter content, which allows for comparison among samples, the total number of seeds is 5418 (Table 2). The density of seeds per 100 g of dry matter (average = 146) is also presented in Table 2. The samples are coded according to the cow number and the sampling day.

For example, sample C1.3 is the sample taken from cow 1 on the third sampling day.

Since *Poa* was extremely dominant in all samples, its fruits and florets are not included in the seed density calculation. Including them would cause the density differences among the samples to be primarily indicative of the fluctuations of a single taxon. Although substantial variation in seed density exists among samples C1.2 to C3.4 (between 69 and 163 seeds per 100 g), the seed density of sample C1.1 stands out. As indicated by the dry matter content (Fig. 6), this animal clearly suffered from diarrhoea that day – which was, in fact, observed during sampling. Although the absolute amount of dry matter in the sample was lower, the diarrhoea appears to have had a positive effect on the seed survival rate, presumably due to the faster rate of passage through the digestive tract.

For a number of taxa, different plant parts were counted separately if encountered as such; seeds and fruits were not counted if they were part of a higher morphological unit. For example, although a complete spikelet of *A. odoratum* undoubtedly contains its caryopsis, the latter is not counted as a fruit also. A number of taxa are present in practically all samples. The ratios between these ubiquitous taxa vary considerably. The fruits of *A. odoratum*, for example, were found in low numbers in samples C2.2 and C3.1. Sample C3.1, however, does contain the highest number of *Carex ovalis* fruits utricles. A remarkable high number of *Juncus effusus* fruits (seeds were not counted because of their very small size) were recovered from sample C2.1. Other noteworthy species are the domesticated *Hordeum vulgare* in samples C1.1 and C1.2, as well as *Atriplex* and *Chenopodium album*, being possible associated arable weeds.

Sheep Pellets

A total of 558 seeds were counted from the sheep pellets; this number was converted to a total of 806 by taking into account the unsorted portion of the 0–5 mm fraction. The sample codes work the same way as those for cows: S1.1. is the sample taken from

Figure 7 'Dung cake' created from one of the cattle dung samples, ca. 40 cm in length.

Table 2 Scaled number of diaspores per sample in dung samples from three cows (C1, C2 and C3), sorted on ubiquity*

Taxon	Plant part	C1.1	C1.2	C1.2	C1.4	C2.1	C2.2	C2.3	C2.4	C3.1	C3.2	C3.3	C3.4
<i>Anthoxanthum odoratum</i>	Fruit	22.7	20.6	28.8	35.3	7.9	3.8	43.2	38	2.3	14	22.8	18
<i>Anthoxanthum odoratum</i>	Floret	25.2	24.7	22.3	25	6.6	14.1	17.6	43.8	8.2	8	27.8	29.2
<i>Carex ovalis</i>	Fruit and utricle	181.4	38.4	5.2	4.4	58.1	23	16.2	4.4	59.6	30	15.2	7.9
<i>Juncus effusus</i>	Fruit	315	63	23.6	48.5	109.6	33.3	31.1	8.8	37.4	50	21.5	4.5
<i>Musci</i>	Vegetative part	xxx	xx	x	xx	x	xx	xx	xx	xx	xx	x	x
<i>Plantago lanceolata</i>	Fruit	12.6	4.1	13.1	38.2	5.3	3.8	10.8	14.6	3.5	4	7.6	2.2
<i>Plantago lanceolata</i>	Seed	45.4	34.3	39.3	26.5	9.2	6.4	19.6	24.8	10.5	10	19	15.7
<i>Poa</i>	Fruit	471.2	164.4	163.8	172	184.8	102.4	222.8	121.2	142.6	155	131.6	164
<i>Poa</i>	Floret	121	82.2	53.7	98.5	62	43.5	85.1	40.9	98.2	44	59.5	49.4
<i>Ranunculus acris/repens</i>	Fruit	32.8	7	9.2	15.6	4.8	1.3	12.3	5.8	16.7	8	11.4	9.5
<i>Galium palustre</i>	Seed	17.6	1.4	6.6	10.3	11.9	5.1		2.9	1.2	1	2.5	2.2
<i>Alopecurus</i>	Floret			1.3	7.4	4	1.3		1.5	1.2			
<i>Festuca</i>	Floret	5		1.3		2.6		1.4	2.9	1.2			
<i>Rhinanthus</i>	Seed		4.1	1.3	4.4			1.4	1.5				2.2
<i>Betula</i>	Fruit		1.4			1.3	1.3				1		1.1
<i>Cynosurus cristatus</i>	Infructescence	2.5	1.4	3.9	1.5						2		
<i>Leontodon autumnalis</i>	Fruit			1.3			0.6		1.5			1.3	1.1
<i>Cirsium</i>	Fruit	2.5			1.5				1.5	1.2			
<i>Rhinanthus</i>	Fruit			1.3	1.5			1.4					1.1
<i>Rumex acetosa</i>	Fruit		2.7	2.6	2.9							1.3	
<i>Cerastium fontanum</i>	Seed								1.5		3		
<i>Cynosurus cristatus</i>	Fruit		1.4									2.5	
<i>Holcus lanatus</i>	Floret			2.6							2		
<i>Hordeum vulgare</i>	Rachis node	15.1	1.4										
<i>Atriplex</i>	Fruit			1.3									
<i>Chenopodium album</i>	Fruit			1.3									
<i>Eleocharis palustris</i>	Fruit	5											
<i>Prunella vulgaris</i>	Fruit								1.5				
Density (per 100 g, excluding <i>Poa</i>)		498	150	121	163	161	69	113	113	104	97	97	69

