Effects of grazing by free-ranging cattle on vegetation dynamics in a continental north-west European heathland

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Summary

1. Abandonment and eutrophication are major threats to traditional pastoral landscapes and their wildlife in Europe. Social and economical developments have rendered traditional pastoralism impracticable. More knowledge is needed about the effects of grazing with free-ranging herbivores, which is increasingly used as a substitute for the traditional herding system.

2. We studied the effects of free-ranging cattle on the recovery of *Calluna* heather, tree encroachment and plant species richness in six habitats in a grass-rich Dutch heathland during a 10-year period. The habitats differed in soil fertility, initial heather–grass ratio and developmental stage of *Calluna*.

3. Despite preferential grass defoliation, cattle grazing neither reduced grass cover in grass heath nor prevented grass invasion in heather. Grass invasion failed only in a nitrogen-poor turf-stripped *Calluna* heath. Grazing induced a substantial *Calluna* recovery in grass heaths on podzolic soils, but its recovery failed in grass heath on a phosphorus-rich medieval arable field. As a consequence, the grass–heather mosaics generated by free-ranging cattle were restricted to habitats of intermediate soil fertility.

4. Grazing did not prevent encroachment by pine and birch. Removal by the site manager prevented conversion of 10–20% of the open heathland to forest.

5. During the first 5 years, grazing induced a significant increase in species richness in all habitats. During the second 5 years, species richness stabilized in grass heath and heather–grass mosaics and it declined in the pioneer *Calluna* heaths.

6. We found indications of various nutrient-mediated grazing effects on the competitive balance between grass and woody pioneers. These suggest that nutrient-mediated feedback might be an important explanatory mechanism for the described vegetation mosaic cycling in heathlands.

7. Free-ranging grazing did not remove the high atmospheric nutrient inputs of the whole area. Substantial amounts of nutrients were redistributed from the grass lawns to the forest.

8. Free-ranging grazing combined with tree cutting appeared to be a suitable management regime for the maintenance of species-rich open heathlands with dynamic grass–heather mosaics.

9. Without tree cutting, free-ranging grazing would have created dynamic tree–grass–heather mosaics in open heathland. Wood–pasture landscapes are fundamentally different from the open heather-dominated heathlands produced by the traditional sedentary farming system. Integrated grazing of heathland, nutrient-rich farmland and forests accelerates this change. Alternative grazing regimes are discussed.

Key-words: biodiversity, *Calluna vulgaris*, *Deschampsia flexuosa*, herbivory, mosaic cycling.

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Introduction

Abandonment in conjunction with atmospheric eutrophication is a major threat to the high conservation values of European traditional pastoral landscapes (Gimingham 1972; Bignal, McCracken & Curtis 1994; Bignal & McCracken 1996; Bignal 1998; Ostermann 1998; Webb 1998). Increased labour costs have rendered traditional herding systems economically unfeasible. Herding is increasingly replaced by more profitable free-ranging systems, using livestock or wild herbivores grazing over extensive areas. Little is known about the long-term effects of this change in grazing patterns on the landscape structure and its conservation values. The design of effective grazing systems for conservation management requires predictive knowledge of the effects on biodiversity and the underlying ecological key processes and factors, e.g. vegetation succession and nutrient availability (McCracken & Bignal 1998). Long-term monitoring provides this information (Illius & Hodgson 1996; Hester & Baillie 1998; Piek 1998; Hester *et al.* 1999) and offers an opportunity for the validation of simulation models (Wallis de Vries & Van de Koppel 1998). This paper assesses the effects of free-ranging cattle on the vegetation dynamics and species richness of open heathland vegetation in the Netherlands, with a special focus on nutrient-mediated mechanisms.

Inland heaths in continental north-west Europe originated mainly by sedentary pastoralism and associated land use (De Smidt 1979; Pott & Hüppe 1991; Pott 1998; Webb 1998). The daily return of the herd to the stable maximized the harvest of manure, which was essential for sustained sedentary arable farming on the nutrient-poor Pleistocene sandy sediments. After the 11th century, the manure was enriched with organic matter from 'plaggen' (sods) from the rangeland. This practice created 'plaggen soils', with a typical thick, black–brown, humic, nutrient-rich topsoil on the arable fields (Pape 1970).

Traditional sedentary herding declined in northwest Europe at the beginning of the 20th century after the introduction of synthetic fertilizers and barbed wire fencing. The abandoned rangelands were transformed into fertilized farmland and forest. In the Netherlands, approximately 40 000 ha of lowland heath (5% of the original 800 000 ha) remained unchanged. The majority of this area is managed today as a nature reserve. An open landscape, low soil fertility and substantial heather cover are considered essential for the survival of many endangered species (Bal *et al.* 1995). Until 1970, management was mainly restricted to the removal of encroaching trees. After 1960, the dominant heather species *Calluna vulgaris* L. and *Erica tetralix* L. were increasingly replaced by the perennial grass species *Deschampsia flexuosa* (L.) Trin. and *Molinia caeru-lea* (L.) Moench (Diemont 1996). Similar changes were reported from surrounding countries (Bülow-Olsen 1980; Marrs, Hicks & Fuller 1986; De Blust & Schneiders 1989; Pott & Hüppe 1991).

The grass invasion and loss of biodiversity were attributed to increased nitrogen deposition and to abandonment by traditional livestock farming (including woodcutting, burning and turf-stripping; Diemont & Heil 1984; Anonymous 1988). Both changes were assumed to favour succession, eutrophication and acidification (Aerts 1993a,b; Bobbink, Hornung & Roelofs 1998; Bakker & Berendse 1999). Grass invasion was accelerated by a positive feedback between nitrogen availability and grass dominance (Berendse 1990, 1994). Turf stripping (removing grass, litter and nitrogen and exposing *Calluna* seeds) appeared to be an effective method for the restoration of heather dominance (Diemont & Lindhorst Homan 1989; Heil & Aerts 1993). However, turf stripping has serious financial and biodiversity drawbacks (Anonymous 1988). This generated new interest in free-ranging grazing as a cheap alternative for sedentary herding and turf stripping.

