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Response of vegetation and soil ecosystem to mowing and sod removal in the coastal dunes 'Zwanenwater', the Netherlands

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Abstract. This paper investigates the effects of mowing and sod removal on vegetation, soil mesofauna and soil profile, and the restoration of these features in the years following sod removal. The sampling site is located in a primary wet dune slack in the northern part of the province of North-Holland. The original vegetation is a heathland with *Empetrum nigrum* and *Calluna vulgaris*, underlain by a Gleyic Arenosol with an O, Ah and (B) horizon development. Above-ground, the vegetation in the dune slack has been mown since 1940. The sod was removed from restricted areas in the slack at various times in the past (1980, 1985, 1987 and 1991).

All three sources of data point to adaptation to wet conditions after mowing and sod removal. The vegetation of the mown area is related to the vegetation in the original heathland, although some species appear to have disappeared. Below-ground, mowing drastically reduces the number and depth of occurrence of microarthropoda. Restriction of depth applies also to the Enchytraeidae. Soil profile development is restricted to an Ah-AC-Cr sequence.

Species diversity both above and below-ground is relatively high in plots where the sod has recently been cut, due to the rapid colonization by the first pioneer species. A time series for the vegetation is difficult to establish because hydrological conditions interfere with years since sod removal. Soil profile evolution after sod cutting is poor but consistent, from an AC-Cr sequence since 1991, to an O-Ah-Cr sequence since 1980.

The management practices were set up with the intention to interrupt the succession to give pioneer species a chance. Neither the vegetation, nor the soil fauna or soil profile have fully recovered during the 13 yr since the first sod removal. So the goal has been reached.

Keywords: Biodiversity; Dune slack; Soil mesofauna; Soil micromorphology.

Nomenclature: For vascular plants van der Meijden et al. (1990); for bryophytes: Gamasina: Karg (1993), Enchytraeidae: Nielsen & Christensen (1959); for soil mesofauna: Corley et al. (1981).

Introduction

Mowing and sod removal are accepted management practices in nature conservation in the Netherlands. They are chosen to restore vegetation types which have suffered from land use changes or environmental deterioration. In the dunes, those two management measures were introduced to re-establish early successional stages and natural, dynamic features of dune ecosystems. The underlying principles of the two measures are different. The aim of mowing is to open the canopy and give the lower vegetation types an advantage over the higher types in the struggle for light, space, nutrients and water (Anderson & Romeril 1992). Sod removal aims at interrupting the succession to give pioneer species a chance. Sod removal is much more drastic than mowing because it truncates the soil profile and destroys practically all soil life.

The aim of this paper is to report on the ecological changes following mowing and sod removal and subsequent restoration of the soil ecosystem in the course of time. Three aspects of the ecosystem have been studied: vegetation, soil fauna and soil profile. These aspects are interdependent. Plants affect the soil ecosystem by uptake and release of organic and inorganic material and by enmeshment of soil particles. Mycorrhiza (Goss 1987), soil fungi and soil microflora have the same effects. Roots and fungal hyphae are important for the formation of aggregates (Molope et al. 1987). Plants and fungi change the soil texture and structure also indirectly by interacting with soil micro and mesofauna (Parkinson et al. 1967; Fitzpatrick 1984).

Dune sands harbour a very diverse soil life. Soil animals may be grouped e.g. by their size (micro, meso and macrofauna: < 0.2 mm, 0.2-4 mm, > 4 mm, respectively), or by their feeding habits. The majority of soil animals feeds on dead plant material (detritus), fungi and bacteria, with a possible preference for certain foodstuffs. Enchytraeidae, small whitish relatives of the earthworms, Oribatei (moss mites) and most Collembola belong to this guild. Particularly from the diverse group of the mites (Acari) many predators are known, like the Gamasina, a systematic division of the Acari. Micro and mesofauna contribute to the function and stability of the soil ecosystem by feeding and excreting, macrofauna also by burrowing (Webb 1977). Further, they affect aggregate formation and formation or restructuring of pores (Seastedt 1984). Plants have a species-specific influence on soil fauna, by their rhizosphere, by effects on soil micromorphology (Babel & Krebs 1991) and by control of the microclimate (Koehler & Born 1989). For the present study, mesofauna living in air-filled soil pores (microarthropods) and in the water film of the pores (Enchytraeidae) was analyzed in more detail.

We were very lucky to be offered an area where experiments with mowing and sod removal have been carried out within a restricted space at various times in the past. This enabled us to compare the two sides of the coin: how was vegetation development above-ground, and what happened to soil life and the soil profile below-ground. The interdisciplinary study reported here is a contribution to the understanding of a characteristic dune ecosystem and to the development of strategies for an ecologically sound and sustainable dune management.

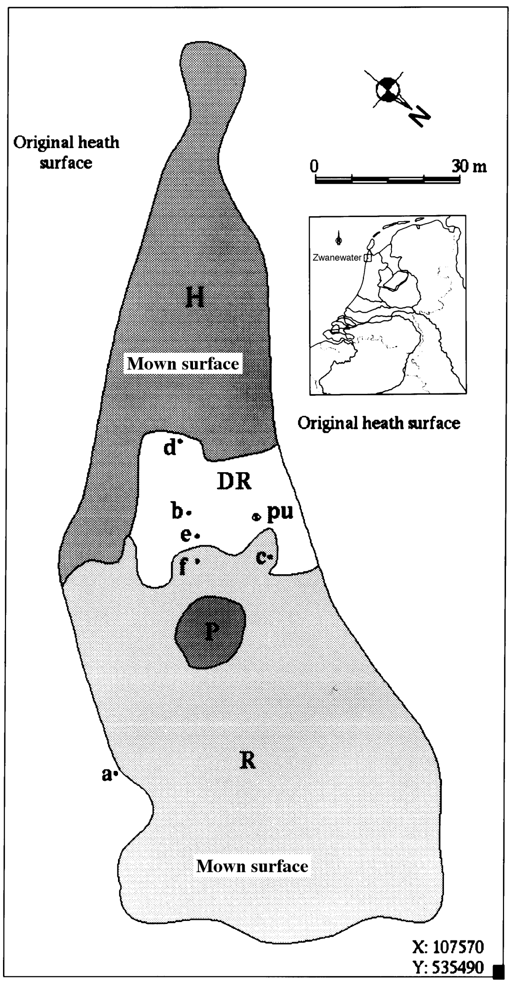

Fig. 1. Location of plots and profiles a to f in the Zwanenwater dunes, Callantsoog, the Netherlands. Legend: a = original heath surface, b = mown heath surface; plot name with sod removed in year: c: 1991, d: 1987, e: 1985 and f: 1980. P = semi-permanent pool; R = vegetation with *Phragmites australis* and *Carex* spp.; DR = vegetation with *Calamagrostis epigejos*; H = vegetation with *Erica tetralix*. PU = location of the piezometer no. 2 of the Department of Environmental Research, University of Utrecht. The black square in the right bottom corner shows the map coordinates.

Site description

The 'Zwanenwater' dunes are owned by the 'Vereniging Natuurmonumenten'. They are situated in the coastal dunes of the northern part of the province North-Holland. When the Heersdiep, an estuary of medieval times, silted up, a sanddike could be constructed in 1793 which connected the mainland with the Wadden Islands Oghe and Huisduinen. To the west of this 'Johan van Oldenbarneveldtdijk' a series of closely spaced sanddikes and dune ridges was formed, with height differences of 5 to 30 m between ridges and slacks (Klijn 1981).

