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Restoration of species-rich dry heaths: the importance of appropriate soil conditions

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SUMMARY

The aim of many rehabilitation projects in degraded ecosystems is to restore biodiversity. In order to achieve this, restoration often focuses on abiotic conditions as they are the main cause for the degradation of the ecosystem. The necessity of restoring the soil conditions for rehabilitation of heathland vegetation is shown by this study. Three dry heathland areas were studied: an acidic species-poor heath which is degrading as a result of atmospheric nitrogen deposition, an acidified matgrass sward and an abandoned grassland. We aimed to restore the characteristic plant communities of the heathlands: a Calluno-Genistion pilosae community in the acidic species-poor heath and a Nardo-Galion saxatilis community in both the acidified matgrass sward and the abandoned grassland. Restoration methods included sod-cutting to the mineral soil layer, liming and a combination of sod cutting and liming. Effects of these methods on top soil chemistry, vegetation development and development and demography of the rare *Arnica montana* are shown and discussed. Furthermore, we discuss the importance of seed availability in relation to the importance of restoring soil conditions for successful rehabilitation of heathlands.

Key-words: *Arnica montana*, liming, nature conservation, soil acidification, sod-cutting.

INTRODUCTION

Degraded ecosystems are restored for many reasons, varying from conservation of rare species and biodiversity to the protection of human health in seriously polluted areas. In all cases, restoration of degraded ecosystems should begin with counteracting the main causes for the decline. However, some ecosystems are affected by a deteriorating factor to such an extent that removal of the cause for decline is insufficient for ecosystem rehabilitation (Hobbs & Norton 1996). For example, soil acidification has a great impact on soil chemistry, but the effects of acidification are easily reversed by the addition of lime. However, as a result of acidification, characteristic plant species of

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an ecosystem may have disappeared. Their return does not only depend on the habitat quality, e.g. the appropriate soil conditions, but also on the capacity of the species to recolonize the habitat. This paper presents data from a restoration experiment, carried out in acidified and eutrophied heathland vegetation, focusing on the question whether dry heath vegetation will recover after restoring the soil conditions.

In the Dutch lowland heathland landscape, different plant communities can be found. Most of the drier parts of the landscape were originally poor in phanerogamic species and dominated by the dwarf shrub *Calluna vulgaris* (Calluno-Genistion pilosae). In other parts, more species-rich matgrass sward communities were found (Nardo-Galion saxatilis), of which many characteristic species are currently rare. Both communities have declined since the beginning of this century, due to changes in land use and atmospheric input of NH_y and SO_x. These atmospheric inputs led to increased nitrogen availability and soil acidification. The dwarf shrub dominated heath communities are very sensitive to increased nitrogen availability: grasses such as *Molinia caerulea* and *Deschampsia flexuosa* benefit more than the heather species from the increased nitrogen availability; consequently, the heathlands are eventually changed into grasslands (e.g. Aerts & Heil 1993). It is not unlikely that a similar process takes place in the species-rich heaths, since the competitive abilities of the Nardo-Galion saxatilis species *Arnica montana* and *Viola canina* in comparison to the grass *Agrostis canina* are strongly reduced by NH_3 input (Dueck & Elderson 1992). Moreover, soil acidification seriously affects many characteristic species of the Nardo-Galion saxatilis communities (Van Dam *et al.* 1986; Fennema 1992; Roelofs *et al.* 1996). Experiments with *A. montana* have shown that especially high aluminium and ammonium concentrations are toxic to this species at low pH (Heijne 1995; De Graaf *et al.* 1997; De Graaf *et al.* 1998). In contrast, the Calluno-Genistion pilosae species occur on more acid soils and are not affected by soil acidification (Houdijk *et al.* 1993; De Graaf *et al.* 1997).

As dry heath and matgrass swards are threatened mainly by nitrogen eutrophication and soil acidification, restoration should focus primarily on counteracting the negative consequences of these processes, as well as on the reduction of the deposition of atmospheric N and S compounds. Removal of accumulated nitrogen can be achieved by sod-cutting ('plaggen'), which removes the aboveground parts of the vegetation and the organic soil layers (Aerts & Heil 1993; Diemont 1994). In the past, sod-cutting of western Europe heathlands was part of a widespread agricultural system, but due to the introduction of artificial fertilizers this practice was abandoned (Gimingham & De Smidt 1983). It has since been reintroduced as an adequate tool for restoration of *C. vulgaris*-dominated heath (Helsper *et al.* 1983; Werger *et al.* 1985). As well as reducing soil nutrients, the bare soil which results from sod-cutting offers suitable germination conditions to many species (Miles 1973). However, sod-cutting does have a serious potential drawback: since heathland species have the greatest proportion of their seeds stored in the upper centimeters of the soil (Putwain & Gillham 1990; Bruggink 1993), a substantial part of the seedbank is removed by sod-cutting. This may restrict the re-establishment of species, especially those with a short-lived seedbank of which all seed is probably present in the upper soil layers. Many Nardo-Galion saxatilis species have such short-lived seedbanks (Bakker *et al.* 1996; Thompson *et al.* 1997).

Liming of the topsoil is a method widely used in agriculture and forestry to counteract soil acidification. In recent decades it has also been used in nature conservation in order to reduce the negative effects of acidic atmospheric deposition in forests and lakes (Laudelout 1993; Kreutzer 1995; Henrikson & Brodin 1995). In general, pH and base cation concentrations of the soil are increased, whereas aluminium concentrations are decreased by applications of lime (Kreutzer 1995). Reports on the effects of liming on heathland species are limited and vary from beneficial (Blom & Wincent 1989; Wilson 1995) to detrimental (Blom & Wincent 1989; Rodenkirchen 1995).

In this study we test sod-cutting, liming and a combined liming and sod-cutting treatment on their ability to rehabilitate the characteristic soil conditions and the typical species-rich vegetation of dry heathlands. The main aim of the experiment was to develop adequate restoration practices for three threatened ecosystems: (1) eutrophied, dry species-poor heath, (2) acidified and eutrophied matgrass sward and (3) abandoned grassland on former heathlands. Based upon the ecological knowledge on characteristic heathland plant species and the actual vegetation, we aimed to regenerate a Calluna-Genistion pilosae community in the eutrophied, species-poor heath and Nardo-Galion saxatilis communities in both the matgrass swards and abandoned grassland. Special attention has been paid to the rare *A. montana* and its response to the different management regimes.

MATERIALS AND METHODS

Site description

The experiments were carried out in 'de Schaopedobbe', a Dutch nature reserve (52° 57′N, 6°16′E), owned and managed by 'It Fryske Gea'. Dry, inland heath (Calluno-Genistion pilosae communities) and matgrass swards (Nardo-Galion saxatilis communities) form a large part of this reserve. These communities are found on sandy soils of Pleistocene origin, in which a podzolic profile developed. Three sites within the nature reserve, with a vegetation as homogeneous as possible, were selected for the experiment: a matgrass sward (Nardo-Galion saxatilis community) in which the original *A. montana* population was declining (referred to as 'matgrass sward'). This decline was probably caused by soil acidification and/or nitrogen eutrophication. The vegetation of the second site ('heath') could be described as Calluno-Genistion pilosae, and lacked *A. montana* plants. The third study site was an abandoned grassland ('grassland'), with a recently expanding *A. montana* population. *Festuca ovina*, *Agrostis canina*, *A. capillaris*, *Holcus lanatus* and *Hypochaeris radicata* were among the most abundant species in this site. In contrast to the other sites, the grassland was used for arable agriculture, and had received fertilizers and lime in the past. After abandonment, a grassland management regime was initiated in order to develop a species-rich grassland vegetation. At the beginning of the experiment (March 1990), the pH of the top soil layer (10 cm) varied between 3·8 and 4·3 in the heath, between 4·1 and 4·7 in the matgrass sward and between 4·2 and 5·1 in the grassland. During the experimental period, all sites were mown anually in August, with the hay being subsequently removed. This was common practice before in the matgrass sward and grassland, but was first carried out in 1990 in the heath.