The (re)introduction of grazing is hindered by the small amount of available information on grazing management methods and their differential effects on lowland heath (Bullock & Pakeman 1997; Webb 1998). Heathland grazing studies refer mainly to British upland areas and to sheep and red deer *Cervus elaphus* L. (Gimingham 1972, 1992; Welch & Scott 1995; Hester & Baillie 1998). Moderate stocking rates are commonly recommended to prevent tree encroachment and allow heather regeneration (Miles 1981; Gimingham 1992; Dolman & Land 1995). Overgrazing may damage the heather canopy, thus precipitating invasion by grass (MacDonald 1990; Gimingham 1992; Hester & Baillie 1998). Undergrazing will lead to *Calluna* degeneration, shrub and tree encroachment and grass invasion (Miles 1981; Loiseau, Ignace & L'Homme 1987; Diemont 1996).

The evidence for grazing-induced heather recovery in grass heath is scarce and conflicting. Examples with little or no heather recovery reported from the Netherlands are all derived from fertilized former heaths, grazed by sheep (Bakker *et al.* 1983), cattle (Wind 1980; Van den Bosch & Bakker 1990) and ponies (Van de Laar & Slim 1981). On former arable fields in the New Forest (southern England), *Calluna and Erica cinerea* recovery is seriously constrained by intensive defoliation and trampling by cattle and ponies (J. Bokdam, personal observations). Successful heather re-establishment has been reported from unfertilized grass heaths, grazed by cattle (Buttenschøn & Buttenschøn 1982; Janssen 1984; Bülow-Olsen, unpublished data; Van Wieren 1988) and sheep or red deer (Bullock & Pakeman 1997; Welch & Scott 1995). The heather recovery in

grazed unfertilized grass heaths conflicts with the sustained low heather cover in grazed wet upland grass heaths (Welch 1997) and with dramatic heather expansion after the relaxation of grazing pressure (Jones 1967; Ball 1974; Anderson & Yalden 1981; Miles 1982).

These different results of grazing in grass heaths might be attributed to differences in site (climate, management history, soil fertility, initial grass–heather ratio, heather and grass species, heather seed bank, developmental stage of heather), grazing regime (including wild herbivores) and spatio-temporal scale of observation. We hypothesized that free-ranging cattle might induce heather recovery, inhibit tree encroachment and increase vascular plant species richness in grass heath on nutrient-poor soils.

The effects of grazing on vegetation tend to be explained primarily by visible, above-ground, changes in the vegetation and litter structure due to defoliation and trampling. Tissue loss and modified light profiles may be major causes of changes in establishment, growth, competitive success and longevity (Ritchie & Olff 1999). Short-term effects of dung and urine are also apparent. Long-term changes in the nutrient availability are less easy to assess (Milchunas & Lauenroth 1993). Nevertheless they might play a key role, especially in nutrient-poor environments (Berendse 1985; Jefferies, Klein & Shaver 1994; Jefferies 1999). Nutrients may affect plant production, nutritional quality and resistance to herbivores and defoliation tolerance (Lambers, Chapin & Pons 1998; Milchunas, Lauenroth & Burke 1998). Herbivores move nutrients directly by ingestion, retention and excretion and indirectly by modifying mineralization, dry deposition, leaching and erosion. They change pathways (De Mazancourt, Loreau & Abbadie 1998), flow rates (Pastor *et al.* 1993) and pools (Milchunas & Lauenroth 1993). Positive nutrient-mediated feedback may stabilize or intensify the grazing pressure on grazing lawns (McNaughton 1984). Negative feedback may induce abandonment after declines in production and nutritional quality, and an increase in the intrinsic resistance. A lower nutrient availability might induce higher lignin and tannin concentrations according to the carbon–nutrient ratio hypothesis (Bryant, Chapin & Klein 1983; Hobbie 1992; Iason & Hester 1993). Neighbouring plants may provide associational resistance or associational palatability (Huntley 1991; Hester *et al.* 1999; Olff *et al.* 1999).

It was hypothesized that replacement of the traditional land use by free-ranging cattle would lead to nutrient redistribution rather than nutrient removal. The resultant soil fertility patterns and the free habitat choice might lead to greater feedback between vegetation development and use by the herbivores.

This might, in turn, lead to the emergence of shifting mosaics.

Materials and methods

STUDY AREA AND HABITATS

The Wolfhezerheide nature reserve is situated on the Veluwe in the centre of the Netherlands, about 12 km east of Wageningen (51°47′N; 5°41′E). Natuurmonumenten has owned this nature reserve since 1966. The grazed area (40 ha of open heathland and 20 ha of forest) covers podzolic soils in fluvio-glacial sand and cover sand, a small area of plaggen soils in cover sand, and some moist podzolic and peat soils on a valley bottom (Vrielink & Van den Hurk 1975). The plaggen soils belonged to the medieval settlement 'Wolfheze'. Spanish soldiers destroyed it in 1585 and its arable fields were mainly used as pasture afterwards (Natuurmonumenten 1996). The annual atmospheric nutrient deposition (wet plus dry) in the open heathland accounted for about 40 kg nitrogen, 1·5 kg phosphorus and 5 kg potassium ha^{-1} (Erisman & Heij 1991). Until 1983, juvenile trees were removed from the open heathland and old heather was occasionally mown (Natuurmonumenten 1996). *Deschampsia* invasion started in about 1960 on the plaggen soil and spread between 1970 and 1980 to the dry podzolic soils (B.W. Jacobs, B. Jansen & W. Aandeweg, personal communication). Some parts of the remaining mature heather were turf-stripped in 1980, other parts were mown in 1982 (Table 1). In 1983, *Deschampsia* covered major parts of the open heathland. Minor parts were covered by mature *Calluna*, pioneer *Calluna* and *Molinia* (Table 1).