The sampling site is very well suited for the purpose of this research because the places where the sod has been removed are confined to a limited area (Fig. 1). The site is located south of Callantsoog, in a primary wet dune slack between the Johan van Oldenbarneveldtdijk and the sea. The sand is well sorted, non-calcareous and with a modal value of 100-250 µm. Patchy occurrence of thin aeolian layers in the soil testifies to the occasional influx of aeolian sand.

Except for very rainy periods, the groundwater level is below the surface of the sample plots most of the time, but varies in depth throughout the year. Groundwater fluctuations at location PU of Fig. 1 were measured by mrs. drs. A.C.D. Ertsen of the ITORS Research Group for 3 yr. Fig. 2 is based on these measurements. The fluctuations reflect the response of the groundwater level to rainfall and to seepage water from the surrounding dunes. The groundwater reaches the surface in a semi-permanent pool (P) in the lowest part of the dune slack (Fig. 1). It is noteworthy that the temporal differences in groundwater level (Fig. 2) are much larger than the differences in height within the investigated part of the dune slack (see 'Sample plots' below).

The original vegetation and soil are characteristic of the dunes of the Dutch mainland north of Bergen, where the $CaCO_3$ content of the sand is low or zero as in our case. The average annual rainfall at the nearby meteorological station Den Helder is 752 mm. The mean temperature is 15.7 °C in summer and 3.1 °C in winter. The

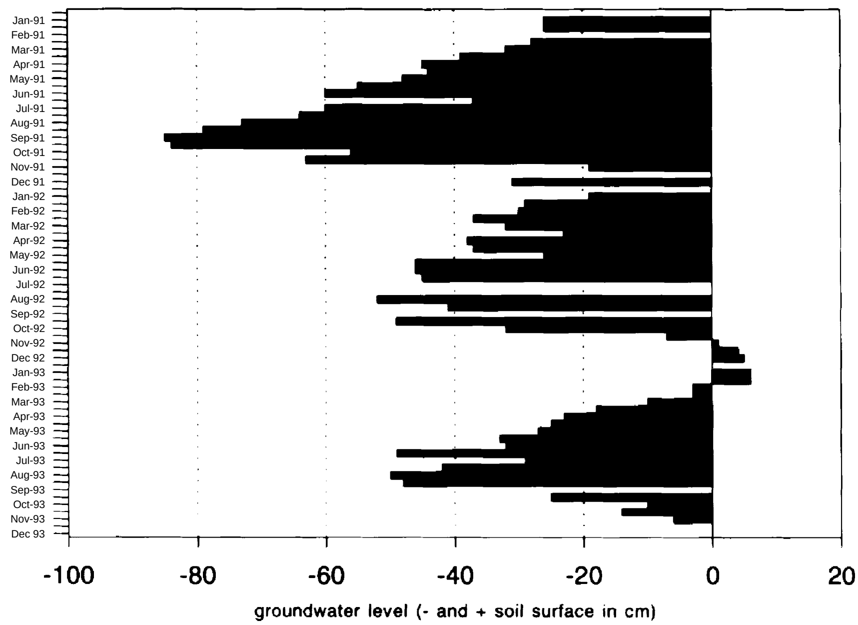

Fig. 2. The fluctuations of the groundwater level at location PU of Fig. 1 (A.C.D. Ertsen, pers. comm. 1994).

dry area surrounding the dune slack is occupied by heathland with *Empetrum nigrum* and *Calluna vulgaris*, together with some *Calamagrostis epigejos*. The original soil of the sampling site was formed under the heath. It is a Gleyic Arenosol according to the FAO/UNESCO soil classification (Anon. 1989), with a thin organic horizon overlying an Ah horizon and a few cm thick incipient spodic horizon (Fig. 3, Plot a). The original dune sand is encountered at a depth of 10 to 20 cm. The subsoil is wet during most of the year. Regarding the general absence of iron segregation in thin sections, this reduced material was interpreted as a Cr horizon. The brown mottles observed in the field are probably clusters of humicol, organic fecal pellets or root mass.

Sample plots

Samples for studying the effect of mowing have been taken near to each other on both sides of the boundary between the original heath and the mown interior of the slack (Fig. 1). The places where the sod was removed are closely spaced within the central part of the slack. The plots are listed below, with height above Ordnance Datum (N.A.P.) in brackets.

Plot a: the original heath surface (3.03 m);
Plot b: irregularly mown since 1940, and yearly since 1973 (2.96 m);
Plot c: sod removed in September 1991 (2.88 m);
Plot d: sod removed in January 1987 (2.88 m);
Plot e: sod removed in November 1985 (2.86 m);
Plot f: sod removed in September 1980 (2.84 m).

Methods

It is one of the characteristics of multidisciplinary research that data are collected and analysed in very different ways. For example, the sampling design for the vegetation survey allows for statistical analysis, but the soil-zoological and micromorphological analyses are too time-consuming to provide the necessary quantitative data. Fecal pellets are an important item of micromorphological research, but their allocation to a specific faunal species is evidently more difficult than determining the presence of that species in soil zoological research. For instance, Babel & Vogel (1989) have shown that discrimination between excrements of Enchytraeidae and Collembola is not possible.

However, the differences in approach are dictated not only by the adopted method and the nature of the research objects, but also by traditions prevailing in the discipline. Further there are practical implications: samples for micromorphological analysis are taken in soil pits and can therefore coincide with soil horizons (Fig. 3, Table 3) whereas samples for soil zoology analysis are taken from an auger which requires sampling at predetermined standard depths (Table 2). The depth of 0-4 cm corresponds only roughly with the Ah horizon which is the main expression of soil profile development in these young soils.

The choice of a common unit of research is one of the principal prerequisites for interdisciplinary research (de Mas & Jungerius 1987). The common units in this case are the six situations each of which is characterized by a specific management history.