*The decimals are the result of correction of all samples to an equal amount of dry matter, normed to sample C3.2. The branches of *Musci* have been quantified into three categories: x, some; xx, many; xxx, very many.

sheep 1 at day 1. In terms of method, it should be mentioned here that the seed analysis from the sheep samples proved much more time consuming than that from the cow samples. Even after sieving, much of the plant material was considerably more entangled, which necessitated manual separation with tweezers to search for seeds.

However, because manual separation was carried out consistently and thoroughly, this initial entangling is not likely to have affected the results.

A striking difference from the cow samples is the much lower number of taxa. We had expected *J. effusus* to be present in low numbers only, because during the feeding regime we observed that the relative proportion of *J. effusus* stems in the hay bucket increased during the day, suggesting avoidance of the stems by the sheep. The cow's physique did not allow for this subtlety. Oddly enough, this observation could not be confirmed by the seed analysis, suggesting that the sheep avoided the *J. effusus* stems more than the infructescences. *S2.2.* stands out for having a higher number of taxa, although all but *Rumex acetosella* are represented by a single seed only.

Pollen Analysis

The full results of the pollen analyses are presented in appendix A. The pollen samples (from cattle and sheep) displayed more taxonomic variation, resulting from the ability of pollen to be dispersed over greater distances. The AP percentages in the dung samples varied from 5.7 to 20.3% (Fig. 8).

The trees that were best represented in the dung samples are *Quercus*, *Betula*, *Corylus* and *Alnus*, which are wind-pollinated taxa. *Quercus*, *Betula* and *Corylus* are the main components of the surrounding hedgerow, and *Alnus* is the dominant tree along the Drentsche Aa stream. Other trees and shrubs that are present in the surrounding hedgerow (*Sorbus*, *Lonicera*, *Rubus*, *Sambucus* and *Salix*) are insect-pollinated taxa. These taxa produce lower quantities of pollen than do wind-pollinated taxa and are therefore less well represented in the dung samples. Pollen from *Fagus*, a wind-pollinated tree that is very well represented in the forest to the east of the sampled grassland, is hardly present in the dung samples, probably as a result of the fact that the prevailing wind originates from the southwest. The regional vegetation as

Figure 8 Proportion of grassland, fen and heathland and arboreal pollen in the pollen samples.

a whole as reconstructed from the pollen diagrams therefore appears somewhat more open than the actual vegetation.