In January 1983, the area was stocked with 17 Dutch Friesian heifers, which from May 1983 were gradually replaced by suckling cows of various breeds. Annual stocking rates were maintained at an equivalent of approximately 0·2 animal units ha^{-1} (1 animal unit = 450 kg). Rates were approximately 30% higher in the summer than in the winter. During the whole study period one to three horses were allowed in the area. Late winter densities of roe deer *Capreolus capreolus* L. (2–4 km^{-2}) and rabbits *Oryctolagus cuniculus* L. (100 km^{-2}) were low. The latter value increased slightly during the study period (B.W. Jacobs, personal communication). From 1984 a minor quantity (1–2 kg dry matter animal^{-1} day^{-1}) of supplementary food (concentrates, hay or corn silage) was provided during late winter.

After 1983, the manager occasionally removed juvenile trees (1–2 m), mainly Scots pine *Pinus sylvestris* L. and silver birch *Betula pendula* Roth. No fires occurred. The winters of 1984–85 and 1985–86 were extremely cold and winter browning of *Calluna* (MacDonald 1990) was observed. Heather beetles

Table 1. Main characteristics of six open heathland habitats at the Wolfhezerheide in 1983

Habitat	CI	CII	CIII	DI	DII	M
Initial vegetation (1983)	Pioneer *Calluna*	Pioneer *Calluna*	Mature *Calluna*	*Deschampsia* (± tussocks)	*Deschampsia* (tussocks)	*Molinia* (tussocks)
Soil	Podzolic	Podzolic	Podzolic	Podzolic	Plaggen	Podzolic, peat
Historical land use	Pasture	Pasture	Pasture	Pasture	Arable field and pasture	Pasture
Previous management	Turf-stripped in 1980	Mown in 1982	–	–	–	–
Grazed plots (serial numbers)	$n=3$ (23, 24, 41*)	$n=2$ (30,35*†)	$n=6$ (22, 25, 26, 34*, 36*, 37*†)	$n=7$ (17, 27, 28† 29, 31†, 32† 38*)	$n=3$ (8, 11, 33‡)	$n=3$ (12, 13, 14)
Ungrazed plots (serial numbers)	–	–	–	–	$n=2$ (39*, 40*)	$n=2$ (43*, 44*)

*Established in 1984; †affected by heather beetles in 1990–91; ‡ affected by supplementary feeding.

Lochmaea suturalis damaged *Calluna* locally in 1991 (personal observation).

MEASUREMENTS

Habitats and treatments

In 1983, we located 21 5×5 m plots randomly in six habitat types in the grazed open heathland (Table 1). The habitats differed in soil, land-use history, previous management and initial vegetation. In April 1984, seven grazed plots and four ungrazed plots were added (Table 1). The ungrazed exclosures (approximately 8×8 m; mesh size 5×5 cm) were constructed in the most heavily grass-dominated *Deschampsia* heath on plaggen soil and in *Molinia* heath.

Plant cover and Calluna density

Plant cover was recorded annually in August–September, using an extended point quadrat method (Goldsmith & Harrison 1976). Pins (diameter 2·5 mm) were lowered through 10 vertical holes at 10-cm intervals in a horizontal plastic tube (diameter 5 cm, length 100 cm, 40 cm above ground level). The tube was located randomly in each plot 10 times, providing 100 pins. Hits for vascular plants (living parts only) were noted. Mosses and lichens were recorded as a group. If a species was hit more than once by the same pin, it was recorded only once. Several species per pin indicated overlap. The number of hits per species by 100 pins reflected the species cover (0–100%). Second and third samples of 100 pins were added until the average cover remained constant ($< 5\%$ change to the average by adding a new series). The cover of species not hit by the pins (i.e. species with a low cover or with foliage above 40 cm height) was estimated visually. Cover measurements in the ungrazed *Molinia* heath started in 1987.

Calluna individuals were counted in the grass heaths to assess the re-establishment rate.

Soil fertility

The soil fertility of the dry habitats was sampled during the winter 1987–88. Samples from A_o (the ectorganic layer, including litter, fermented horizon and humic horizon) were taken at 50 random locations within 5 m around each plot. At each location, thickness was measured on the four sides of a 1-dm^2 sod. The A_o material was transported in plastic bags to the laboratory for chemical analysis. The thickness of the A_m horizon (grey–blackish mineral horizon between A_o and the brownish B horizon) was measured using an Edelman auger (diameter 7 cm) at eight locations around each plot. Volume samples from A_{10} (the upper 10 cm of A_m) and the total A_m

were collected at eight locations around each plot with a gouge auger (diameter 30 mm). Samples were mixed per plot. Laboratory treatments followed Houba *et al.* (1986). Subsamples of A_o were dried at 70 °C for 7 days, grounded and sieved. Mineral soil samples were only sieved (mesh size 2 mm). For all horizons, organic matter content was measured as loss-on-ignition. The pH was assessed after adding 1 M KCl solution to the soil. Total N and P concentrations (spectro-photometrically) and the total K concentration (flame-photometrically) in the soil were measured after digestion in H_2SO_4–salicylic acid–H_2O_2 and selenium. Extractable $NH4^+$-N, $NO3^-$-N, P and K in the topsoil ($A_o + A_{10}$) were measured after digestion in 0·01 M $CaCl_2$, using a Technicon Auto-analyser (Skalar, Breda, the Netherlands).