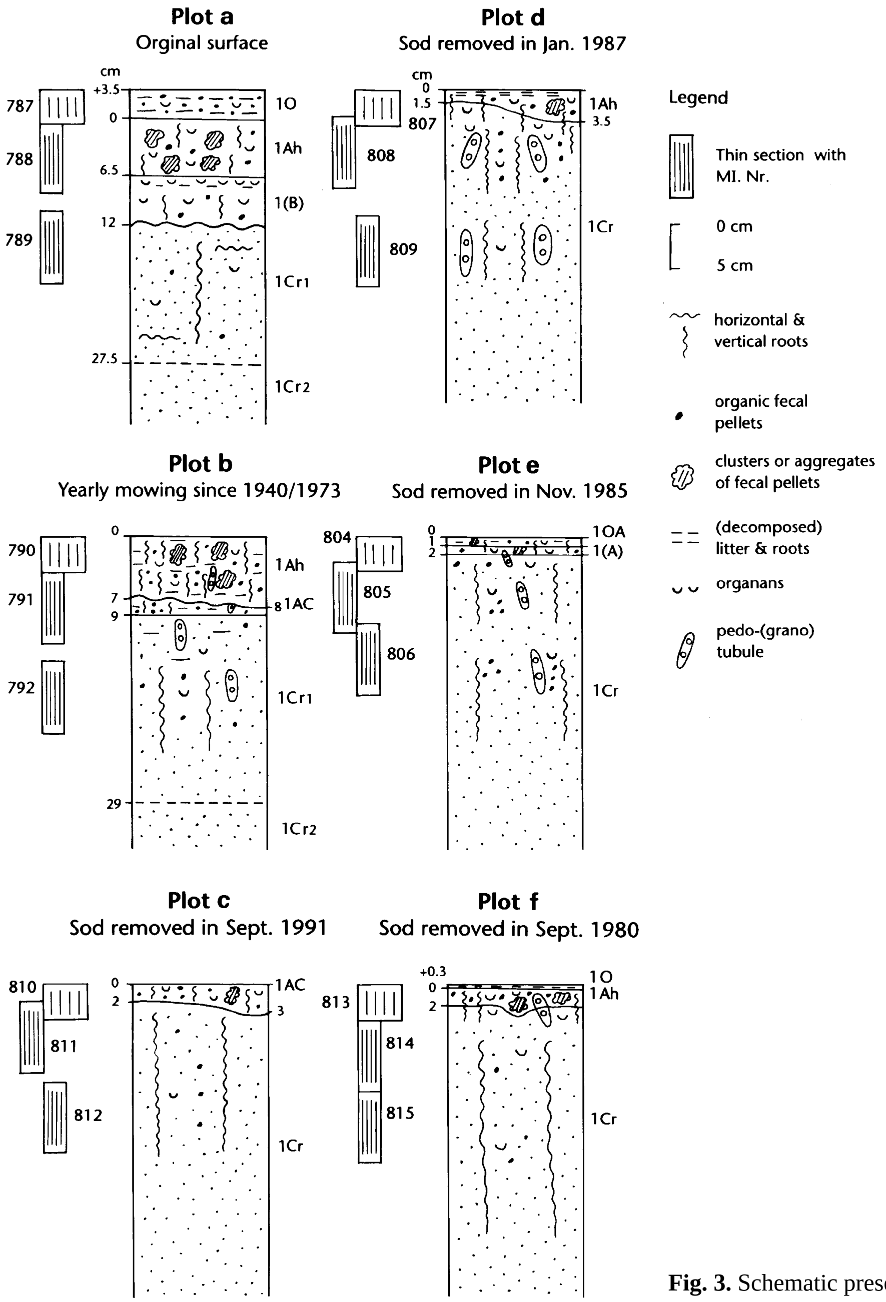

Fig. 3. Schematic presentation of the soil profiles.

Vegetation

The vegetation was analyzed in 21 locations. Three of these locations were situated in the original wet heath (including Plot a). Sampling of 1 m × 1 m was done pairwise selected in the sod-removal sites and adjacent non-cut control areas which are mown each year: two pairs in the 1991 sod-removal area (including Plot c), four pairs in the 1987 sod-removal area (including Plot d), one pair in the 1985 sod-removal area (including Plot e), and two pairs in the 1980 sod-removal area (including Plot f). The relevés were made in July 1993, according to Braun-Blanquet with cover values of individual species transformed to a scale of 1 to 9 (Westhoff & van der Maarel 1973). Percentage cover of total vegetation and the herb and bryophyte layers were estimated.

Differences in species composition between sod-removal and control plots were analyzed using Correspondence Analysis with standard options, as implemented in the programme CANOCO (ter Braak 1988).

In addition, the correlation of the CA-axes with environmental factors such as sod removal and surface height was analyzed. Species diversity was calculated as N2 diversity which is the inverse of the Simpson index (Hill 1973). Statistical analysis of the effects of sod removal and time since sod removal on vegetation cover and species diversity values were carried out with SAS (Anon. 1985) with general linear models and least square means tests.

Soil fauna

Samples for the analysis of the soil fauna were taken in two ways. For microarthropods two samples were taken per plot, at 0-4, 4-8 and 8-12 cm depth. Cores were taken with a soil corer driven into the soil with a hammer. Sample size is 100 cm^3 for volume, 25 cm^2 for surface, and 4 cm for height. Abundances are given as individuals per sample; m^2-values for comparison with literature data can be obtained by multiplying the abundances with 400.

For Enchytraeidae, soil blocks about 15 cm × 15 cm and 20 cm deep were taken with a spade and brought to the laboratory. From these blocks one soil core per site was used for quantitative analysis (depth, sample size and data presentation as for microarthropods). In the remaining material the last author identified the Enchytraeidae species. This material was not suitable for stratified sampling. Species abundances are given as classes.

Soil microarthropods were sampled from the soil by dry dynamic extraction according to MacFadyen (for details see Koehler 1984). Enchytraeidae were extracted with a wet procedure after O'Connor with modifications (Born 1993). The two extraction methods are not suitable for very small soil animals (Protozoa, Rotatoria, Nematoda) and large animals (Lumbricidae, insect larvae, Diplopoda, Formicidae). The efficiency for Harpacticidae (Crustacea) is unknown.

Microarthropods and Enchytraeidae were counted under the binocular. Gamasina species were identified for all samples. Enchytraeidae species were identified in the Institut für Angewandte Bodenbiologie GmbH, Hamburg. In spite of methodological shortcomings, findings of Nematoda (estimates after counting a fraction) and other soil animals were noted. Because of small sample sizes, no statistics were applied and emphasis is put on qualitative information.

Soil micromorphology

For soil profile descriptions, small pits about 50 cm deep were dug at each of the six sampling plots. The profiles were described following the FAO (Anon. 1977) Guidelines (App. A) and checked with the thin section analysis. Fig. 3 shows a schematic representation of the soil profiles, with a revised horizon designation based on combined field and laboratory evidence. The same pits were used for sampling undisturbed soil for micromorphological purposes. Three vertical soil samples were taken from each profile. The thin sections are about 8 cm × 6 cm in size, and about 20 μm thick. The thin sections were prepared according to the methods described by Jongerius & Heintzberger (1975) and analyzed microscopically, mainly using the terminology of Brewer (1976) unless otherwise stated. Concerning the micromorphological terminology and definitions only the frequently used terms in this paper are explained.

Humiskel: organic residues that are essentially undecomposed or chemically preserved (Barratt 1969);
Humicol: strongly decomposed organic residues of colloidal size (Barratt 1969);
Organan: coating of humicol on grains or walls of voids;
Pedotubule: a pedological feature consisting of soil material with a tubular external form, with relatively sharp boundaries (Brewer 1976).

The terrain elevations were measured with a SOKKIA tachymeter, using the SET4B Electronic Total Station.

Results

The results of the three ecosystem components are described separately in this section. As in all truly integrated research, a balance has to be found between the amount of information that each participant feels is expected in his or her discipline, and the much smaller amount of information that can be processed in a multidisciplinary approach. An attempt to integrate the information with emphasis on the temporal aspect, i.e. the changes in the course of time after sod removal, is made in the discussion.