Experimental design

Eight plots ($5 \times 10\,m^2$) were laid out in each of the studied sites, in March 1990. In four plots per site the topsoil layer, including aboveground parts of the vegetation, was removed by sod-cutting to the mineral soil layer. At each site, two sod-cut and two-non-sod cut plots were limed: in one plot limestone (chalk, 100% $CaCO_3$, grain diameter

0·1–10 mm) was applied, in the other we applied dolomite (80% $CaCO_3$, 20% $MgCO_3$, grain diameter <0·1 mm). In order to increase the base saturation of the top soil layer to 80%, 150 kg ha^{-1} lime (limestone or dolomite) was applied to the grassland plots, 300 kg ha^{-1} to the Matgrass sward plots and 600 kg ha^{-1} to the heath plots. Lime applications were repeated in July 1991. In each plot, two control plots were not limed; a 5-m-wide zone separated the limed and unlimed.

The effects of sod-cutting and liming on topsoil chemistry (10 cm) were studied twice a year from March 1990 to August 1995. Soil samples were taken with an auger (diameter 3 cm, eight subsamples per plot); subsamples were mixed and stored in polyethylene bags at 4°C until analysis. In all samples, water-extractable pH, Al, Ca, Al/Ca-ratio, NO_3^- and P were measured, as were exchangeable Ca, Mg, K and NH_4^+. Total mineral nitrogen concentrations (N_{min}) are the sum of water-extractable NO_3^- and exchangeable NH_4^+. In addition, soil pH was determined every 2 months during the first year of the experiment. The soil organic matter content was determined immediately in March 1990, by weight loss after ignition (550°C, 4 h).

The vegetation of the plots was described in the summers of 1990, 1992, 1994 and 1995, using the Braun–Blanquet approach (Westhoff & Van der Maarel, 1978); the total area of 5 × 10 m was treated as one relevé. As vegetation development was slow, only the data of 1990 (non-sod-cut plots) and 1995 (all plots) are presented. More specific information on the effects of liming on the performance of established *A. montana* populations in the matgrass sward was gained by counting the numbers of rosettes and flower buds of the plants in the non-sod-cut plots. These observations were made at the end June of 1991, 1994, 1995 and 1996. We were unable to study the effects of liming on established *A. montana* populations in the grassland, due to the fact that these were only present in the control plots. No established *A. montana* plants were present in the heath.

In the sod-cut plots of the matgrass sward, an additional experiment was set up to study the effects of liming on the demography of *A. montana* in detail. A hundred seeds were sown in a grid (0·5 cm below the soil surface, 10 cm distance between individual seeds) in July 1991. The seeds of *A. montana* were collected 2 weeks earlier in the direct neighbourhood of the experimental plots; 98% of the seeds sampled germinated under laboratory conditions (20°C). Germination of the seeds and survival of the seedlings and plants were regularly noted until June 1996 (monthly during the first year except during the winter, in May and September during the second year and in June in the following years). From 1994 onwards biomass was estimated annually with a non-destructive method which consists of multiplication of the maximum leaf length with the maximum leaf width and the number of leaves. This method proved to be a good estimation of biomass of *A. montana* (R=0·77, P<0·001, greenhouse conditions). An identical experiment was carried out in 1992 in the control and dolomite-treated plots of the heath; seeds were again collected a few weeks before sowing in the direct neihbourhood of the heath plots (95% germination under laboratory conditions). As in the matgrass sward, biomass estimations on *A. montana* began 3 years after sowing.

Extraction methods and chemical analyses

Seventy grams of thoroughly mixed fresh soil was mixed with 200 ml bi-distilled water (for determination of water-extractable elements) or 200 ml 0.2 M NaCl solution (for determination of exchangeable elements). The mixtures were shaken for 1 hour (120

Table 1. Soil characteristics (geometrical means) with (+) and without (−) sod-cutting of unlimed plots, 2 weeks after sod-cutting (March 1990). pH and P are determined in water extracts, Ca+Mg+K in 0·2 M NaCl extract. $N_{mineral}$ is the sum of water extractable NO_3^- and NaCl-extractable NH_4^+. All nutrients are expressed in μmol kg^{-1} dry soil, except Ca+Mg+K, which is in μeq kg^{-1} dry soil. Significance: NS: P>0·1, *: P<0·05, **: 0·01<P<0·05, ***: P<0·01. If 0·1<P<0·05 then the P-value is indicated. N=4

	Heath			Matgrass sward			Grassland		
Sod-cutting	-	+		-	+		-	+	
pH	4·01	4·31	*	4·48	4·43	NS	4·65	4·64	NS
Al	93	82	NS	41	130	NS	110	72	**
Ca_{exch}	2015	544	***	1656	760	*	2475	925	**
Mg_{exch}	683	564	***	695	594	*	691	570	**
Base cations	6351	1978	***	6246	2812	*	7681	2762	**
NO_3^-	3·3	47·1	0·09	137·5	73·6	NS	69·6	51·2	NS
$NH_4^+{}_{exch}$	713	422	NS	502	305	NS	517	268	**
$N_{mineral}$	808	482	NS	647	387	NS	639	322	*
P	8·5	0·0	***	6·4	0·0	*	18·0	8·0	*
% org. matter	17·5	7·0	***	14·1	11·8	*	7·6	5·5	NS

movements min^{-1}), after which pH of the solution was measured (Radiometer type PHM 82 pH-meter). Hereafter, the solution was centrifuged (12 000 r.p.m., 20 min) and the supernatant was stored in polyethylene bottles at -28°C. Al, Ca, Mg and P concentrations were measured using an ICP (type IL Plasma 200), NO_3^- and NH_4^+ concentrations were determined colorimetrically with a continous-flow autoanalyser (Technicon AAII system) and K concentrations were quantified with flame photometry (Technicon Flame photometer IV).

Statistical analyses

To determine the effects of sod cutting, an analysis of variance (GLM procedure, SAS 6·0) was performed on soil data; data were log-transformed in order to fit a normal distribution. The effects of liming on soil chemistry in the separate plots were tested with a regression analysis (GLM procedure, SAS 6·0); a separate slope model was used in order to detect differential time effects between treatments.

Germination and survival of sown *A. montana* plants were tested with a PHREG procedure (SAS 6·0). This is a regression analysis of survival data based on the Cox proportional hazards model. Three years after sowing and onwards, the effects of liming on the estimated biomass of the living *A. montana* plants were tested with an analysis of variance (GLM procedure, SAS 6·0) following log transformation.