Calluna seed bank

To explain different rates of *Calluna* recovery, we assessed the *Calluna* seed bank in A_o and A_5 (the top 5 cm of A_m) in grass heath on podzolic soil (three plots) and plaggen soil (two plots) in June 1991. Two-hundred soil samples were taken with a gouge auger (diameter 30 mm) within a 5-m distance around each plot. The A_o (without unfermented litter) and A_5 material were placed on perforated dishes. The dish area per plot and horizon was 1414 cm^2 and the resulting thickness of the soil material on the dishes was 1 cm for the A_o material and 5 cm for the A_5 material. The dishes were placed in full daylight in a non-heated, ventilated, greenhouse. They were kept moist and cool (< 35 °C) by daily sprinkling for 130 days (28 June−4 November 1991). Emerging seedlings were removed with minimal soil disturbance. Their number was expressed per m^2 dish area, approximating the density of viable seeds per unit exposed area under field conditions. Our method did not yield an estimate of the seed bank per unit volume, as the material was not stirred, dried and remoistened during the germination period (Hester, Gimingham & Miles 1991; Bruggink 1993).

Plant height

The defoliation pressure on grass and heather in the *Deschampsia* heaths on podzolic and plaggen soil was approximated by measuring the plant height of *Deschampsia* (20 random locations per plot) and *Calluna* (20 individuals or all available individuals). A perforated foam disc (diameter 10 cm; weight 8 g) was slowly lowered down a vertical measuring rod on to the plant canopy.

DATA ANALYSIS

Calluna died in some plots in 1991–92 due to a heather beetle outbreak. This necessitated separation

of affected and unaffected plots (Table 1). One of the plots in the grazed *Deschampsia* heath on plaggen soil was omitted because vegetation and soil had been severely affected by trampling and excretion during supplementary feeding at the site (Table 1).

The measured data were tested for normality using a one-sample Kolmogorov–Smirnov test (Norusis 1993). Viable seed numbers were log-transformed. The seed bank of the A_o as a percentage of the total seed bank was arcsine-transformed. Differences between habitats or treatments were tested using two-sample *t*-tests or ANOVA followed by Student–Newman–Keuls multiple comparisons. Homogeneity of variance was checked using Levene's test. Differences between time series of grazed habitats were tested using ANOVA with year as covariate. Grazing–year interactions were detected by comparing two test designs. When two-way or higher order interactions were absent, main effects were tested with a one-way ANOVA with year as covariate.

Results

SOIL FERTILITY

All habitats were very acid (Table 2). The extreme soil fertility values occurred in the pioneer *Calluna* heath on podzolic soil and in the *Deschampsia* heath on plaggen soil (Table 2). The A_o thickness and organic matter pool were significantly lower ($P < 0·05$) in the two pioneer *Calluna* heaths than in the other habitats. The extractable nitrogen was also lower, but only significantly so ($P < 0·05$) in the turf-stripped *Calluna* heath. The grazed *Deschampsia* heath on plaggen soil differed significantly ($P < 0·05$) from the one on podzolic soil in its thicker A_m layer, higher A_o phosphorus pool and higher extractable phosphorus. The latter value was also significantly higher in the grazed than in the ungrazed treatment ($P < 0·05$).

HEATHER AND GRASS COVER

The cover of *Calluna* and *Deschampsia* displayed different trends in the four grazed habitats on podzolic soil (Fig. 1a–d; habitat × year effect, $P < 0·001$; Table 3). In the turf-stripped pioneer *Calluna* heath (Fig. 1a), *Calluna* cover increased during the study period to nearly 90%. This contrasted with the persistently low *Deschampsia* cover. In the mown pioneer *Calluna* heath, cover of both species increased (Fig. 1b). In the mature *Calluna* heath (Fig. 1c), *Calluna* declined initially, particularly between 1985 and 1986, but it recovered afterwards. Similar declines occurred between 1985 and 1986 in the other *Calluna* habitats. *Calluna* also recovered after the crash due to heather beetles in 1991–92 (Fig. 1b–d). *Deschampsia* cover increased or stabilized at a high

Table 2. Soil characteristics of five grazed and one ungrazed dry heathland site at the Wolfhezerheide (for site descriptions see Table 1 and text). Values in a row with a same letter are not significantly different (one-way ANOVA and Student–Newman–Keuls test, $P < 0.05$). A_o = ectorganic horizon (L + F + H); A_m = humus-rich mineral horizon; A_{10} = upper 10 cm of the A_m. Extractable nutrient values concern the topsoil ($A_o + A_{10}$)

Sites (n)	Grazed turf-stripped pioneer *Calluna* heath (2)	Grazed mown pioneer *Calluna* heath (2)	Grazed mature *Calluna* heath (5)	Grazed *Deschampsia* heath (7)	Grazed *Deschampsia* heath (2)	Ungrazed *Deschampsia* heath (2)
Soil type	Podzol	Podzol	Podzol	Podzol	Plaggen	Plaggen
Thickness A_o (cm)	0·10a	0·33a	1·70b	1·93b	1·97b	3·07c
Thickness A_m (cm)	31·7ac	26·5abc	30·0a	27·3a	55·5c	54·0bc
Organic matter A_o (ton ha^{-1})	–	3·5a	34·8b	33·7b	37·8b	40·2b
Organic matter A_{10} (ton ha^{-1})	111·2b	106·4ab	94·0ab	89·6ab	82·3ab	74·2a
Organic matter A_m (ton ha^{-1})	219·1	194·2	211·9	210·1	323·0	354·6
pH KCl A_o	–	3·09	3·00	3·06	3·14	3·14
pH KCl A_{10}	3·40ab	3·32ab	3·39b	3·40b	3·11ab	3·04a
Nitrogen pool A_o (ton ha^{-1})	–	–	0·75	0·88	1·01	1·05
Nitrogen pool A_{10} (ton ha^{-1})	2·27	2·28	2·04	1·99	2·01	1·90
Nitrogen pool A_m (ton ha^{-1})	4·91	3·78	4·84	4·68	7·51	7·69
Phosphorus pool A_o (ton ha^{-1})	–	–	0·04ab	0·04a	0·06b	0·03ab
Phosphorus pool A_{10} (ton ha^{-1})	0·41	0·26	0·34	0·33	0·45	0·37
Phosphorus pool A_m (ton ha^{-1})	0·87	0·55	1·01	0·93	2·36	1·94
Potassium pool A_o (ton ha^{-1})	–	–	0·07	0·09	0·10	0·07
Potassium pool A_{10} (ton ha^{-1})	0·99	0·88	1·01	0·92	0·93	0·92
Potassium pool A_m (ton ha^{-1})	2·87	2·41	3·23	2·80	4·88	4·29
Extractable nitrogen (kg ha^{-1})	3·2a	12·8ab	36·0c	26·2bc	33·1bc	18·9abc
Extractable phosphorus (kg ha^{-1})	0·39a	0·46a	5·27a	3·49a	16·55b	5·38a
Extractable potassium (kg ha^{-1})	24·7a	24·6a	74·3b	49·8ab	58·3ab	83·3b