Vegetation

The results of the vegetation survey are summarized in Table 1. The species encountered in the heathland surrounding the dune slack include *Erica tetralix*, *Calamagrostis epigejos, Salix repens, Phragmites australis, Carex nigra, C. arenaria, Hypnum cupressiforme* and *Empetrum nigrum*. The vegetation in the dune slack which has been mown since 1940, shows a gradient from heathland with *Calluna vulgaris*, *Erica tetralix* and *Empetrum nigrum* in the drier parts, towards more

Table 1. Vegetation relevés of the original heath surface and pairs of sod-cut plots and adjacent control plots. Plot type: co = control plot; sr = sod-removal plot. Replicate: similar numbers belong to the same pair of sod-removal/control plots. Plot code: correspondence with the plots used in the soil analyses (Fig. 1). Cover values are based on Braun-Blanquet cover values, transformed to a scale from 1 to 9 (Westhoff & van der Maarel 1973).

Year sod removal	Original surface			1991				1987								1985		1980			
Plot type	co	co	co	sr	co	sr	co	sr	co	sr	co	sr	co	sr	co	sr	co	sr	co	sr	co
Replicate	1	2	3	1	1	2	2	1	1	2	2	3	3	4	4	1	1	1	1	2	2
Plot code	a			c				d								e				f	
Pseudoscleropodium purum	-	6	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lythrum salicaria	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ranunculus repens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-
Carex serotina	-	-	-	6	-	6	-	3	-	-	-	-	-	3	-	5	-	-	-	6	-
Sagina procumbens	-	-	-	-	-	4	-	3	-	-	-	-	-	-	-	4	-	-	-	-	-
Juncus articulatus	-	-	-	5	-	4	-	4	-	3	-	4	-	5	-	5	-	-	-	5	-
Radiola linoides	-	-	-	7	3	4	-	7	-	3	-	5	-	6	-	3	-	-	-	-	-
Ranunculus flammula	-	-	-	3	-	-	-	-	-	-	-	-	-	3	-	-	3	3	-	5	-
Euphrasia stricta	-	-	-	3	-	-	-	3	-	-	-	-	-	3	-	-	-	3	3	5	-
Calliergonella cuspidata	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	4	-	7	-	6	-
Molinia caerulea	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-
Polygala serpyllifolia	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-
Pellia endiviifolia	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-
Rumex acetosella	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-
Cladonia foliacea	-	-	-	-	-	-	-	-	-	3	-	6	-	-	-	-	-	-	-	-	-
Cladonia cf. *furcata*	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-
Eleocharis palustris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	3	-
Festuca ovina	-	-	-	-	3	-	-	2	-	3	5	-	-	-	-	-	-	-	-	-	-
Pedicularis palustris	-	-	-	-	-	3	-	4	-	3	3	-	3	3	-	-		-	-	-	3
Sanionia uncinata	-	-	-	5	-	-	-	6	7	4	3	-	-	-	-	-	-	6	-	-	-
Agrostis stolonifera	-	-	-	3	-	4	-	-	-	3	-	3	-	-	3	5	-	3	3	3	-
Carex panicea	-	-	-	5	6	4	7	5	5	7	5	5	5	6	7	4	6	6	6	6	-
Erica tetralix	7	-	6	5	6	-	5	7	8	8	8	5	9	7	7	-	-	3	5	3	6
Carex disticha	-	-	-	-	-	-	-	3	4	-	-	-	-	-	-	-	-	5	-	-	-
Calamagrostis epigejos	8	8	8	5	4	-	7	4	5	3	5	4	5	5	7	-	6	5	6	5	6
Hydrocotyle vulgare	-	-	-	6	6	4	7	3	3	3	3	3	3	3	-	4	6	6	6	6	6
Potentilla erecta	-	4	-	8	6	3	6	4	6	5	5	5	6	6	7	3	6	3	6	3	6
Salix repens	4	6	2	6	8	4	7	3	8	3	8	-	6	-	7	5	7	8	8	8	6
Galium palustre	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
Holcus lanatus	-	-	-	3	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lotus uliginosus	-	-	-	3	3	-	-	3	-	-	-	-	-	3	-	-	3	-	3	3	3
Galium uliginosum	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	3	3	4	5	-	3
Phragmites australis	2	2	4	-	-	4	5	-	-	-	-	-	-	-	-	-	-	5	5	4	6
Carex nigra	2	-	2	-	6	-	7	-	-	-	-	-	-	-	6	-	6	7	7	-	6
Luzula multiflora	-	-	-	-	3	-	3	-	-	-	-	-	-	-	2	-	3	-	-	-	6
Poa trivialis	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	6	-	6	-	6
Sieglingia decumbens	-	-	-	-	-	-	3	-	-	-	-	-	3	-	-	-	-	-	-	-	-
Mentha aquatica	-	-	-	-	-	3	6	-	-	-	-	-	-	-	-	-	6	-	6	-	6
Lycopus europaeus	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	3	-	6	-	3
Dicranum scoparium	-	-	3	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
Pohlia nutans	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
Cirsium palustre	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-
Genista sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-
Prunella vulgaris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	3
Leontodon saxatile	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
Rhinanthus minor	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-
Trifolium repens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
Empetrum nigrum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carex arenaria	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hypnum cupressiforme	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

moist vegetation with *Carex* spp. and *Salix repens* towards the pool in the centre of the valley.

Twinspan analysis suggests that the original heathland is related to the adjacent control in the mown area where the sod was not removed. The exception is formed by *Carex arenaria*, *Empetrum nigrum* and *Hypnum cupressiforme* which are absent in the control plots (Table 1). Species which are generally restricted to the mown control plots are e.g. *Carex nigra*, *Luzula multiflora*, *Poa trivialis* and *Lycopus europaeus*.

The removal of the sod has a clear effect on the species composition of the vegetation (Fig. 4): the vegetation relevés were separated into the sod-removal and the mown control plots along the first axis of the Correspondence Analysis (eigenvalue 0.37). The correspondence with the factor sod cutting ('sodcut') points also in this direction. The plots are further divided along the second axis of the Correspondence Analysis (eigenvalue 0.27). This axis represents the hydrological gradient of the plots, as illustrated by the vector 'height', which is

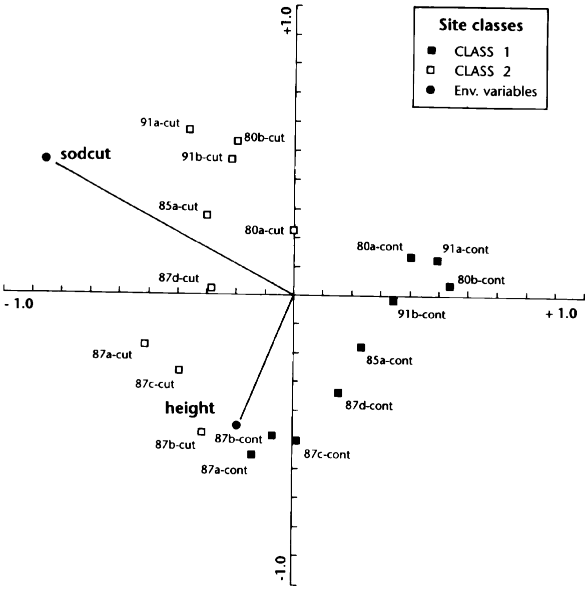

Fig. 4. Correspondence Analysis of vegetation relevés of the Zwanenwater area, classified in two groups: Class 1 = control plots, Class 2 = sod-removal plots. Sod-cut plots and control plots with the same prefix are paired observations of a sod-removal plot of a particular year and its control plot immediately adjacent to the sod-cut area. Environmental variables are: sodcut = sod-removal; height = elevation of the soil surface, representing a measure of soil moisture.