All samples are dominated by grassland taxa, especially Poaceae, *P. lanceolata*-type, Asteraceae Liguliflorae (which includes *L. autumnalis*), and *Ranunculus acris*-type. Other grassland taxa are present in lower proportions. Within the grassland taxa, there is a noteworthy variation between the *P. lanceolata* and Poaceae values in the cow samples. The *P. lanceolata* pollen values in the day 4 samples are remarkably lower than those in the day 1 samples. The pollen from *C. vulgaris* (3.9–9.8%) comes from patches of grassy heathland located in the western and southern areas of the sampled grassland.

Discussion

Comparison Between the Dung Samples and the Vegetation

This study explores the effectiveness of using dung from hay-fed livestock in order to reconstruct the surrounding standing vegetation, as opposed to using archaeological dung to study prehistoric farming methods (Karg 1998; Akeret *et al.* 1999). With this objective in mind, three main factors are relevant for fully understanding vegetation reconstruction: vegetation, hay and dung. Hay as such has not been the subject of this study, primarily because it is rarely encountered in archaeobotany. Moreover, it would require a considerable amount of extra lab work and substantial extra discussion, which is beyond the scope of this paper. We recommend it be the topic of future studies.

The dung samples of both sheep and cattle correspond well with the vegetation as recorded in the field (Table 4). In Table 4, we chose to merge *R. acris/repens* for the vegetation category, although they were mostly identified to the species level in the vegetation. We assumed that *Rhinanthus* in the seed samples most likely represents *Rhinanthus*

angustifolius and that *Cirsium* represents *Cirsium palustre*, in accordance with the sampled vegetation. This results in a total of 35 taxa.

Twelve of these taxa were found in the vegetation, the cow dung samples and the sheep pellets. Of these, *A. odoratum*, *P. lanceolata* and *R. acris/repens* are found in almost all samples. These three taxa possess relatively large, easily identifiable seeds – as do most of the taxa that were so ubiquitously present. *G. palustre*, less frequent in the vegetation than in the cow dung samples, stands out in terms of its ecology and growth form. Its small fruits do not occur in spikes, like they do in most grasses in this experiment (see also Fig. 10) and in *P. lanceolata*. Nor are its multiple fruits implanted into the receptacle of one flower, like they are in *Ranunculus* species (Cappers and Bekker 2013). Whereas Poaceae, *P. lanceolata* and *Ranunculus* would potentially result in the consumption of about 30 seeds in a single bite, for *G. palustre* this would be only two seeds (numbers from LEDA, Kleyer *et al.* 2008). This difference in growth form is probably at least as significant for understanding the seed composition in dung as is seed production.

Seed counts are highly problematic for additional reasons. Using seed production to address the ratio between taxa in actual vegetation is problematic because of the high interspecific variability among samples. Moreover, seed production is already highly variable at the intraspecific level, influenced by such factors as differences in reproductive allocation and effort (Bazzaz *et al.* 1992), pollination failure (Fenner 1985) and pre-dispersal seed predation (Crawley 1992).

Alopecurus is occasionally found in the cattle and sheep dung samples, but has not been witnessed in the standing vegetation. *C. ovalis* is found in the dung samples in both high frequency and high numbers. This species is known to occur in grasslands like the ones that were part of this study but to disappear through ongoing oligotrophication of hay fields (Weeda *et al.* 1994, 334–335). In combination with the incidental finds of ruderal plants and even some rachis fragments of barley (*H. vulgare*), these finds indicate either that the grassland was more nutrient-rich when the hay was cut or, more likely, that the hay contained at least some material from richer grasslands.

The presence of *Betula* fruits in the cattle dung samples indicates that such diaspores not only end up in the soil, where they can eventually germinate (Fig. 5), but also easily become attached to the standing vegetation. In this way, they become part of the diaspore composition of hay and thus part of the dung. They do not relate to the specimens in the field (such as shown in Fig. 5), as these seedlings would not be fruiting yet. The morphology of *Betula* fruits allows them to be transported over great distances. In palaeolimnological studies, they are a

prime example of one of the few taxa usually found near the centre of deep lakes (Birks 1973, 180). In other words, the adhesion of seeds to upright plants should also be considered for species with diaspores that are not equipped for adhesion – for example, needles or the bristle-shaped pappi in the Asteraceae family.