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(a) Grazed turf-stripped pioneer *Calluna* heath on podzolic soil

(b) Grazed mown pioneer *Calluna* heath on podzolic soil

(c) Grazed mature *Calluna* heath on podzolic soil

(d) Grazed *Deschampsia* heath on podzolic soil

% cover

(e) Grazed *Deschampsia* heath on plaggen soil

(f) Ungrazed *Deschampsia* heath on plaggen soil

(g) Grazed *Molinia* heath on podzolic/peat soil

(h) Ungrazed *Molinia* heath on podzolic/peat soil

Year

Fig. 1. (a–h) Cover change of potential dominant species in six heathland habitats at the Wolfhezerheide. (a–d) Grazed pioneer and mature *Calluna* and *Deschampsia* heaths on podzolic soils. (e–h) Grazed and ungrazed *Deschampsia* heath on plaggen soil and *Molinia* heath on podzolic–peat soil. Vertical bars indicate SE. Filled squares = *Calluna*; diamonds = *Erica*; triangles = shrubs and trees; circles = *Deschampsia*; open squares = *Molinia*; continuous lines = plots not affected by heather beetles; broken lines = plots affected by heather beetles.

Table 3. *F*-values and significance levels of main effects of habitat, year and habitat × year on the cover of *Deschampsia* and *Calluna* and on the species richness in four grazed *Calluna* habitats on podzolic soils during the period 1983–93 (ANOVA, ***$P < 0.001$)

Response variable	d.f.	*Deschampsia* cover	*Calluna* cover	Species richness
Source of variation				
Habitat	3	12.6***	15.9***	9.0***
Year	1	24.8***	82.5***	14.0***
Habitat × year	3	13.1***	16.6***	9.0***

level in all *Calluna* habitats, except in the turf-stripped pioneer *Calluna* heath.

The effect of grazing on the recovery of *Calluna* differed significantly between the *Deschampsia* heath on plaggen soil and the *Molinia* heath (Fig. 1e–h; habitat × grazing interaction, $P < 0.01$; Table 4). *Calluna* recovery failed in the grazed *Deschampsia* heath on plaggen soil (Fig. 1e). In the *Molinia* heath, cover reached 20% in 1993 (Fig. 1g). The *Deschampsia* cover in the ungrazed *Deschampsia* heath on plaggen soil declined after the tree invasion (Fig. 1f).

No other herbaceous species became dominant at the habitat scale. On individual plots, the non-nitrophilous species *Carex pilulifera* L., *Galium saxatile* L. and *Rumex acetosella* L. occasionally reached a 10% cover level.

CALLUNA DENSITY IN GRASS HEATHS

The measured density in the grass heaths reflected the net establishment success, as plots did not contain juveniles in 1983. Between 1983 and 1990 density increased in the *Deschampsia* heath on podzolic soils significantly more than on plaggen soils (Fig. 2; ANOVA, habitat × year, $F = 4.34$, $P < 0.05$). After 1990 the rates were no longer significantly different. *Calluna* density in the grazed *Molinia* heath was also higher than in the *Deschampsia* heath on plaggen soil (ANOVA, habitat × grazing effect, $F = 10.5$, $P < 0.01$). No significant difference occurred between the grazed and ungrazed *Deschampsia* heath on plaggen

soil. In the ungrazed *Deschampsia* heath one seedling emerged, in the ungrazed *Molinia* heath none. *Calluna* density (Fig. 2) and *Calluna* cover (Fig. 1d,e,g) were significantly correlated in 1993 ($R^2 = 0.91$).

SHRUBS AND TREES

Young trees (see the Appendix) established in the grazed treatments, but their cover remained low (< 1%), partly because of browsing and partly as a result of removal by the site manager (see the Discussion). The ungrazed exclosures displayed different results. In the ungrazed *Deschampsia* heath on plaggen soil, trees started to invade after the winter of 1985–86 (Fig. 1f). In 1993 the mean cover had reached 20%. Tree seedlings were occasionally observed in the ungrazed *Molinia*, but they did not survive. Statistical tests were not carried out for tree cover, as the values in the grazed treatments were affected by tree removal.

The frequency of shrub and tree species remained rather constant; only birch and bramble *Rubus fruticosus* L. increased substantially (see the Appendix).