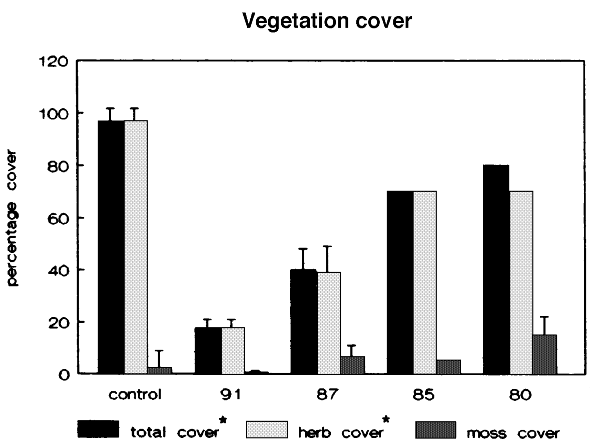

Fig. 5. Cover values of total cover, herb layer and bryophyte layer in sod-removal plots and control plots. Mean values and standard deviations are given; n = 9, 2, 4, 1 and 2 for the control plots and the sod-removal plots of 1991, 1987, 1985 and 1980 respectively. An asterisk indicates significant differences ($p < 0.05$) from the control plot.

the elevation of the surface.

Species that occur primarily in sod-removal plots are *Carex serotina, Sagina procumbens, Juncus articulatus, Radiola linoides, Euphrasia stricta* and *Ranunculus flammula* (Table 1). These are mostly pioneer species occurring under relatively wet conditions. The latter is not surprising considering that the soil surface has been lowered with a few cm. *Carex oederi* and *Juncus articulatus* are restricted to the plots of 1985 and younger.

Summarizing, there are clear differences in species composition between the plots, but the hydrological factor interferes with the response to age since sod removal. The evidence provided by the cover values is more unambiguous. Total cover and herb cover are higher in the control plots in all years of sod-removal (Fig. 5). The cover increases gradually to 80% after 13 yr. Changes in species diversity also occur (Fig. 6). In the recently cut plots species diversity is higher than in the adjacent control plots, but after 13 yr the diversity of sod-removal and control plots are the same.

Soil fauna

Numbers of soil animals recovered from the samples are listed in Table 2. For microarthropods (columns 3 to 8), the mowing effect is drastic, reducing abundances roughly by factor 15-20. This is not the case for Enchytraeidae. The colonization by microarthropods (and Nematoda) is in agreement with the age of the plots after sod removal. Reasons for low Enchytraeidae abundances of Plot b and Plot e are unclear. The findings for other soil animals indicate a colonization of all sites particularly by insect larvae and Nematoda. Occurrence of Harpacticidae suggests more humid conditions in Plot c and Plot d.

The stratified evaluation in the lower part of Table 2 documents a strong decrease of abundances with depth, with the exception of Plot a with its well-developed root system. Oribatei mainly occur in the upper 4 cm. Gamasina, with the exception of Plot a, have been found near the surface exclusively. Surprising are the findings in Plot c where the deeper soil layer yielded considerable numbers of Enchytraeidae.

The analysis of Enchytraeidae on the species level reveals a major impact of mowing and sod removal, partly as a consequence of changes in the humus layer (Fig. 7). Plot a is inhabited by two acid-tolerant species (*Cognettia sphagnetorum* and *Achaeta aberrans*) belonging to the typical community of mor profiles (*Achaeto-Cognettietum*, Graefe 1993). On the other plots, these species are less dominant or absent and substituted by species indicating more or less neutral soil conditions. Compared to mowing, sod removal has a strong effect. The occurrence of *Cognettia glandulosa* as domi-

Table 2. Soil mesofauna individuals per sample (mites, primitive insects, potworms) and other soil fauna (individuals/25 cm^2). Mites: Ac = Acari (Gamasina and Oribatei included); Ga = Gamasina; Or = Oribatei; Primitive Insects: Coll = Collembola (Arthropleona and Symphypleona); Sym = Symphypleona; Prot = Protura; Ench = Enchytraeidae (potworms); Others = Other soil fauna: Nema = Nematoda (estimates); Larv = insect larvae; Various = various soil fauna: Diplo = Diplopoda; Form = Formicidae (ants); Lumb = Lumbricidae (earthworms); Harp = Harpacticidae (Crustacea).

Plot	Depth (cm)	Mesofauna							Others		
		Ac	Ga	Or	Coll	Sym	Prot	Ench	Nema	Larv	Various
a	0 - 12	338	14	6	263	6	1	466	1500	3	Form, Diplo
b	0 - 12	21	2	8	11	5		28	1100		Lumb
c	0 - 12	17		1	1			198	800	3	Harp
d	0 - 12	9	1	3	2			236	700	3	Lumb, Harp
e	0 - 12	8	2	3	7	5		64	600	3	
f	0 - 12	12	3	7	4	3		284	800	1	
a	0 - 4	49.5	11.0	3.0	74.5	5.0	0.5	293.0	500		Form, Diplo
a	4 - 8	199.0	2.5	2.5	180.0	0.5	0.5	100.0	500	2.5	Form
a	8 - 12	89.5			8.0	0.5		73.0	500		
b	0 - 4	18.0	2.0	8.0	9.5	4.5		25.0	500		Lumb
b	4 - 8	1.0			1.0	0.5		3.0	400		
b	8 - 12	2.0			0.5				200		
c	0 - 4	3.0		0.5				160.0	500	3.0	Harp
c	4 - 8	13.5			0.5			14.0	200		
c	8 - 12	0.5						24.0	100		
d	0 - 4	3.5	1.0	2.5	1.5			236.0	500	2.5	Lumb, Harp
d	4 - 8	5.0			0.5				100		
d	8 - 12	0.5							100		
e	0 - 4	6.0	1.5	2.5	6.5	4.5		63.0	500	2.5	
e	4 - 8	1.5		0.5					100		
e	8 - 12	0.5			0.5			1.0			
f	0 - 4	8.5	3.0	4.5	3.0	2.0		284.0	500		
f	4 - 8	2.0		2.0	0.5	0.5			200		
f	8 - 12	1.5		0.5					100		

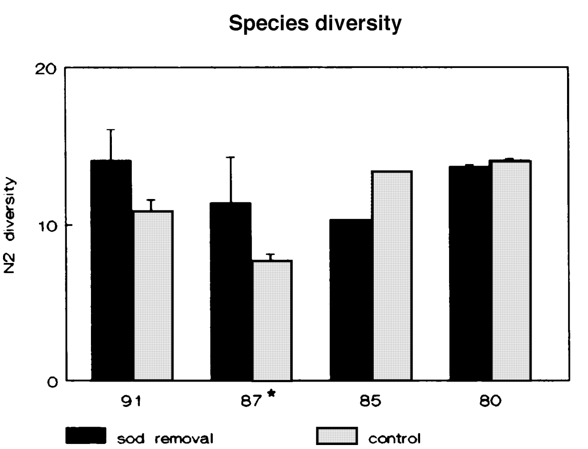

Fig. 6. Species diversity in sod-removal plots and adjacent control plots with respect to different years of sod removal. Mean values and standard deviations are given; n = 2, 4, 1 and 2 for sod removal in 1991, 1987, 1985 and 1980 respectively. An asterisk indicates significant differences ($p < 0.05$) between sod-removal and control plots.

nant species on all sod removal plots and of *Marionina argentea* on Plot c indicates wet conditions, which is partly due to the lowering of the soil surface with a few cm. These wet conditions have consequences for humus form, pH and nutrients. *M. argentea* is found in more or less neutral soils, under humid conditions with decaying plant matter, but also in agricultural soils (Dawod & Fitzpatrick 1993) and in decaying sea weed on the shore (Nielsen & Christensen 1959). This may be an indication that *M. argentea* is an early colonizer under certain conditions. Species composition of the enchytraeid community after sod removal tends towards the alliance of *Eiseniellion* community, typical of frequently water-saturated, badly aerated soils (Graefe 1993).