RESULTS: EFFECTS ON SOIL CHEMISTRY

Sod-cutting

Sod-cutting instantly reduced the concentrations of most nutrients and organic matter content in the top soil layer (Table 1). P concentrations were strongly reduced, and not detectable in the sod-cut plots of the heath and matgrass sward. The mineral nitrogen concentrations decreased with 40% compared to the intact vegetation. The topsoil pH

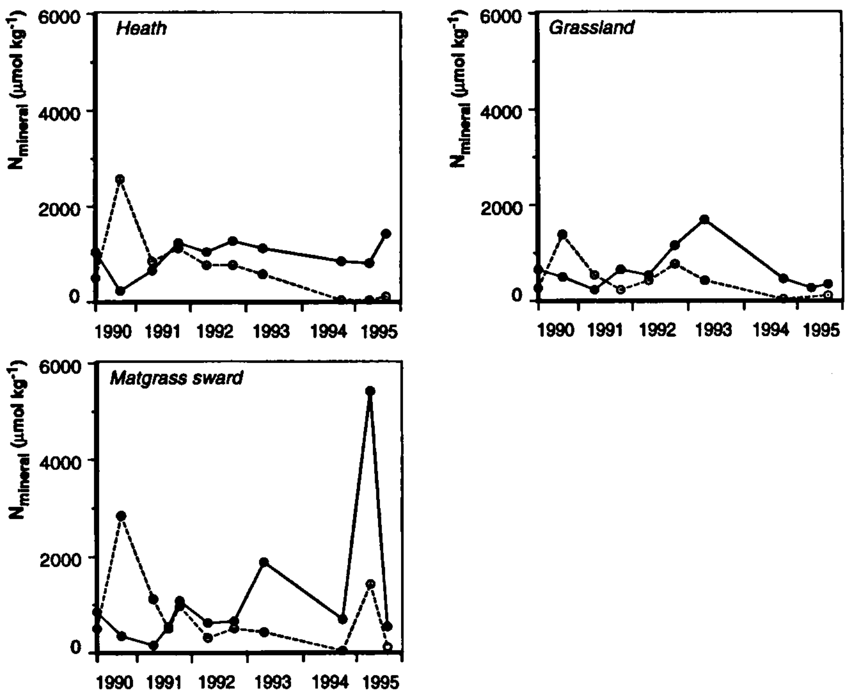

Fig. 1. The effects of sod-cutting on mineral nitrogen concentration ($N_{mineral}$) in the unlimed plots. Closed circles, solid line: non-sod-cut plots, open circles, dashed line: sod-cut plots.

of the heath increased to 4·3, whereas in the non-sod-cut parts of the heath pH remained at 4·1. In the matgrass sward and the grassland, pH was not affected by sod-cutting.

During the 5 years following sod-cutting, the concentrations of most nutrients in the sod-cut plots remained below those of the concentrations in the soils under intact stands, although some nutrients showed considerable fluctuations (Figs 1 and 2, data for P not shown). However, mineral nitrogen concentrations increased considerably to 1500–3000 µmol kg^{-1} dry soil during the first year after sod-cutting (Fig. 1), compared to 500–1000 µmol kg^{-1} dry soil in the non-sod-cut plots. Both ammonium and nitrate concentrations were enhanced by sod-cutting (Table 2), but the increase in ammonium concentrations was especially high in the heath and matgrass sward (up to 2500 µmol kg^{-1} dry soil). In all sites the NH_4^+/NO_3^--ratio was in the same order of magnitude in the sod-cut and non-sod-cut plots. One year after sod-cutting, mineral nitrogen concentrations reverted to the initial values after sod cutting and remained low for the rest of the experimental period (<100 µmol kg^{-1}). These mineral nitrogen concentrations are always lower than those measured in the non-sod-cut sites. In the matgrass sward, a second peak in $N_{mineral}$ was measured after the winter of 1995, both in the sod-cut and in the non-sod-cut plots.

Liming

The effects of liming (treatments with dolomite or limestone) are presented as comparisons between limed and control (unlimed) plots, within the same site, with or without sod-cutting. The effects of liming were, generally, most pronounced in the

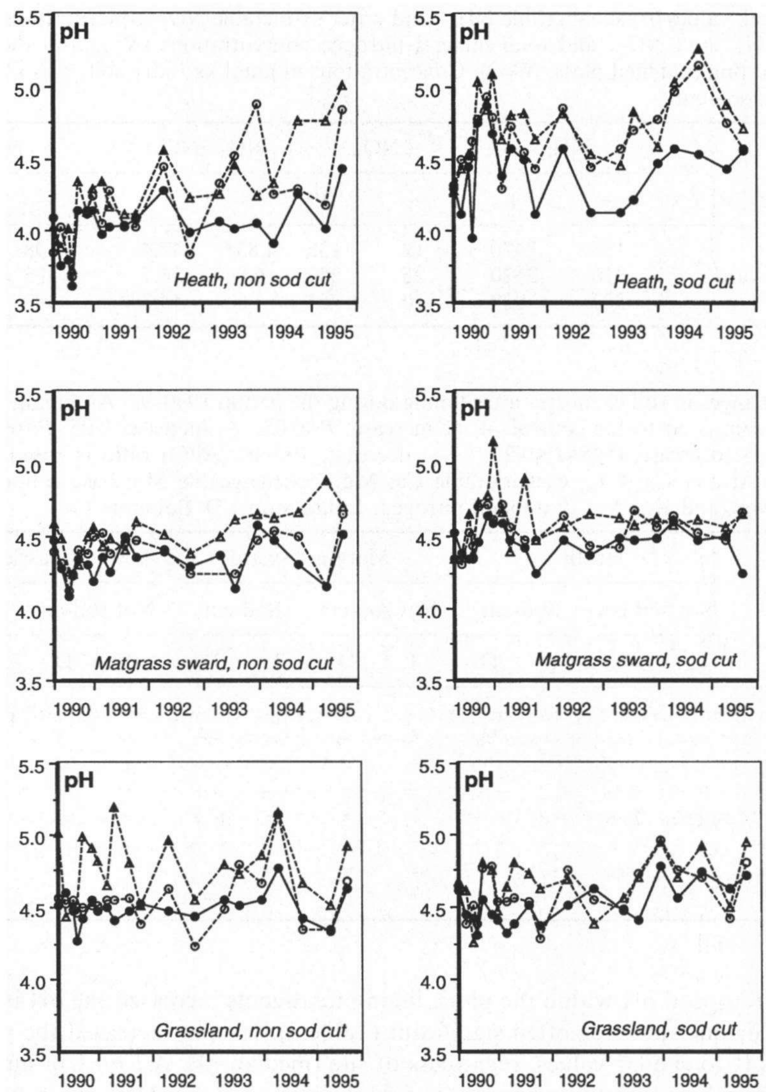

Fig. 2. The effects of sod-cutting and liming on topsoil pH. Closed circles: control (unlimed) plots; open circles: limestone-treated plots; open triangles: dolomite-treated plots.

heath, followed by the matgrass sward. In the grassland, hardly any significant effects of liming on topsoil chemistry were found (Table 3). Liming affected soil chemistry more in sod-cut plots than in plots with vegetation cover. The two liming materials, dolomite and limestone, affected soil chemistry in similar ways. Therefore, they will be discussed together, except where the results differed considerably between dolomite and limestone treatments.

The response of soil factors related to the buffering capacity to liming was rapid (Figs 2 and 3): pH and base cation concentrations increased almost immediately following the addition of limestone or dolomite in 1990 and 1991. Despite considerable

Table 2. Peak values in exchangeable NH_4^+ and water extractable NO_3^- concentrations, the ratio between NH_4^+ and NO_3^- and total mineral nitrogen concentrations ($N_{mineral}$) in the first year after sod-cutting (unlimed plots, $N=2$). Concentrations in μmol kg^{-1} dry soil. *: $N=1$. −: non-sod-cut; +: sod-cut

	NH_4^+		NO_3^-		NH_4^+/NO_3^-		$N_{mineral}$	
Sod-cutting	−	+	−	+	−	+	−	+
Heath	186	2426	12	135	4.85*	47.4	198	2562
Matgrass sward	310	2520	25	252	16.9	16.7	335	2772
Grassland	383	929	110	761	4.6	14.3	493	1691

Table 3. Changes in soil chemistry after liming during the period 1990–95. All liming treatments have been compared to the control. + +: increase, $P<0{\cdot}05$; +: increase, $0{\cdot}05<P<0{\cdot}25$; =: no difference; −: decrease, $0{\cdot}05<P<0{\cdot}25$; − −: decrease, $P<0{\cdot}05$. Al/Ca ratio is based on water-extractable Al and Ca; Ca_{ex}: exchangeable Ca; Mg_{ex}: exchangeable Mg; base cations: sum of 2^*Ca_{ex}, 2^*Mg_{ex} and K_{ex}. $N_{mineral}$: mineral nitrogen. L: limestone; D: dolomite