CALLUNA SEED BANK

The number of emerged seedlings from the A_o of the grass heath on podzolic soil (1324 ± 1039 m^{-2}) and plaggen soil (96 ± 76 m^{-2}) differed remarkably, but the difference was not statistically significant (P

Table 4. *F*-values and significance levels of main effects of habitat, grazing and year and interactions on the cover of *Deschampsia*, *Molinia*, *Calluna* and on species richness in grazed and ungrazed *Deschampsia* heaths on plaggen soil and *Molinia* heaths on podzolic–peat soil 1983–93

Response variable	d.f.	*Deschampsia* cover	*Molinia* cover	*Calluna* cover	Species richness
Source of variation					
Habitat	1	10.0**	2.0^{NS}	6.7*	0.4^{NS}
Grazing	1	10.8**	0.4^{NS}	6.9^{NS}	23.4***
Year	1	1.1^{NS}	3.7^{NS}	8.1**	29.5***
Habitat × grazing	1	7.0*	0.4^{NS}	7.2**	0.9^{NS}
Rest design 1: habitat × year + grazing × year + habitat × grazing × year	3	5.4*	2.7*	11.7***	10.2***
Rest design 2: habitat × year + habitat × grazing × year	2	2.1^{NS}	4.0*	12.9***	1.5^{NS}

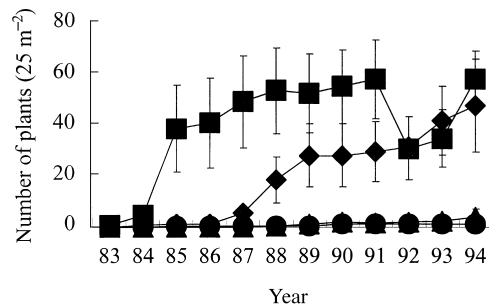ANOVA *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$; NS = not significant.

Fig. 2. Re-establishment of *Calluna* from seed in grass heaths after the introduction of free-ranging cattle at the Wolfhezerheide site. Squares = grazed *Deschampia* heath on podzolic soil; triangles = grazed *Deschampsia* heath on plaggen soil; diamonds = grazed *Molinia* heath on podzolic–peat soil; circles = ungrazed *Deschampsia* heath on plaggen soil. In ungrazed *Molinia* heath, no *Calluna* established. Vertical bars indicate SE.

$= 0.078$; Fig. 3) due to the low number of replicates. The differences between the A_5 seed banks were less distinct: $175 \pm 145\,m^{-2}$ for podzolic soil and $89 \pm 86\,m^{-2}$ for plaggen soil (Fig. 3).

Linear regression yielded a significant relationship between the A_o seed bank and *Calluna* density in 1990 ($R^2 = 0.97$, $n = 5$, $P < 0.01$; Fig. 4) and between the A_o seed bank and *Calluna* cover in 1990 ($R^2 = 0.95$, $n = 5$, $P < 0.01$).

PLANT HEIGHT OF *DESCHAMPSIA* AND *CALLUNA*

Between 1991 and 1993, the average plant heights of *Deschampsia* and *Calluna* in the *Deschampsia* lawns were significantly lower on the plaggen soil than on the podzolic soil (Fig. 5; *Deschampsia*: $F = 8.0$, $P < 0.01$; *Calluna*: $F = 11.3$, $P < 0.01$).

SPECIES RICHNESS

After an initial rise during the first 5 years in all grazed habitats, species richness declined during the last 5 years in the two pioneer *Calluna* habitats (Fig. 6a). Species richness more or less stabilized in the
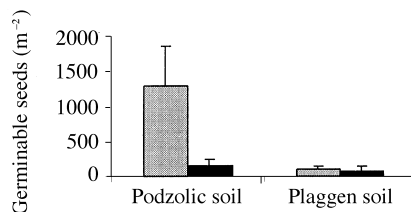
Fig. 3. Seed banks of *Calluna* in A_o (shaded bars) and A_5 (solid bars) in *Deschampsia* heaths on podzolic and plaggen soils at the Wolfhezerheide (1990). Vertical bars indicate SE.
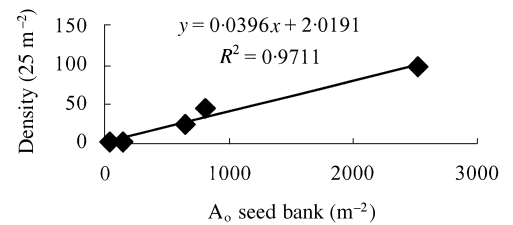

Fig. 4. Linear regression of *Calluna* density after 7 years of grazing (1990) on the *Calluna* seed bank in the A_o in *Deschampsia* heaths. $y = 2.01 + 0.040x$; $R^2 = 0.97$; $P < 0.01$.

mature *Calluna* heath and in the other habitats (Fig. 6a,b). The effect of grazing was most clearly shown by comparing the grazed and ungrazed treatments of the *Deschampsia* heath on plaggen soils and the *Molinia* heath (Fig. 6b and Table 4; grazing × year effect, $P < 0.001$). Species richness increased in the grazed treatments from 3·0 to 8·0 (*Deschampsia* heath) and from 3·7 to 9·3 (*Molinia* heath).

It may be argued that the increase in species richness by grazing is mainly due to the introduction of dung and urine. The plant species in the plots (see the Appendix) were classified as nitrophilous species ($I_N > = 6$) and non-nitrophilous heathland species ($I_N < 6$) according to their Ellenberg's nitrogen indication value, I_N ($1 = < I_N > = 9$; see the Appendix; Ellenberg 1979). The group of non-nitrophilous herbs displayed the strongest increase in species richness, and nitrophilous herbs the smallest (Fig. 7a,b). None of the 11 nitrophilous species increased by more than 10% between 1983 and 1993 (see the Appendix). Among the 19 non-nitrophilous heathland species, 10 species (see the Appendix) increased more than 10%, e.g. bramble (0–48%), birch (29–71%) and buckthorn *Frangula alnus* Mill. (29–41%). No species disappeared from the plots (see the Appendix). Some rare species established after 1983 outside the plots (e.g. *Lycopodium clavatum* L. and *Ophioglossum vulgatum* L.).
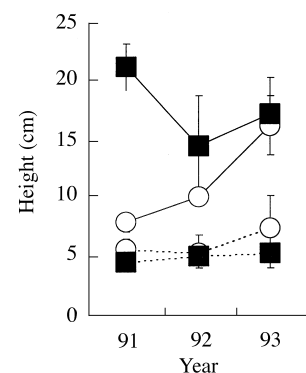