As shown in Tables 1 and 4, most of the taxa that were identified in the relevés but not retrieved from the dung were present in low abundance and frequency in the standing vegetation. Other factors influencing this ‘lack of visibility’ are seed size – for example, in *Dactylorhiza majalis* subsp. *majalis* (because the microscopic seeds of most orchids pass through the smallest sieves used in this study) – and lack of seed production due to the phenophase of the plant (*Quercus*; see Fig. 5). There are also taxa, such as *Trifolium*, whose absence in the samples is more surprising. In our experience, this member of the Pea family is highly appreciated by grazing animals, and its diaspores (seed embedded by fruit and calyx) are generally easy to identify.

A prime difference between the cattle dung and the sheep dung is the lower presence of larger seeds in the sheep pellets. This difference is in line with the findings by Wallace and Charles (2013), who observed that relatively few seeds exceeding 2.0 mm were recovered from the sheep dung intact. Note that hardly any residue remained on the 2.0 mm sieve (Fig. 9) and that relatively large diaspores, such as the seeds produced by *P. lanceolata* or the fruits of *R. acris/repens*, were indeed found in lower numbers in the sheep pellets than in the cow dung (Tables 2 and 3). Owing to the fact that fragments of seeds can also mostly be identified to species level, these do not

cause differences between the combined sheep samples and the combined cattle samples on the presence/absence level (Table 4).

The main differences between the cattle and sheep samples are in taxa that have been found in only low numbers and frequencies in the cattle dung as well, such as *Betula*, *Cerastium fontanum* and *C. album*.

The variety of dominant taxa within the combined sheep samples and the combined cattle samples, respectively, emphasises a remarkable effect. Despite the fact that the hay had been cut, turned over several times in the field, wrapped, consumed by the animals, and sieved over a stack of sieves, the plant dispersal units still tended to retain a form of clustering. By ‘a form of clustering’ we mean that despite all the taphonomic potential mixing processes mentioned above, the composition of the dung had not yet reached a point where the ratios among the dominant taxa were more or less the same.

The results from the pollen samples are very consistent with those from the seed samples. ‘Type’ identifications for *P. lanceolata*, *R. acris* and *R. acetosa* probably pertain to these respective species. The high numbers of Poaceae pollen correspond well with *A. odoratum*, *Poa*, *Cynosurus cristatus* and *H. lanatus* in the standing vegetation. An increase in the *P. lanceolata* values for samples C1.4 and C2.4 can also be observed in the seed samples. The results fit very well with the vegetation pattern beyond the sampled grassland as established through the RSAP survey, which was characterised as open to semi-open. The variation in AP values may be explained by differences in the origin of the hay, with the higher AP percentages coming from the east (forest edge) side of the grassland. It is an important finding that the pollen

Figure 9 Relative proportion of total amount of organic residue by sieve aperture size. C, cattle; S, sheep. Black, 2.0 mm sieve; grey, 1.0 mm sieve; white, 0.5 mm sieve.

Table 3 Number of diaspores per sample in sheep pellets from three sheep (S1, S2 and S3) sorted on ubiquity and within that alphabetically*