	Heath				Matgrass sward				Grassland			
	Not sod-cut		Sod-cut		Not sod-cut		Sod-cut		Not sod-cut		Sod-cut	
Liming	L	D	L	D	L	D	L	D	L	D	L	D
pH	=	=	+	+ +	=	+	=	+ +	+ +	=	+ +	+
Al	=	−	=	=	=	−	=	+	=	=	=	=
Al/Ca	− −	− −	− −	− −	=	=	=	− −	+	=	=	=
Ca_{ex}	+ +	+ +	+ +	+ +	=	=	+ +	+ +	=	=	+	+
Mg_{ex}	+	+ +	+ +	+ +	=	=	=	+ +	=	=	=	+ +
Base cations	+ +	+ +	+ +	+ +	=	=	+ +	+ +	=	=	=	+ +
$N_{mineral}$	=	=	−	−	=	=	=	=	=	=	=	−
P	=	=	− −	− −	=	=	=	=	=	=	=	=

variation in topsoil pH within the plots, liming treatments increased the pH in all plots (Fig. 3). This increase was often significant (Table 3). Liming increased the pH of the sod-cut plots to similar values, regardless of site (median pH: $4{\cdot}7 \pm 0{\cdot}1$ in limed plots; $4{\cdot}5 \pm 0{\cdot}1$ in unlimed plots), whereas the initial differences in pH between areas were still noticeable after liming in the non-sod-cut plots (median pH: 4·2, 4·5 and 4·6 in limed and 4·0, 4·3 and 4·5 in unlimed heath, matgrass sward and grassland plots, respectively; differences in median pH between dolomite and limestone treatments did not exceed 0·1 pH value).

Liming significantly increased base cation concentrations in all heath plots, in the sod-cut plots of the matgrass sward and only in the dolomite treated, sod-cut plot of the grassland (Table 3, Fig. 2). The increase was mainly due to an increase in exchangeable calcium concentration; magnesium concentrations increased only in the dolomite-treated plots and in most limed heath plots (Table 3). Towards the end of the experiment, base cation concentrations tended to decrease in all limed plots. This decrease was significant in the limestone treatment in both the heath vegetation (non-sod-cut) and the dolomite treatment in the sod-cut matgrass sward.

Although liming did not cause a significant decrease in aluminium concentrations

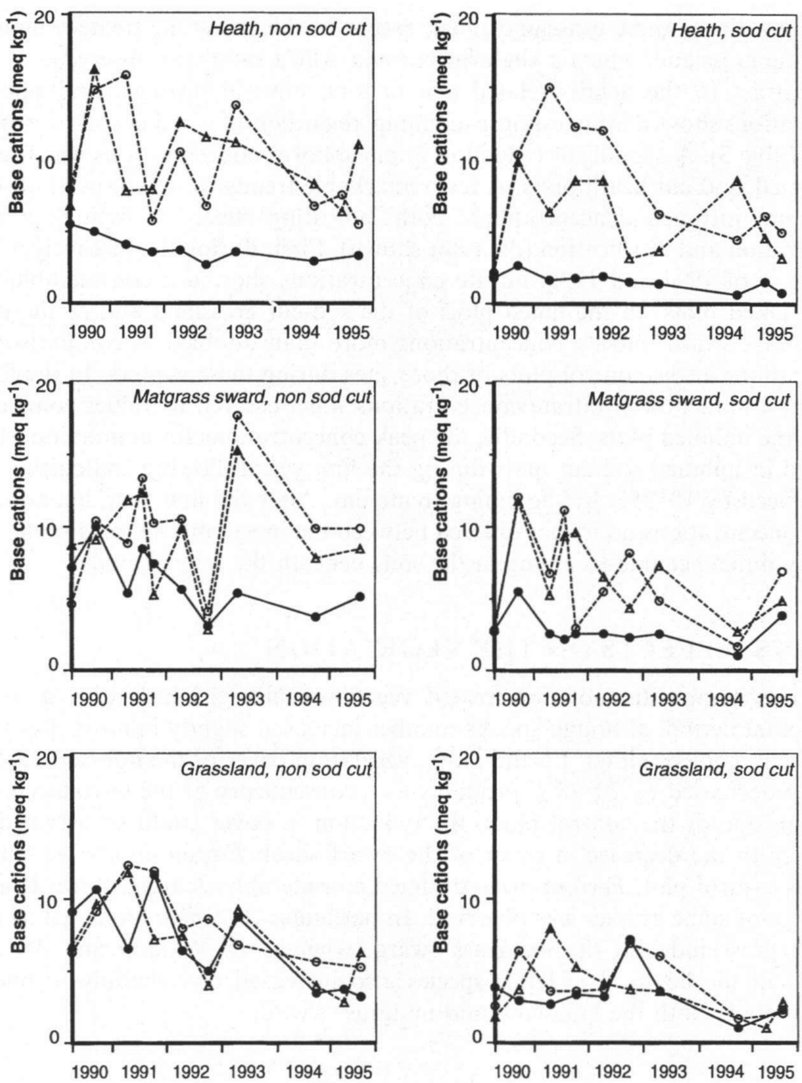

Fig. 3. The effects of sod-cutting and liming on base cation concentrations (Ca + Mg + K, in meq kg^{-1} dry soil). Closed circles: control (unlimed) plots; open circles: limestone-treated plots; open triangles: dolomite-treated plots.

(Table 3), the plant-important Al/Ca-ratio did decrease as a result of liming in the heath and in the dolomite-treated, sod-cut part of the the matgrass sward. The decrease is caused mainly by the increase in calcium concentrations of the topsoil layer after liming. Much variation in Al/Ca-ratio was observed throughout the experimental period but, in general, Al/Ca-ratios of the limed plots in the heath and matgrass sward did not exceed 5·0 and were often less than 1·0 (data not shown). In the control plots of these sites, higher values of the Al/Ca-ratio than 5·0 were frequently observed. In the grassland, Al/Ca-ratios were always rather low (generally <5·0). Liming did not affect the Al/Ca-ratio of these grassland plots, except in the limestone-treated, non-sod-cut part of the grassland, where a slight increase in Al/Ca-ratio was observed.

In contrast to the acidity-related soil factors, mineral nitrogen and phosphorus concentrations showed little response to liming, regardless of whether sods were removed or not (Table 3). A significant reduction in phosphorus concentrations was found only in the limed, sod-cut heath plots. A few remarkable trends were, however, observed in the mineral nitrogen concentrations, both indicating effects of liming on nitrogen mineralization and nitrification (data not shown). First, during the relatively warm and wet winters of 1994 and 1995, nitrate concentrations showed a considerable increase in some limed plots. In the limed plots of the sod-cut grassland and of the non-sod-cut matgrass sward, nitrate concentrations more than doubled in comparison to the concentrations in the control plots of those sites during these winters. In the following summers, a reduction in nitrate concentrations was observed to values comparable to those in the unlimed plots. Secondly, the peak concentrations for ammonium that were measured in unlimed sod-cut plots during the first year following sod-cutting (Fig. 1) were reduced by 10–25% by the liming treatment. After the first year, ammonium and nitrate concentrations no longer differed between the limed and unlimed plots, nor was there any difference due to liming in the soils beneath the intact stands.