The effect of management becomes evident not only on the level of the decomposer community, but also on the higher trophic level of the predacious Gamasina (Fig. 8). There is no overlap of the species spectrum of Plot a with the other plots which emphasizes the particular edaphic conditions of this site. Three of the species found here are surface predators (*Lysigamasus vagabundus, Pergamasus norvegicus, Veigaia nemorensis*), the remaining two species live hemedaphically (*Veigaia exigua, Leioseius bicolor)*. The species spectra of the other sites show slight differentiations. *Cheiroseius*

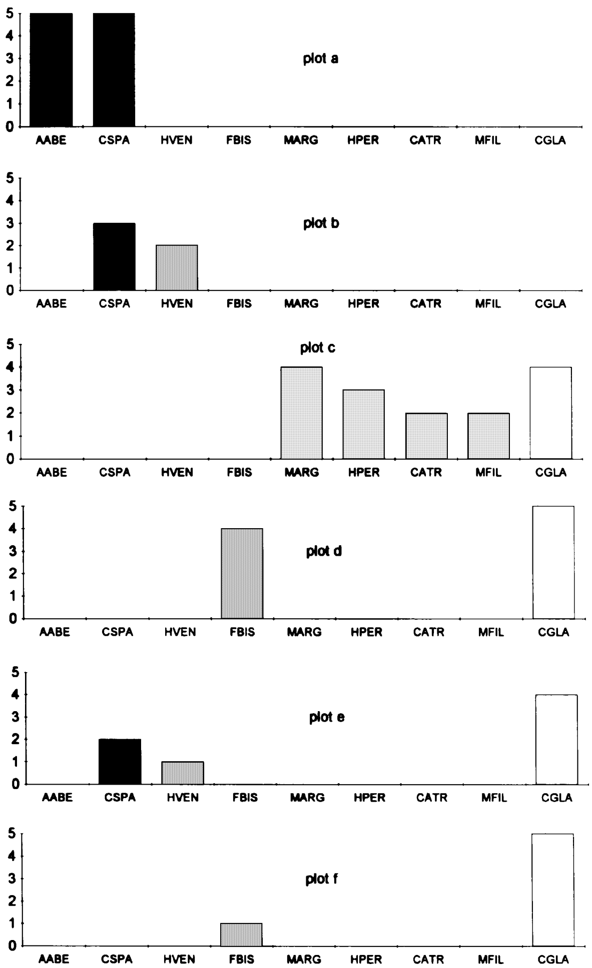

Fig. 7. Enchytraeidae species, abundance values (individuals/ m²) in classes: 1 = < 1000; 2 = 1-3000; 3 = 3-10 000; 4 = 10-30 000; 5 = > 30 000.

AABE = *Achaeta aberrans*
CATR = *Cernosvitoviella atrata*
CGLA = *Cognettia glandulosa*
CSPA = *C. sphagnetorum*
FBIS = *Fridericia* cf. *bisetosa*
HPER = *Henlea perpusilla*
HVEN = *H. ventriculosa*
MARG = *Marionina argentea*
MFIL = *M. filiformis*

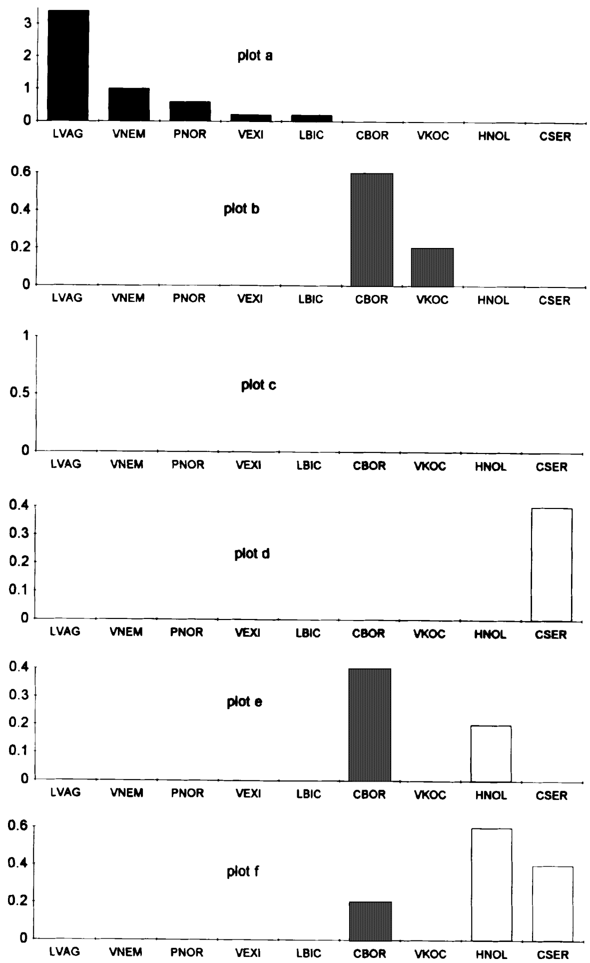

Fig. 8. Gamasina abundance values (0-12 cm depth, individuals/25 cm²).

CBOR = *Cheiroseius borealis*
CSER = *C. serratus*
HNOL = *Hypoaspis nolli*
LBIC = *Leioseius bicolor*
LVAG = *Lysigamasus vagabundus*
PNOR = *Pergamasus norvegicus*
VEXI = *Veigaia exigua*
VKOC = *V. kochi*
VNEM = *V. nemorensis*

borealis is known to occur in meadows, *C. serratus* in sandy sites. With *Veigaia kochi,* these surface predators prefer very wet sites. From humic, very wet sandy soils, hemedaphic *Hypoaspis nolli* is known (Karg 1993).

Soil micromorphology

The results of the micromorphological analysis are summarized in Table 3. For a field description of the soil profiles, see App. 1. Fig. 3 shows the position of the thin sections in the soil profiles.

The main process in the O-horizon of the soil of Plot a in the original heath vegetation is faunal activity: the formation of channels, pedotubules and organic fecal pellets, all of which result in a spongy microstructure (Bullock et al. 1985). The decomposition by fungi is less important. The fecal pellets are produced by (a) Enchytraeidae and/or Collembola, (b) Oribatei, and (c) Isopoda

Table 3. Various biotic and abiotic characteristics, expressed in % by volume, and related distribution pattern in thin section of the soil horizons. ENCH/COLL = Enchytraeidae and/or Collembola, ORI = Oribatei, ISOP/LARV = Isopoda and/or Diptera larvae.