Taxon	Plant part	S1.1	S1.2	S2.1	S2.2	S3.1	S3.2
<i>Poa</i>	Fruit	68.2	43.3	162.6	57.6	55.5	30.8
<i>Poa</i>	Floret	72.1	15.2	38.4	12.0	21.7	10.6
<i>Anthoxanthum odoratum</i>	Fruit	6.4	7.7	2.4	11.4	4.9	16.9
<i>Anthoxanthum odoratum</i>	Floret	5.4	8.0	4.0	4.0	1.0	1.5
<i>Juncus effusus</i>	Fruit	13.0	3.0	15.4	5.8	8.0	
<i>Carex ovalis</i>	Fruit and utricle	13.3	1.7	16.3		9.0	1.8
<i>Ranunculus acris/repens</i>	Fruit		2.0	1.0	1.5	0.7	0.7
<i>Plantago lanceolata</i>	Fruit	4.0	5.0	2.0	4.0	2.0	
Musci	Vegetative part	x	x		x	xx	xx
<i>Festuca</i>	Floret		1.0	2.0	1.0	2.0	1.0
<i>Plantago lanceolata</i>	Seed	7.2		1.0	2.0	3.0	
<i>Galium palustre</i>	Fruit	1.8		2.0			
<i>Rhinanthus</i>	Seed			1.0			1.0
<i>Holcus lanatus</i>	Floret				1.0		1.8
<i>Alopecurus</i>	Floret				1.0		
<i>Cynosurus cristatus</i>	Infructescence				1.0		
<i>Cynosurus cristatus</i>	Fruit				1.0		
<i>Rumex acetosa</i>	Fruit				2.8		

*The branches of Musci have been quantified into two categories: x, some; xx, many.

Table 4 Comparison of standing vegetation (v), cattle dung samples (c), and sheep dung samples (s) on a presence/absence level*

Taxon	Vegetation	Cow dung	Sheep dung	cnt.
<i>Anthoxanthum odoratum</i>	*	*	*	31
<i>Plantago lanceolata</i>	*	*	*	29
<i>Ranunculus acris/repens</i>	*	*	*	29
<i>Poa</i>	*	*	*	24
<i>Juncus effusus</i>	*	*	*	21
<i>Carex ovalis</i>	*	*	*	18
<i>Holcus lanatus</i>	*	*	*	17
<i>Rhinanthus angustifolius</i>	*	*	*	17
<i>Galium palustre</i>	*	*	*	16
<i>Rumex acetosella</i>	*	*	*	15
<i>Cynosurus cristatus</i>	*	*	*	13
<i>Festuca pratensis</i>	*	*	*	13
<i>Leontodon autumnalis</i>	*	*	*	16
<i>Cirsium palustre</i>	*	*	*	14
<i>Cerastium fontanum</i>	*	*	*	8
<i>Betula</i>	*	*	*	6
<i>Alopecurus</i>	*	*	*	7
<i>Dactylorhiza maj. maj.</i>	*	*	*	4
<i>Cardamine pratensis</i>	*	*	*	3
<i>Hypochaeris radicata</i>	*	*	*	3
<i>Trifolium pratense</i>	*	*	*	3
<i>Trifolium repens</i>	*	*	*	3
<i>Agrostis capillaris</i>	*	*	*	2
<i>Deschampsia cespitosa</i>	*	*	*	2
<i>Quercus</i>	*	*	*	2
<i>Bellis perennis</i>	*	*	*	1
<i>Luzula campestris</i>	*	*	*	1
<i>Phragmites australis</i>	*	*	*	1
<i>Ranunculus flammula</i>	*	*	*	1
<i>Rubus fruticosus</i>	*	*	*	1
<i>Hordeum vulgare</i>	*	*	*	2
<i>Eleocharis palustris</i>	*	*	*	1
<i>Atriplex</i>	*	*	*	1
<i>Chenopodium album</i>	*	*	*	1
<i>Prunella vulgaris</i>	*	*	*	1

*The taxa are ordered in groups. Group 1, v + c + s; group 2, v + c; group 3, c + s; group 4, v; group 5 = c.

samples from dung in this experiment seem to correspond quite well with surface samples from comparable landscapes (see Groenman-van Waateringe 1986).

Implications for Archaeological Vegetation Reconstruction

The comparison between the standing vegetation and the dung samples, in terms of both seeds and pollen, as presented above, specifically deals with the degree of similarity between the samples. This experiment was set up in order to see to what extent these samples would lead to a correct reconstruction of the vegetation.