Fig. 5. Plant height in late summer of *Deschampsia* (circles) and *Calluna* (squares) in grazed *Deschampsia* heaths on podzolic soil (continuous line) and plaggen soil (broken line). Vertical bars indicate SE.
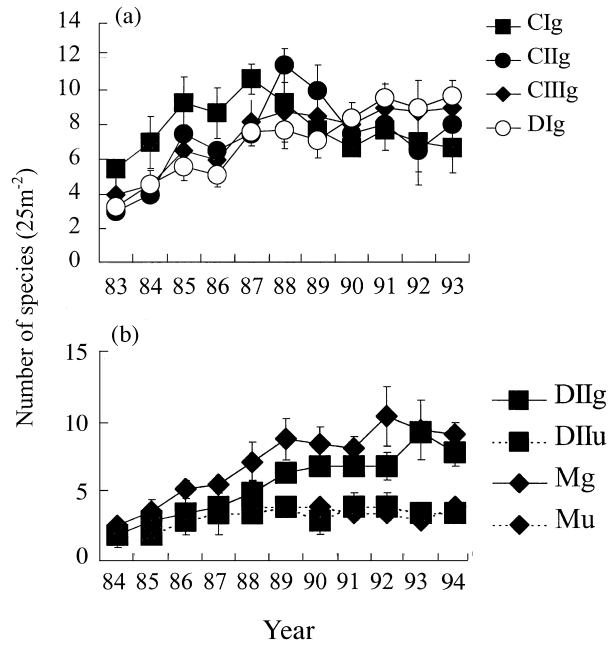
Fig. 6. (a) Changes in the (vascular plant) species richness of grazed *Calluna* and *Deschampsia* heaths on podzolic soil at the Wolfhezerheide. Squares = turf-stripped pioneer *Calluna* heath (CIg); filled circles = mown pioneer *Calluna* heath (CIIg); diamonds = mature *Calluna* heath (CIIIg); empty circles = *Deschampsia* heath (DIg). Vertical bars indicate SE. (b) Changes in the (vascular plant) species richness of grazed (continuous lines) and ungrazed (broken lines) *Deschampsia* heath on plaggen soil (squares) (grazed, DIIg; ungrazed, DIIu) and *Molinia* heath on podzolic–peat soil (diamonds) (grazed, Mg; ungrazed, Mu). Vertical bars indicate SE.

Discussion

HABITAT USE BY CATTLE

The cattle used habitats and dominant species in an uneven fashion. Time–budget studies and records of numbers of bites over 24-h periods between 1983 and 1985 (Bokdam, Gleichman & Batterink 1986; J.

Bokdam, unpublished data) showed that the cattle grazed grass preferentially during the growing season. Between November and March, *Calluna* was added to their grass diet, reaching a maximum of 50% of all bites in January. The annual foraging pressure, based on foraging time and expressed in animal units ha^{-1}, was higher in *Deschampsia* heath
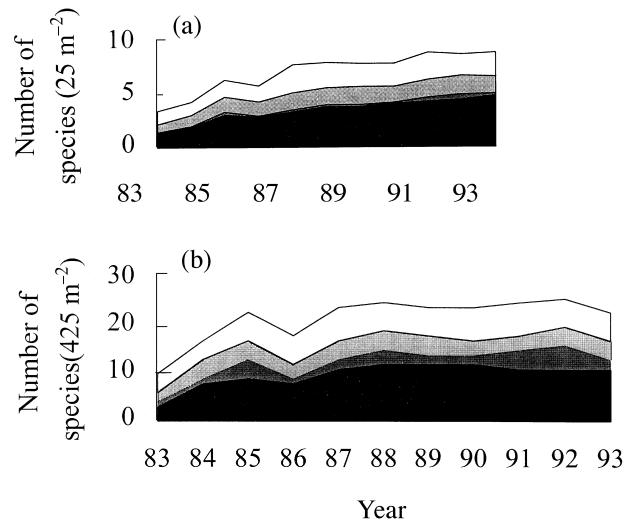

Fig. 7. Changes in the (vascular plant) species richness per ecological group in open heathland after the introduction of free-ranging cattle: black = non-nitrophilous herbs; dark grey = nitrophilous herbs; light grey = dwarf shrubs; white = shrubs and trees. For ecological groups see text and the Appendix. (a) Average of 17 plots (25 m^2); (b) species pool of 17 lumped plots (425 m^2).

(0·28) than in *Calluna* heath (0·23), *Molinia* heath (0·16) and forest (0·12). Forest was intensively used as a shelter during the night.

SOIL FERTILITY

Soil fertility displayed a gradient across the four habitats on podzolic soils, and significant differences were found between the podzolic and plaggen soils. The increase in the amount of organic matter in the topsoil and extractable nitrogen across the podzolic soils was caused by mechanical removal before the start of grazing. The low amount of organic matter in the A_o of the mown pioneer *Calluna* heath may have been due to the interrupted litter production or to litter removal by wind or run-off.

The different thickness of the A_m and extractable phosphorus level (grazed treatments only) between *Deschampsia* heaths on podzolic and plaggen soil were explained as long-lasting effects of differential use as common pasture and arable field, respectively, during the Middle Ages.

The significantly higher extractable phosphorus and (not significantly) higher extractable nitrogen in the grazed *Deschampsia* heath on plaggen soil compared with the ungrazed treatment indicates accelerated decomposition and mineralization by grazing. Similar effects were found by Kemmers *et al.* (1996) in *Deschampsia* swards in pine forest.