RESULTS: EFFECTS ON THE VEGETATION

The species composition of non-treated vegetation changed little during the 6-year experimental period, although species number increased slightly in most sites (Table 4; non-sod-cut, control plots). Furthermore, vegetation cover of the non-sod-cut parts of the heath decreased by 20–25%, probably as a consequence of the introduced mowing regime. In one of the control plots, the reduction in cover could be ascribed almost exclusively to the decrease in cover of the dwarf shrub *Empetrum nigrum* whereas in the other control plot, *Festuca ovina* declined considerably. A trend towards a greater abundance of some grasses was observed. In particular *A. canina* increased its cover in both the grassland and the matgrass sward, whereas *D. flexuosa* and *M. caerulea* increased in the heath. The latter species also increased considerably in one of the control plots in both the grassland and matgrass sward.

Sod-cutting

Five years after sod-cutting had created a bare soil surface, the vegetation cover of the matgrass sward and grassland equalled that of the parts that were non-sod-cut (80–90% in the sod-cut and 80–95% in the non-sod-cut parts; Table 4). In the sod-cut heath vegetation, the canopy was not yet closed in 1995 (50–70% cover). Almost all plant species present in the non-sod-cut plots in 1990 had returned in 1995. In most sod-cut plots, species number was higher in 1995 than in the plots that had not been sod-cut. The dwarf shrub *Calluna vulgaris* benefited especially from sod-cutting: in all sites, this species became more abundant in the sod cut than on the non-sod-cut plots. In the heath, *C. vulgaris* had become the dominant species at the end of the experimental period. In contrast, the other dominant dwarf shrub, *E. nigrum*, failed to significantly reestablish after sod removal in the heath, and did not even return in one sod-cut, unlimed plot (C1, Table 4). The characteristic heathland species *Genista anglica* increased in abundance after sod-cutting of the matgrass sward. The abundances of *M. caerulea*

Table 4. Vegetation the heath (Table 4A), matgrass sward (Table 4B) and grassland (Table 4C) in 1990 and 1995. Trees and species in the category 'remaining species', which only appear in one or two plots with a low abundance (r, +), are omitted. In each site, the unlimed plots were replicated (C1, C2), not the limed plots (L: limestone-treated; D: dolomite-treated). –: non-sod-cut plot; +: sod-cut plot. * Characteristic species of the Nardo-Galion saxatile; †: characteristic species of the Calluna–Genistion pilosae. [1]: subspecies *congesta*

Experimental plot	C1	C1	C1	C2	C2	C2	L	L	L	D	D	D
Year	1990	1995	1995	1990	1995	1995	1990	1995	1995	1990	1995	1995
Sod-cut	–	–	+	–	–	+	–	–	+	–	–	+
A												
Heath												
Vegetation cover (%)	90	55	70	90	70	50	80	80	60	85	85	55
Number of species	13	15	21	14	15	17	11	17	24	12	15	21
Matgrass sward species												
Agrostis canina	1	+	2m	1	+	2a	1	2a	2a	1	2m	2a
Agrostis capillaris			r			+			+			
*Arnica montana**			+						+			r
*Danthonia decumbens**	1	+	1	1	+	+	+	+	1	1	+	+
*Galium saxatile**	1	1	+	2m	1	+	2m	2a	+	2m	2m	1
Hieracium pilosella			+		r			+	1		+	1
*Nardus stricta**	r	1		+	+	+	+	1		+	+	
*Potentilla erecta**			+			r		+	+			+
*Veronica officinalis**												r
Heathland species												
Calluna vulgaris†	2a	2a	4	2a	2b	3	2a	2a	3	2b	2b	3
Empetrum nigrum	4	2a		2a	2a	r	2m	+		+	+	
Erica tetralix									+			+
Genista anglica†	+	+	+	r	r							
Genista pilosa†			r			r		r	+			r
Frequently found species in matgrass swards and heathland vegetations												
Carex pilulifera	+	2m	2m	2m	2m	2a	1	2m	2a	2m	2m	2a
Deschampsia flexuosa	r	2a	+		+	+	3	2a	+	+	1	r
Festuca ovina	2a	2b	2m	3	2a	1	3	3	2a	3	3	2a
Molinia caerulea	+	2a	1	3	3	1	2a	2a	1	2b	2a	+
Rumex acetosella		1	+	r	1	1	2m	2m	+	+	2m	+
Remaining species												
Hieracium laevigatum			r						+			+
Hypochaeris radicata		+	1	r	+	1		2m	2m	r	2a	2m

continued

Table 4—*continued*

Experimental plot	C1	C1	C1	C2	C2	C2	L	L	L	D	D	D
Year	1990	1995	1995	1990	1995	1995	1990	1995	1995	1990	1995	1995
Sod-cut	–	–	+	–	–	+	–	–	+	–	–	+
B												
Matgrass sward												
Vegetation cover (%)	90	80	75	90	80	80	95	90	80	95	80	85
Number of species	17	22	20	15	20	20	14	24	25	14	26	23
Matgrass sward species												
Agrostis canina	2m	2b	2a	2a	2a	2b	2a	2b	2b	2a	2b	2a
Agrostis capillaris		1	+			+		+	+			+
*Arnica montana**	1	1		1	1	r	1	1	+	1	1	r
*Danthonia decumbens**	1	1	2a	2a	2a	2a	2a	1	1	2a	2a	+
Euphrasia stricta											r	
*Galium saxatile**	2b	2a	2m	2b	2m	2m	2b	2m	2m	2b	2m	2m
Hieracium pilosella		r	1					+	2m		1	2m
*Nardus stricta**			r	+	+			+			2a	
Polygala serpyllifolia						+		+	1		1	1
*Potentilla erecta**	+	+	1	r		1		+	2a		+	2m
Heathland species												
Calluna vulgaris†	2a	2a	3	2a	2a	3	2a	1	3	2a	1	4
Erica tetralix	r	+			r						r	
Genista anglica†	+	+	2m	+	+	1	r	+	2m	1	+	2m
Genista pilosa†									r			
Frequently found species in matgrass swards and heathland vegetations												
Carex pilulifera	2b	2a	2a	2a	2m	2a	2b	2a	2a	2a	2a	2a
Deschampsia flexuosa		r			r							
Festuca ovina	3	2a	2m	3	2a	2m	3	2b	2m	3	2b	2a
Molinia caerulea	2b	3	1	3	3	2a	2b	3	1	3	2b	1
Rumex acetosella	1	1	1		+	+	+	1	+	+	1	+

continued

Table 4—*continued*

Experimental plot	C1	C1	C1	C2	C2	C2	L	L	L	D	D	D
Year	1990	1995	1995	1990	1995	1995	1990	1995	1995	1990	1995	1995
Sod-cut	–	–	+	–	–	+	–	–	+	–	–	+
Remaining species												
Amelanchier lamarckii			r		r							r
Anthoxanthum odoratum	+	+	+							+	+	+
Cerastium fontanum	r							+			+	
Hieracium laevigatum						1			+			+
Hieracium umbellatum	+	+		r	+	+	r	+	r	r	+	+
Hypochaeris radicata	r	+	1	r	r	1	+	1	2m	r	1	2m
Luzula multiflora[1]				+	+	r	+	+				
Taraxacum officinale s.s.								+		r	r	
C												
Grassland												
Vegetation cover (%)	80	95	85	90	95	85	92	90	90	92	80	90
Number of species	25	21	30	23	29	27	25	27	31	28	27	25
Matgrass sward species												
Agrostis canina	2m	2b	2b	2m	2b	2b	2m	2b	2a	2m	2b	2b
Agrostis capillaris	2m	2a	+	+	2a	1	2a	2a	2m	2m	2m	2a
*Arnica montana**	1	+	2m	+	+	r			+			
*Danthonia decumbens**	r	+	+	2a	2a	2a	2a	2a	+	2a	2a	
*Galium saxatile**	2b	2b	2m	2m	2m	1	2m	2a	2m	2m	2a	1
Hieracium pilosella	+	2a	3	2b	2b	2m	+	1	2a	2m	2a	+
*Nardus stricta**		r				r						
Polygala serpyllifolia	+		1	+	r	+	+	r	1			1
*Potentilla erecta**	1	2a	+	+	+	+	2m	2a	+	1	+	+
Succisa pratensis					r	r						
*Veronica officinalis**				+	2m			r		+	2m	