				Biological features in vol. %					Abiotic features % by volume		
				Fecal pellets							
Profile no.	Soil horizon	Depth (cm)	Humiskel	ENCH/ COLL	ORI	ISOP/ LARV	Fungi Hyphae	Pedotu- bules	Humicol	Organans	Related distribution patterns
a	1O	+ 3.5 - 0	10	5	2	2	2	2	15	2	spongy
	1Ah	0 - 6.5	5	15	-	< 1	-	-	5	2	agglomeroplasmic
	1(B)	6.5 - 12	3	2	-	-	-	-	1	4	granular
	1Cr	> 12	2	2	-	-	-	-	-	1	granular
b	1Ah	0 - 7/8	15	20	2	2	2	2	5	2	agglomeroplasmic
	1AC	7/8 - 9	5	5	-	-	1	1	-	22	granular
	1Cr	> 9	2	2	-	-	1	1	-	1	granular
c	1AC	0 - 2/3	5	2	-	-	-	-	2	5	granular
	1Crr	> 2/3	2	1	-	-	-	-	-	1	granular
d	1Ah	0 -	8	2	< 1	-	-	-	1	2	granular
	1Cr	1.5/3.5 > 1.5/3.5	2	1	< 1	-	-	2	-	1	granular
e	1OA	0 - 1	15	2	-	-	1	-	2	2	granular
	1(A)	1 - 2	5	1	-	-	1	2	5	5	granular /chlamydomorphic
	1Cr	> 2	2	1	-	-	1	1	1	1	granular
f	1O	+ 0.3 - 0	30	-	-	-	-	-	-	-	loose
	1Ah	0 - 2	15	15	-	-	2	2	-	2	spongy
	1Cr	> 2	2	2	-	-	1	-	-	1	granular

and larvae. The latter type occurs mainly deeper than 1.5 cm. The faunal activity in the Ah horizon is much less although sufficient to destroy the original lamination of the sand. Very fine to medium-sized sand grains are abundant, with few organic granules and some fresh root fragments. Locally discontinuous, very thin (<20 µm) organans occur around the sand grains. The occurrence of organans is most pronounced in the upper part of the horizon below the Ah, which suggests a weak development of a B-horizon. The C-horizon consists of aeolian, non-calcareous fine and medium sand with local intercalations of coarse sand grains. Soil formation is restricted to root channels and fecal pellets of Enchytraeidae and/or Collembola.

After mowing (Plot b), there is no longer an O horizon. The soil profile changes from a complete, be it thin ABC profile to an AC profile. Traces of B-horizon formation are absent, giving the soil profile a less-developed appearance. The role of the O-horizon is to some extent taken over by the Ah-horizon at the surface. The same types of fecal pellets are found. An important difference with the soil of Plot a is that hyphae of fungi and pedotubules are found deeper in the profile, indicating stronger bioturbation than in Plot a.

After sod removal, not much is left of the soil profile. It took two years to develop a weak organic horizon in the parent material between 2 and 3 cm of Plot c. It is covered by an aeolian deposit in which again a weak organic horizon is forming. Besides channel formation, the biological activity is limited to the production of rare organic pellets of Enchytraeidae and/or Collembola. Further soil development is restricted to the formation of free grain organans, and some organic infillings. The mineral matter below 2 to 3 cm has hardly been affected by soil-forming processes. Root growth is hampered by the dense packing.

Seven years after sod removal a weak Ah-horizon has formed in the upper few centimetres of the soil (Plot d). Plant fragments are common only in the upper 0.5 cm, but the production of fecal pellets, mainly by Enchytraeidae and/or Collembola, is very limited. The bioturbation has reached a depth of 20 cm. The related distribution pattern is still largely granular.

The soil formation in Plot e which lost its sod in 1985, is clearly more advanced. In the eight years since sod removal the production of pedotubules, humiskel and humicol (Barratt 1969) is restored to the level of the reference profile of Plot b where the sod never was removed (Table 3). Based on the decreasing quantity of humiskel with depth, the distribution of the humicol and the related distribution patterns, a distinction has been made between an OA and an (A) horizon. The A symbol is placed between brackets because the development of this horizon is weak. It is slightly banded indicating aeolian influx of sand during soil formation.

Finally, Plot f shows the level of restoration after 13 yr since sod removal. Although the Ah-horizon below the very thin O-horizon is < 2 cm thick, it contains common plant and root fragments, mycelium hyphae, organans, and fecal pellets of Enchytraeidae and/or Collembola.

Discussion

When integrating the three sources of data - vegetation, soil mesofauna and micromorphology - one should bear in mind that there are fundamental differences in the character of the evidence they produce. This is due not so much to the contrast biotic for vegetation and fauna, versus abiotic for soil, because many of the soil components are also biotic in origin. It is more important that vegetation and soil fauna analysis deal with live individuals whereas the soil reflects present as well as past biological activities. This dimension of time is not unambiguous: some micromorphological features such as fecal pellets and plant roots are shorter-lived than the individual plant or animal that produced them, others, in contrast, survive the individual as organic granules and pedotubules. This means that the vegetational and faunal activity cannot always be directly inferred from the thin sections. The micromorphologist deals with the problem of determining the time of formation of the excrements: are they inherited or produced after sod removal? The period of time of survival and thus microscopic recognition of excrements in a certain soil environment is unknown. Van der Drift (1964) concluded that identification of excrements in the thin section is a precarious matter, and that some oribatids do not leave the slightest trace of their activities. In our case, only a fraction of the soil fauna was investigated and we do not know anything about seasonal changes.

The results of the three sources of information can be evaluated as follows:

Sod removal affects the species composition of the vegetation; a number of small pioneer species occur in sod-removal plots only. A time series of these changes in species composition is however difficult to assess, since hydrological conditions interfere with years since sod removal. A few centimetres difference in soil elevation in wet dune slacks may have relatively large effects on the duration of flooding and thus on the vegetation. It is possible that the soil fauna is affected to some extent as well, but these are more mobile. Unfortunately no samples of soil fauna were taken in the driest part of the dune slack. Vegetation cover gradually increases with time since sod removal, but after 13 yr it has not reached the 100 % cover values of the control plots. Species diversity in sod-removal plots is higher than in control plots in early stages after sod removal, but is the same after 13 yr.

Abundances of microarthropods of the original soil surface (Plot a) are within the range of findings from other coastal dune sites (Koehler & Weidemann in press). Abundances on the mown and sod removal plots are extremely low. The hemiaquatic Enchytraeidae, however, occur in large numbers in all plots, abundances in the original soil surface (Plot a) being matched only by findings from raw humus forests (Fründ & Graefe 1992). Dawod & Fitzpatrick (1993) describe their effect under the prevailing low pH conditions to be the production of a large number of small fecal pellets, which later fuse to form the soil matrix. On the species level, Plot a hosts members of communities known from raw humus forest and heathland. The species composition on the other plots differs profoundly, the Gamasina indicating very wet conditions. There is little similarity with typical white or grey dune communities, but they are known from secondary successions (Dawod & Fitzpatrick 1993; Koehler 1984).