There are several ways to approach vegetation reconstruction, ranging from loose descriptions to a comparison with detailed descriptions of present day plant communities (Schepers *et al.* 2013). Loose descriptions are mostly based on the botanical knowledge of the archaeobotanical analyst, which would undoubtedly lead to the identification of a grassland here. If we take a standard system for ecological groups for the Netherlands as a reference (Arnolds and Van der Maarel 1979), both the vegetation relevés and the dung samples are dominated by species from eutrophic soils (category 2a) and manured grasslands (5a). The tree signal is only poorly represented in the seed samples, by the presence of *Betula* fruits, whereas the heathlands are absent. It is only the combination of the pollen and the seed analysis that leads to a rather complete reconstruction of both local (the meadow) and regional vegetation.

Very detailed vegetation reconstruction of the hay land is more easily executed based on the cow dung than on the sheep pellets, especially when trying to match the results of the analysis to present-day plant communities. This is because in plant communities, the combination of taxa is of high relevance, whereas in standard ecological grouping, the individual characteristics of a taxon are leading. A higher number of species will therefore lead to a more reliable reconstruction.

General Conclusions

In general, this study has shown that on the presence/absence level, dung produced by hay-fed animals is very well suited for a reconstruction of local vegetation through the analysis of seeds and pollen. Seed counts, however, should be used with caution. As this study shows, they can be highly variable and are not necessarily directly related to the ratios among taxa in the standing vegetation. The seed counts should therefore not be used to calculate the absolute ratios among taxa in vegetation. A relevant interpretation based on the seed counts that does seem valid, however, is that the source vegetation must have been patchy, as was found to be the case in the vegetation relevés. The ratio among seeds from dung samples is likely to be

Figure 10 *Cynosurus cristatus* in different phenophases in relevé 1. From left to right: flowering, withered, and fruiting.

the result of a mixture of patches with different ratios for taxa that are present in both.

That pollen and seeds are produced and dispersed in different phenophases of a plant considerably influences the botanical content of the dung. With specific regard to hay, late seed setters, in particular, are less likely to be in seed at the time of year when hay is typically harvested (although we acknowledge that this timing is also determined by the decisions of farmers). To a lesser extent, this also goes for early seed setters. Moreover, the different phenophases do not happen simultaneously for all individuals (Fig. 10).

Most dung-vegetation experiments in ecology focus on free-ranging animals and on seed germination. As a vehicle for plant dispersal, cattle dung will definitely be better suited than sheep dung, at least as far as relatively big seeds are concerned. Moreover, at least in cattle, diarrhoea tends to have a positive effect on the seed survival rate. The archaeological relevance of this observation is limited to the fact that it emphasises once more that there are many uncontrollable and probably unrecognisable factors that determine the composition of dung, especially in relation to seed counts.

A future experiment would require better control of the exact source of all hay and, ideally, a comparison with dung from livestock grazing on standing vegetation in the same location. Despite the limitations of this study, we believe that analysing the botanical content of dung from animals fed with hay provides a good picture of the source grassland.