continued

Table 4—*continued*

Experimental plot	C1	C1	C1	C2	C2	C2	L	L	L	D	D	D
Year	1990	1995	1995	1990	1995	1995	1990	1995	1995	1990	1995	1995
Sod-cut	–	–	+	–	–	+	–	–	+	–	–	+
Heathland species												
Calluna vulgaris†	r	+	2a	2a	2a	3	2a	2a	3	2a	2a	2a
Empetrum nigrum							+	+		r	+	
Erica tetralix			r		+		r	+	r	r	r	
Genista anglica†			+		+				+	r	+	
Vaccinium vitis-idaea				+	+							
Frequently found species in matgrass swards and heathland vegetations												
Carex pilulifera	2m	+	2m	2m	2m	2m	2m	2m	2a	2m	2m	2m
Deschampsia flexuosa	+	1	+		+	+	2a	2a	+	r	+	+
Festuca ovina	3	3	2a	3	2b	2a	3	2b	2b	3	2b	2a
Molinia caerulea	+	2a			+	+	+	+	+			+
Rumex acetosella	1	+	1	1	+	2m	1		1	1	+	1
Remaining species												
Achillea millefolium			r	+		r		+	+	2m	2m	+
Aira praecox			2m			2m			2m			2m
Anthoxanthum odoratum			+	2m	1	+	+	1	+	2m	2m	+
Chamerion angustifolium	+		+	r	+	+	+	r	+	1	+	+
Hieracium laevigatum	1	2m	+	+	1	+	2a	2a	1	1	2m	+
Hieracium umbellatum	r	+	+	+	+	r	+	+	+	+	+	r
Holcus lanatus	2m	+	1		+	+	+	+	+	+	+	+
Hypochaeris radicata	2a	2a	2m	2a	2m	3	2b	2a	2b	2b	2a	3
Leontodon autumnalis			+	r					+	r	+	
Luzula multiflora[1]	+	1	+	1	1	+		+				
Plantago lanceolata									+	r	+	+
Rubus fruticosus	2a	3	r				+	+		r	r	+

were lower in 1995 in most sod-cut plots than in the intact vegetation in 1990 and 1995. In contrast, *A. canina* was more abundant in the sod-cut, unlimed plots in 1995, regardless of the original vegetation.

Liming

Similarly to the soil chemical parameters, no major differences between liming with limestone or dolomite were observed. Therefore, dolomite and limestone treatments will be discussed together, unless stated otherwise.

Liming without sod-cutting caused an increase in species number in both the heath and the matgrass sward, but not in the grassland. In all experimental plots, most of the newly established species were characteristic for matgrass swards. In the matgrass sward, new establishments of *Polygala serpyllifolia*, *P. erecta*, *Nardus stricta* and *Hieracium pilosella* were found after liming. The expansion of *A. canina* in the limed plots of the matgrass sward and grassland was equal to the increase in the unlimed plots of these sites. An increase in abundance of *A. canina* was also observed in the limed heath plots, but it was absent in the unlimed plots of this site. The abundance of some typical heathland species, e.g. *C. vulgaris* and *G. anglica*, was reduced after liming in the matgrass sward.

The effects of the combination of sod-cutting and liming were most pronounced in the matgrass sward. The heath vegetation responded to a lesser degree to this combination of treatments, whereas in the grassland, the effects of a combined liming and sod-cutting treatment were almost similar to the effects of sod-cutting (Table 4, sod-cut, limed plots). In the heath and matgrass sward, the combination of both treatments increased species number considerably compared to the intact vegetation in 1990 and the unlimed sod-cut plots. Compared to sod-cutting only, the number of characteristic matgrass sward species increased. Some of those species, e.g. *P. erecta* and *H. pilosella* had higher abundances than in either one of the treatments alone. Remarkable is the large abundance of *Hypochaeris radicata* in all sod-cut, limed sites. Especially in the matgrass sward, a large increase in the abundance of *H. radicata* was observed. As in the unlimed sod-cut plots, the dwarf shrubs *C. vulgaris* and *G. anglica* benefited clearly from sod-cutting, but no additional effect due to liming treatments was observed.

Effects of liming on Arnica montana *performance in established vegetation*

Detailed observations on the *A. montana* population in the non-sod-cut parts of the matgrass sward showed that the population in the unlimed plots declined from 1991 until 1996 (Table 5). During this period, the number of rosettes in the unlimed plots gradually decreased by almost 70%, and a decrease in the number of flower buds was also noted. As an indication of the seed-producing potential of the population, the ratio between flower buds and rosettes was calculated ('flower/rosette ratio'). Although this flower/rosette ratio fluctuated between years, it was always less than 0·5. In the limed plots, the *A. montana* population expanded during the same period, as can be seen from the rosette numbers (Table 5). In the same period, the number of flower buds increased even more, resulting in a higher flower/rosette-ratio (always >0·5) in the limed compared to the unlimed vegetation. Limestone increased the number of rosettes more than dolomite, whereas the latter treatment improved the flowering density of *A. montana* more than in the limestone treatment.

In the grassland, *A. montana* was only present in the control plots. In these plots,

Table 5. Performance of *Arnica montana* in non-sod-cut parts of the matgrass sward during the period 1991–96. Number of rosettes, flower buds and flower/rosette ratio. Rosettes and flower buds expressed as percentages from 1991, with absolute values in 1991 between brackets. Flower/rosette-ratios are derived from absolute values. C = control (no lime), L = limestone, D = dolomite

	Rosette			Flower buds			Flower/rosette		
	C	L	D	C	L	D	C	L	D
1991	100	100	100	100	100	100	0·21	0·51	0·47
	(99)	(72)	(82)	(20)	(37)	(39)			
1994	77	107	95	106	249	303	0·34	1·19	1·51
1995	51	153	111	31	186	197	0·12	0·63	0·85
1996	32	132	101	71	203	187	0·46	0·79	0·88

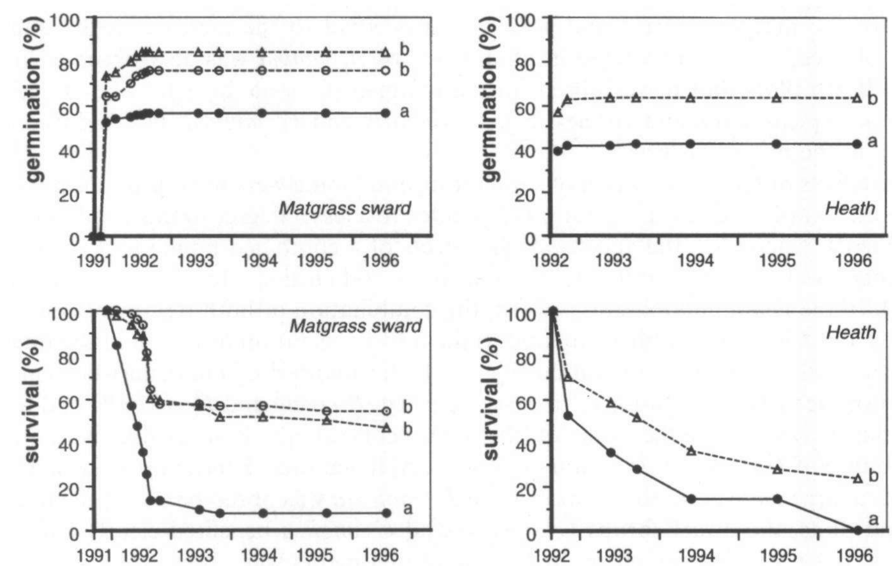

Fig. 4. The effects of liming on germination and survival percentages of sown *Arnica montana* in the matgrass sward and heath. Mean percentages, $N=4$ (except in controls of matgrass sward, $N=8$). Different letters indicate significant differences ($P<0·05$) between treatments within a plot. Closed circles: control (unlimed) plots; open circles: limestone-treated plots; open triangles: dolomite-treated plots.

the number of rosettes increased from 1991 to 1995 by 62% (from 25 to 41 rosettes per plot, mean values). Since the flower bud number increased only by 7% during the same period, the flower/rosette ratio was somewhat lowered (from 1·93 to 0·58). Nevertheless, this ratio was similar to the limed plots of the matgrass sward and much higher than in the unlimed plots of that site (Table 5).