Table 4 summarizes the recovery of the main micromorphological phenomena to the situation after sod removal, in reference to Plot b which is only mown. Generally there is an increase in soil development with the age of sod removal, but even after 13 yr the Ah horizon is no more than a fraction of its original thickness. The trend is not the same for all soil constituents. The volume of organans needs no more than 2 yr to be restored to the original level. Other pedological features such as humiskel, pedotubules and humicol need more time, but after 8 yr most of the characteristics of the mown heathland soil appear to be restored. Hyphae of

Table 4. The restoration of soil features as a function of time since sod removal. A square indicates recovery to the original situation (in % volume) of reference Profile b (mown for more than 50 yr without sod removal).

Profile	Years after sod removal	Humiskel	Enchytraeidae excr.	Oribatei excr.	Isopoda/Diptera excr.	Fungi/Hyphae	Pedotubules	Humicol	Organans
c	2								■
d	7								
e	8	■					■	■	
f	13		■			■			

fungi gain full strength only after 13 yr. There is a gradual increase in the expression of soil structure in the Ah-horizon, from granular to spongy, but the agglomeroplasmic fabric of the original Ah horizon was not recovered.

If the results of the three sources of data are compared, we see at once similarities and differences. The transition from heath to mown surface, and from mown surface to sod removal represent the two major breaks both in the above-ground and in the below-ground parts of the ecosystem.

For the vegetation, the effects of mowing are not surprising as these are the aim of the management practice: the restoration of a pioneer vegetation adapted to wet dune slack conditions. It is less obvious that the transition from the original heath to the mown situation also involves a radical change in the composition of the soil fauna. The number of indiviuals drops drastically and the new species that appear are particularly adapted to humid soil conditions. In this way there is a clear resemblance in the above-ground and below-ground effects of mowing. The fact that the original soil (Plot a) is hardly different with respect to depth to groundwater level, suggests that other soil properties, e.g. the composition of the organic material, determine the living conditions of soil fauna in well-developed soils. Micromorphological analysis established clearly the effect of mowing on the course of the pedological processes, and the evidence of enhanced fungal activity after mowing is interpreted as increase in the weight of the hydrological factor. In short: all three sources of data point to adaptation to wet conditions after mowing. This may be due to topography, causing differences in closeness to the groundwater table, but this is not backed by investigations of the groundwater and the lower soil profile. More likely, changes of vegetation by management measures affect soil micromorphology (see Babel & Krebs 1991) and microclimate (Koehler & Born 1989), both being responsible directly for water conditions and indirectly for soil biota colonization.

The nature of the second measure, sod removal, is as drastic as expected. Again there is some analogy in the reaction of the above-ground and below-ground parts of the ecosystem. In both cases the species diversity is relatively high in plots where the sod has recently been cut. This is due to the rapid establishment of the first pioneer species. A consistent time series of the changes in composition in the subsequent period is difficult to establish. It was the goal of the management practices to interrupt the succession to give pioneer species a chance. Neither the vegetation, nor the soil fauna or soil profile have fully recovered in the 13 yr since the first sod removal. So the goal has been reached.

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Appendix 1. Short soil profile descriptions.

Field description of the soil profiles. For location see Fig. 1. Soil colours moist unless indicated otherwise. Depth in cm. Depth of groundwater table at time of description (April/May 1992). Fig. 3 shows the schematic representation of the soil profiles revised on the basis of micromorphological analysis.

Plot a: (original surface)
Slope: flat;
Groundwater table at 30 cm depth;
Groundcover: 100%.

+1-0	O	brown-black organic material;
0-8	1Ah	very dark brown (10YR2/2), very humic sand, weak medium crumb, abundant rootlets. Lower boundary abrupt and smooth;
8-11	1E	dark grayish-brown (10YR4/2) sand, few to common roots. Lower boundary clear and weak wavy;
11-19	1C1u	brown (10YR5/3) sand (very moist), few roots and very few iron mottles. Lower boundary abrupt and smooth;
19-19.5	1C2u	black (10YR2/1) massive organic (?) layer. Lower boundary abrupt and smooth;
19.5-30	1C3g	pale brown (10YR6/3), wet, sand with many iron mottles, and few roots. Lower boundary abrupt and smooth;
>30	1C4g	very pale brown (10YR7/3), wet, non-sticky and non-plastic, sand.

Plot b: (irregularly mown between 1940 and 1972, and yearly mown since 1973)
Slope: flat;
Groundwater table at 29 cm depth;
Groundcover: 100%;

0-8	1Ah	black (10YR2/1), very humic sand with abundant rootlets. Lower boundary abrupt and smooth;
8-17	1AE	very dark grayish-brown (10YR3/2), sand with common fine roots. Very moist. Lower boundary clear and weak wavy;
17-29	1C1u	dark grayish-brown (10YR4/2), sand with common to many medium roots. No iron mottles observed. Lower boundary abrupt and smooth;
>29	1C2r	very pale brown (10YR7/3) wet, non-sticky and non-plastic sand.

Plot c: (sod removed in September 1991)
Slope: flat;
Groundwater table at 22 cm depth;
Groundcover: <2%;

0-2	1A	dark grayish-brown (10YR4/2), slightly humic sand, massive, very friable, few medium roots. Lower boundary clear and smooth;
2-8	1AC	brown (10YR5/3) slightly humic sand, massive, very friable, common medium roots (phragmites); Lower boundary gradual and smooth;
8->26	1Cr	pale brown (10YR6/3), wet sand, massive, non-sticky, non-plastic, common medium roots above 20 cm, and few below 20 cm.

Plot d: (sod removed in January 1987)
Slope: flat;
Groundwater table rising to 26 cm;
Groundcover: 90%;

0-3	1Ah	dark grayish-brown to very dark grayish brown (10YR4-3/2) humic sand with many light coloured grains, massive, very friable, many very fine roots. Lower boundary abrupt and wavy;
3-9.5	1AC	grayish-brown (10YR5/2) slightly humic sand, massive, very friable, few medium, distinct, very dark grayish-brown (10YR3/2) mottles, common very fine roots. Lower boundary clear and smooth;
9.5->30	1Cr	light gray (10YR7/2), wet sand, massive, non-sticky, non-plastic, common very fine roots above 17 cm, and few below 17 cm.

Plot e: (sod removed in November 1985)
Slope: flat;
Groundwater table rising from 22 to 17 cm;
Groundcover: 100%;

0-0.5	1Ah	black (10YR2/1) humic sand, massive, very friable, abundant very fine roots forming sod. Lower boundary abrupt and smooth;
0.5-9	1ACg	brown (10YR5/3) slightly humic sand, massive, very friable, many medium distinct diffuse, very dark grayish-brown (10YR3/2) mottles, common fine roots. Lower boundary clear and smooth;
9-28	1Cr	pale brown (10YR6/3), wet sand, massive, non-sticky, non-plastic, few medium, faint and diffuse dark grayish-brown (10YR4/2) mottles and few fine, distinct and clear, dark brown to brown (7.5YR4/4) mottles, mostly vertical around root channels, common fine roots decreasing in number downwards.

Plot f: (sod removed in September 1980)
Slope: flat;
Groundwater table at 27 cm depth;
Groundcover: 100%;

0-4	1Ah	black (10YR2/1), very humic sand with abundant roots and firm. Lower boundary abrupt and smooth;
4-14	1AC	light brownish-gray (10YR6/2), moist to wet sand with common roots (3 mm and thinner),very friable and massive, no lamination. Lower boundary abrupt and smooth;
14->30	1Cr	light gray (10YR7/2), wet sand with few roots, non-sticky and non-plastic, massive, without mottles.