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Appendix A

Sample name Number (N) and percentage (%)	C1.1 N	C1.1 %	C1.4 N	C1.4 %	C2.1 N	C2.1 %	C2.4 N	C2.4 %	S1.1 N	S1.1 %	S1.2 N	S1.2 %
Totals												
Arboreal pollen (AP)	80	17.4	30	6.7	66	13.8	45	6.9	59	20.3	15	5.7
Non-arboreal pollen (NAP)	379	82.6	421	93.3	414	86.3	603	93.1	232	79.7	250	94.3
Total pollen count (AP + NAP)	459	100.0	451	100.0	480	100.0	648	100.0	291	100.0	265	100.0
Pollen concentration N/ml (AP + NAP)	45.090		35.874		26.073		45.727		65.616		78.987	
Trees and shrubs												
<i>Betula</i>	16	3.5	8	1.8	16	3.3	15	2.3	21	7.2	5	1.9
<i>Alnus</i>	25	5.4	8	1.8	15	3.1	13	2.0	24	8.2	5	1.9
<i>Carpinus betulus</i>	1	0.2		0.0		0.0	1	0.2		0.0		0.0
<i>Corylus</i>	9	2.0	7	1.6	10	2.1	4	0.6	3	1.0	1	0.4
<i>Fagus</i>	1	0.2		0.0		0.0	1	0.2	2	0.7		0.0
<i>Fraxinus excelsior</i> -type	1	0.2		0.0	1	0.2	1	0.2		0.0		0.0
<i>Juniperus communis</i> -type	2	0.4		0.0		0.0		0.0		0.0		0.0
<i>Pinus</i>	9	2.0		0.0	5	1.0	4	0.6	3	1.0	1	0.4
<i>Quercus</i>	15	3.3	4	0.9	16	3.3	4	0.6	5	1.7	3	1.1
<i>Salix</i>		0.0		0.0	1	0.2		0.0		0.0		0.0
<i>Sorbus</i> -group		0.0	1	0.2		0.0	2	0.3		0.0		0.0
<i>Tilia</i>	1	0.2	2	0.4	1	0.2		0.0	1	0.3		0.0
<i>Ulmus</i>		0.0		0.0	1	0.2		0.0		0.0		0.0
Cultivated plants												
<i>Hordeum/Triticum</i> -type	1	0.2		0.0	2	0.4	1	0.2		0.0	1	0.4
<i>Secale</i>	1	0.2		0.0		0.0	1	0.2		0.0		0.0
Grassland												
Asteraceae liguliflorae	12	2.6	67	14.9	14	2.9	105	16.2	5	1.7	90	34.0
<i>Filipendula</i>		0.0		0.0		0.0		0.0	1	0.3	1	0.4
<i>Plantago</i>	1	0.2		0.0		0.0	3	0.5		0.0		0.0
<i>Plantago lanceolata</i> -type	60	13.1	150	33.3	98	20.4	244	37.7	56	19.2	82	30.9
Poaceae	230	50.1	165	36.6	223	46.5	211	32.6	125	43.0	59	22.3
Poaceae >40 µm	2	0.4		0.0		0.0		0.0	2	0.7		0.0
<i>Ranunculus acris</i> -type	16	3.5	8	1.8	13	2.7		0.0	5	1.7	1	0.4
<i>Rumex acetosa</i> -type	1	0.2	4	0.9	4	0.8		0.0	1	0.3	1	0.4
<i>Rumex acetosella</i>	1	0.2	1	0.2		0.0		0.0	1	0.3		0.0
<i>Succisa</i> -type		0.0		0.0		0.0		0.0		0.0	1	0.4
Ruderals and weeds												
<i>Artemisia</i>	3	0.7		0.0		0.0		0.0		0.0		0.0
Chenopodiaceae pp		0.0		0.0	1	0.2	1	0.2		0.0		0.0
<i>Urtica dioica</i> -type	2	0.4	5	1.1	4	0.8		0.0	3	1.0		0.0
Fen and heathland												
<i>Calluna vulgaris</i>	37	8.1	18	4.0	47	9.8	25	3.9	23	7.9	11	4.2
<i>Erica tetralix</i> -type		0.0	1	0.2		0.0		0.0		0.0		0.0
Ericaceae	3	0.7	1	0.2		0.0	5	0.8	1	0.3	1	0.4
<i>Myrica gale</i>		0.0		0.0		0.0	2	0.3		0.0		0.0
<i>Sphagnum</i>	3	0.7		0.0		0.0	2	0.3	6	2.1		0.0
<i>Dryopteris</i> -type		0.0		0.0		0.0		0.0		0.0	1	0.4
Nonspecific ecology												
Cyperaceae		0.0		0.0	2	0.4		0.0		0.0	1	0.4
Apiaceae		0.0		0.0	1	0.2		0.0		0.0		0.0
Asteraceae tubuliflorae		0.0		0.0	1	0.2		0.0	2	0.7		0.0
Brassicaceae	3	0.7		0.0	1	0.2	2	0.3		0.0		0.0
<i>Carduus/Cirsium</i>		0.0		0.0	1	0.2	1	0.2		0.0		0.0
Fabaceae pp	1	0.2		0.0		0.0		0.0		0.0		0.0
Rubiaceae	2	0.4	1	0.2	2	0.4		0.0	1	0.3		0.0
Not identifiable	6	1.3	5	1.1	14	2.9	10	1.5	8	2.7	4	1.5

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