Effects of liming on germination and survival of Arnica montana

Most *A. montana* seeds germinated during the first autumn after sowing in the sod-cut plots and only a few next spring; after this, no germination of *A. montana* was observed (Fig. 4). Between the limed and unlimed plots a clear difference in germination was observed: whereas 76–84% of the seeds germinated in the limed plots, only 56% of the

Table 6. Mean estimated biomass of sown, living *Arnica montana* plants in June 1994, 1995 and 1996 in the sod-cut matgrass sward and in the sod-cut heath. Biomass is estimated by the multiplication of maximum leaf length, maximum leaf width and the number of leaves (mm^2). Significant differences in biomass between treatments per year (row) are indicated by different letters. *: in 1996, all plants in the control treatment in the heath-site had died

	Treatment		
	Control	Limestone	Dolomite
Matgrass sward			
1994	1370 ab	2568 b	958 a
1995	1844 a	4702 b	1394 a
1996	3261 a	7383 b	2437 a
Heath			
1995	533 b	.	299 a
1996	0*	.	580

seeds germinated in the unlimed plots of the matgrass sward. In the sod-cut heath, germination of *A. montana* was somewhat lower after liming (63%) but still higher than in the control treatment (42%). A drastic effect of liming was also observed on the survival of the plants: 4 years after germination, only 8% of the *A. montana* plants were alive in the unlimed treatment, whereas 53% and 46% of the plants were still present in the limestone and dolomite treatments, respectively (Fig. 4). Biomass production of the *A. montana* plants was clearly higher in the limestone-treated plots than in the unlimed and dolomite-treated plots (Table 6). In the heath, *A. montana* plants were even bigger in 1995 in the unlimed plot than when dolomite was applied. However, all the plants in the unlimed plot died during the next year, in contrast to the plants in the dolomite treatment. The first flowering of the sown *A. montana* plants in the matgrass sward was noted in 1996, 5 years after the start of the experiment. No correlation between the percentage of flowering individuals with liming treatment was observed, but the statistics may have been biased by the very low number of plants in the control treatment. In the heath, no flowering of *A. montana* was observed.

DISCUSSION

Habitat requirements of different heathland vegetations

In this study we have tested restoration strategies used to rehabilitate the characteristic soil conditions and the typical vegetation of dry heathlands. We aimed to regenerate two vegetations: a Calluna-Genistion pilosae community and a Nardo-Galion saxatilis community. Both communities appear on nutrient-poor soils (Fennema 1992; Aerts & Heil 1993; Houdijk *et al.* 1993; Roelofs *et al.* 1996). In a field survey by Houdijk *et al.* (1993) it was shown that mineral nitrogen concentrations in the topsoil under different heathland species varied from 300 to 1050 μmol kg^{-1} dry soil, with the lowest concentrations in the Calluna-Genistion pilosae vegetations. A field study by Roelofs *et al.* (1996) has shown differences in ammonium concentrations between the heathland vegetations: under well-developed Nardo-Galion saxatilis communities significantly lower ammonium concentrations were found than under deteriorating Nardo-Galion saxatilis communities (50 vs. 150 μmol kg^{-1} dry soil, respectively). The ammonium concentrations in the Calluna-Genistion pilosae community were similar to those in declining Nardo-Galion saxatilis communities. Experiments with the characteristic *A. montana* (Nardo-Galion saxatilis community) showed that high ammonium concentrations (>100 μmol l^{-1}) are toxic to this species (De Graaf *et al.* 1998). In contrast, many species of the Calluna-Genistion pilosae community even prefer ammonium as a nitrogen source and ammonium toxicity has not been shown, not even at ammonium concentrations as high as 500 μmol l^{-1} (Troelstra *et al.* 1995, De Graaf *et al.* 1989). Thus, in order to restore different heathland vegetations, not only the amount of mineral nitrogen needs to be reduced, it is also necessary to restore low ammonium concentrations in the topsoil in order to rehabilitate a Nardo-Galion saxatilis community.

Furthermore, the characteristic species of the Nardo-Galion saxatilis community require moderately acidic soils (4·2<pH < 6·0), in which aluminium concentrations and aluminium to calcium ratios are not too high (Al/Ca <5·0; Houdijk *et al.* 1993; De Graaf *et al.* 1994). It was shown in water culture experiments that aluminium may become toxic to *A. montana* at 50 μmol l^{-1} (De Graaf *et al.* 1997), whereas aluminium toxicity in Calluna-Genistion pilosae species has only been shown at extremely high aluminium concentrations (>400 μmol l^{-1}; Hackett 1965; De Graaf *et al.* 1997).

Restoration of heathlands

The results of this study showed that in all three sites the aimed heathland vegetation could be restored by restoring the soil conditions: in sites where soil acidity already matched the requirements of the vegetation before restoration, e.g in the heath and the grassland, sod-cutting was sufficient for rehabilitation of the vegetation. When soil acidity was increased by atmospheric deposition, as had happened in the matgrass sward, liming was needed in order to reverse the soil acidification.

Ecosystem functioning is generally affected by sod-cutting in two ways: first, nutrient concentrations in the soil are reduced to sufficiently low levels for heath vegetations (Table 1; Houdijk *et al.* 1993). Secondly, a bare substrate for germination and seedling establishment is created by sod-cutting.

Sod-cutting reduced almost all nutrient concentrations in the topsoil layer: not only were N and P reduced, but Ca and Mg concentrations were also lower in the sod-cut than in the non-sod-cut parts. Although these base cations are important to the buffering capacity of these acid soils (Scheffer & Schachtschabel 1992), pH was not influenced by sod-cutting in the matgrass sward and grassland. In the heath, pH of the mineral top 10 cm soil increased due to the removal of the most acidic organic top centimetres.

The initial decrease in mineral nitrogen immediately after the sods have been removed was, however, followed by a large increase in mineral nitrogen to up to three times the nitrogen concentration in the non-sod-cut soils, to values far above those which are considered apropriate for Nardo-Galion saxatilis communities (Fig. 1). This might be due to an initial increase in nitrogen mineralization; Berendse (1990) measured high N mineralization rates during the first two years after sod-cutting, which were probably caused by the mineralisation of roots that were excised with the removal of the sods. Since these remaining living roots have relatively high N contents, the C:N ratio of the organic material in the soil is temporarily decreased, which consequently leads to an increase in mineralization (Berendse 1990). As plant uptake of N is negligible during the first year after sod-cutting, the mineral nitrogen formed by the mineralization can reach high values in the top soil. High ammonium concentrations may arise from the fact that, in acidic heathlands, nitrate is almost exclusively formed in the humus layer, whereas the formation of ammonium also occurs in the mineral soil layers (De Boer *et al.* 1989). Removal of the organic soil layers thus negates the nitrification capacity, resulting in enhanced ammonium concentrations. These high ammonium concentrations may affect the establishment of *A. montana* in the first year after sod-cutting, since these are detrimental to this species (De Graaf *et al.* 1998). The establishment of more acid-tolerant species, e.g. *C. vulgaris*, *E. nigrum*, *D. flexuosa* and *M. caerulea*, will probably be unaffected due to their preference for ammonium as a nitrogen source (Troelstra *et al.* 1995; De Graaf *et al.* 1998).

In dry heath vegetation, gap formation is important for the establishment of seedlings of many species (Miles 1974; Fennema 1990). Experiments on sod-cutting in Scottish heath showed that most species present in the original vegetation had returned 3 years after sod removal (Miles 1973). In addition, Miles observed that a higher number of species became established on more fertile, less acidic heathland soils than on the more acid soils, including some typical matgrass sward species (e.g. *Galium saxatile*, *Veronica officinalis*, *Polygala serpyllifolia* and *P. erecta*). Our results are in agreement with this: after sod-cutting nearly all species returned and most species established on the grassland, followed by the matgrass sward, whereas the lowest number of species established on the heath. Most of these species were present in the plot before sod-cutting and are thus likely to have emerged from the soil seed bank (Table 4). Other newly found species were either present in the surroundings of the plot or were ruderals (grassland).

Apart from the species number, the relative abundance of species is also affected by sod-cutting. As in many species-poor heathlands, the abundance of *D. flexuosa* and/or *M. caerulea* is largely reduced in favour of *C. vulgaris* (Table 4; Diemont & Linthorst-Homan 1989). The establishment of *E. nigrum* was, however, seriously restricted by sod-cutting. This indicates that in grass heaths formerly dominated by *E. nigrum*, sod-cutting should be applied only after careful consideration.

Heathland restoration on abandoned grasslands has its own specific problems. During the years of agricultural use, lime and fertilizers have often been applied. Effects of such liming practices on soil pH, exchangeable calcium and, possibly, on mineralization, are detectable long after lime applications have been ceased and may hamper heathland restoration on abandoned fields (Pywell *et al.* 1994). In this study, the soil conditions in the grassland still reveal the signs of former liming: soil pH and base action contents are higher than in the adjacent heathland site. In fact, they are suitable for a Nardo-Galion saxatalis vegetation. Additional experimental liming with very low doses had hardly any effect on soil chemistry or vegetation (Tables 3 and 4). The soil fertilty of the abandoned grassland has slowly decreased since the cessation of agricultural practices, due to the practice of yearly mowing of the vegetation with removal of the hay. Despite this, many species which are characteristic of more fertile grasslands are still present, although some of these species, e.g. *Holcus lanatus*, are now declining. The results of this experiment show that the restoration of heathland on abandoned grassland can be accelerated by sod-cutting (Table 4).

Without interference, the decline of the *A. montana* population in matgrass sward plots continued throughout the experimental period (Table 5, unlimed, non-sod-cut plots). This decline was probably due to soil acidification: during the experimental period, base cation concentrations in the unlimed, non-sod-cut plots were reduced by 50% (Fig. 3) and ammonium concentrations increased to values markedly above those on which well developed Nardo-Galion saxatilis communities usually occur (Roelofs *et al.* 1996). Moreover, it is unlikely that the decline of *A. montana* is caused by competitive interactions with grasses, since the total cover of the grasses in the controls of the non-sod-cut plots did not change considerably during the experimental period.

Liming served to reverse soil acidification and after liming, soil conditions in the matgrass sward closely resemble those on which vital Nardo-Galion saxatilis communities occur (Houdijk *et al.* 1993; Roelofs *et al.* 1996). The beneficial effects of liming on *A. montana* are clearly shown by the improved vitality of the established population in the matgrass sward (Table 5) and the better germination, establishment and vitality of *A. montana* sown in the sod-cut parts of the heath and matgrass sward (Fig. 4, Table 6). The apparent contradiction on the abundance of *A. montana* after liming in Table 4B (no effects of liming) and Table 5 (increased abundance after liming) are to be ascribed to the rather crude Braun–Blanquet method, which is unable to distinguish between small changes in abundance. Moreover, liming increased the species number, which was largely due to an increase in species characteristic of Nardo-Galion saxatilis communities, again indicating that these species favour less acidic soils than the characteristic Calluna-Genistion pilosae species.

The effects of lime applications on ecosystem functioning are, however, not always beneficial. First, not all species respond well to liming: the abundance of *C. vulgaris* is largely reduced in the limed plots of the matgrass sward. A reduction in abundance of acid-tolerant species after liming has previously been observed by Blom & Wincent (1989) in acidic grasslands in Sweden, which were treated with 1000–2000 kg ha^{-1} dolomitic lime. Secondly, in non-sod-cut ecosystems, liming may enhance N-mineralization and nitrification (Nyborg & Hoyt 1978), which may eventually lead to leaching of nitrate to the groundwater (Kreutzer 1995) and to a transition from dwarf-shrub-dominated heath to monotonous grass stands (Heil & Aerts 1993). Although we did not measure mineralization rates in this experiment, some observations indicate that nitrogen mineralization increased, at least temporarily, in the limed plots. The most obvious indications for the enhanced nitrogen mineralization and nitrification were the increased nitrate concentrations in the winters of 1994 and 1995. It is likely that the vegetation readily took up this nitrate during the following summer, since the nitrate concentrations in the limed plots did not differ from those in the unlimed plots in autumn. Leaching of NO_3^- only occurs if the retention capacity of the ecosystem for nitrogen is exceded (Kreutzer 1995). Normally, nitrate leaching from heathlands is very low (Van der Maas 1990). It is probably even lower in sod-cut heaths, since it was found that after sod-cutting of a species-poor dry heath, all incoming atmospheric nitrogen accumulated in the system for a period of 30 years (Berendse 1990). Nevertheless, we recommend a combined liming and sod-cutting treatment in order to minimize the risk of unwanted eutrophication effects.

CONCLUDING REMARKS

It is concluded that restoration of the soil conditions is necessary for the rehabilitation of various heath vegetations. However, if the long-term conservation of the restored heathland vegetation is to be assured, the inputs of atmospheric pollutants must decrease below set critical loads (e.g. Bobbink & Roelofs 1995).

The success of restoring species-rich heathland vegetation is, however, not only dependent on the restoration of abiotic conditions. Re-establishment of endangered species also depends on the availability of seeds. A positive situation exists in these experimental sites, but seed availability is a limiting factor in many restoration projects. In this experiment we did not observe the establishment of Nardo-Galion saxatilis species that were absent from the seed bank or in the nearby surroundings of the experimental plots. Even *Thymus serpyllum*, which was found 300–500 m from the experimental plots, was not found after rehabilitation of the soil. As soil conditions were suitable for the establishment of this and other species characteristic of this community (Houdijk *et al.* 1993; Houdijk 1993), the absence of the species must be caused by the absence of seeds due to limited dispersal and/or due to the lack of a viable seed bank. Unfortunately, most of the rare species of the Nardo-Galion saxatilis comunities lack long-term seed banks (Bakker *et al.* 1996), thus diminishing the chances for successful re-establishment after restoration of the soil. Sadly, this is shown by the results of a similar experiment with combined sod-cutting and liming in another Dutch heathland: although we were able to restore soil conditions the rare Nardo-Galion saxatilis species, which had disappeared 10 years previously, did not return due to the absense of viable seeds or nearby seed sources (Roelofs *et al.* 1996). This emphasizes the importance of saving seed-setting plants from restoration practices such as sod-cutting, in order to provide nearby seed sources after restoration. Otherwise, deliberate reintroduction of plant species is probably the only way to establish complete Nardo-Galion saxatilis communities in heathlands in which soil conditions will have been restored in the near future.

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