TRANSITIONS BETWEEN GRASS AND HEATHER

Grazing did not stop the ongoing invasion of *Deschampsia* in the non-turf-stripped *Calluna* habitats (Fig. 1b,c). The failed grass invasion in the turf-stripped pioneer *Calluna* heath (Fig. 1a) was attributed to nitrogen deficiency. Ageing and accumulation of litter and nitrogen may allow *Deschampsia* to invade in the future in gaps in this habitat. Grazing may have accelerated grass invasion in the mature *Calluna* (Fig. 1c). The mature and degenerating stages of *Calluna* are less tolerant of defoliation and trampling than the pioneer and building stages (MacDonald 1990). The prostrate growth forms, developed by layering and grazing (MacDonald *et al.* 1995), also seemed to be tolerant to trampling.

In the grazed grass heaths, *Deschampsia* cover did not decline despite intensive defoliation (Fig. 1d,e,g). This indicates a high tolerance of defoliation. Trampling, urine scorching and digging by rabbits and dung beetles created small gaps in the grass sward. The only declines of *Deschampsia* cover by defoliation occurred in the *Deschampsia* heath on plaggen soil, before the first measurement. Grazing of the tussocks exposed the bare intertussock areas, which were colonized by the grass after 1983 (Fig. 1e,g). Competition by taller *Molinia* (Fig. 1h) and trees (Fig. 1f) caused all other declines

of *Deschampsia* cover. Until 1993, *Deschampsia* was only locally suppressed by expanding *Calluna* (Bokdam 1996).

Grazing induced a significant recovery of *Calluna* in the grass heaths on podzolic and peat soils (Fig. 1d,g), but not on plaggen soils. Key mechanisms were a successful establishment from the seed bank (Fig. 5), seedling survival and expansion. Recovery included four phases. (i) During the lawn development phase, grazing changed the grass tussocks into a lawn by defoliation and trampling. (ii) In the heather establishment phase, the first seedlings emerged in litter gaps. They probably originated from the seed bank. During later years recruitment was also found on compacted litter and in open lawn patches. These seedlings may have derived from seed rain. Rabbits heavily browsed *Calluna* seedlings and juveniles in localized areas. (iii) During the building phase, *Calluna* plants expanded in height and width (Fig. 1a–d), despite substantial browsing by cattle and rabbits. Browsing kept the plants more or less in a prostrate or creeping growth form with adventitious roots (MacDonald *et al.* 1995). Browsing and trampling may have stimulated layering and the development of adventitious roots in the moss-rich grass turf. It may also have favoured a dense canopy and increased the ability of *Calluna* to 'walk' over short-cropped grass lawns. Unbrowsed *Calluna* plants displayed the well-known, classical, developmental stages (Watt 1955). Layering and vegetative regeneration may have had a positive effect on the longevity of *Calluna*. Rabbits created flat, shaved, *Calluna* cushions, described earlier by Welch & Kemp (1973). (iv) In the final mosaic phase, which became apparent after 5 years of grazing, *Calluna* shrubs coexisted with grass in a dynamic mosaic (Bokdam 1996).

The failure of *Calluna* to colonize *Deschampsia* lawns on plaggen soil (Figs 1e,f and 2) was attributed to inhibition of germination, caused by the thick grass-rich A_o (Table 2), and to intensive browsing of the young plants (Figs 1e, 2 and 5). The inhibitory effect of the tough grass litter on the plaggen soil became obvious after a simple additional turf-stripping experiment. In two plots, each of $20\,m^2$, the turf was removed in 1986. The turf stripping triggered the germination of *Calluna* and resulted in a mean *Calluna* cover of 50% by 1993. The lower plant height of *Deschampsia* and *Calluna* (Fig. 5) and the cushion form of *Calluna* confirmed the more intensive defoliation by cattle and rabbits on the nutrient-rich plaggen soil. Our findings agree with the higher grazing pressure by sheep and red deer on heather plants near grass patches (Hester & Baillie 1998; Palmer & Hester 2000). Impoverishment of the seed bank was not judged to be of great importance, as the low germinable seed density (96 m^{-2} from the A_o) did not prevent a successful recovery in the turf-stripped plots.

TREE ENCROACHMENT

Cattle browsed and suppressed all tree species (see the Appendix) except the unpalatable pine and silver birch. To maintain open heathland, the site manager had to remove several hundreds of young trees, mainly from heather stands. Without removal, 10–20% of the open area might have been colonized by trees (W. Aandeweg, personal communication). Similar removals are practised in other heathland areas with free-ranging cattle (Westerhoff 1992). The observed differential tree encroachment in grass and *Calluna* heaths, and the frequency of bite marks, suggested that pine and birch juveniles were more severely suppressed in grass lawns than in *Calluna* heaths, more on plaggen soils than on podzolic soils, and more by rabbits than by cattle.

Scots pine, buckthorn, silver birch, rum cherry *Prunus serotina* Ehrh. and goat willow *Salix caprea* L. invaded in the ungrazed *Deschampsia* heath on plaggen soil (Fig. 1f). Their establishment followed substantial *Deschampsia* die-off after a prolonged snow cover during the winter 1985–86. The establishment after die-off and the failure of tree invasion in the vigorous ungrazed *Molinia* (Fig. 1h) suggest a threshold for tree invasion in ungrazed tall grass swards. Causal factors may be shading, small rodents and fungi. Runways and bite marks revealed the presence of small rodents in our exclosures.

Despite the increased frequency of bramble (see the Appendix), its cover remained low (< 1%). Nutrient deficiencies and browsing by rabbits, roe deer and horses may have checked its expansion. Cattle avoided bramble (J. Bokdam, unpublished data).

During the study, more than 20 adult trees in the forest and open heathland died as a result of ageing and wind-throw. They were all replaced by grass because cattle had suppressed the shade-tolerant mid-successional pedunculate oak *Quercus robur* L. and rowan *Sorbus aucuparia* L.

SPECIES RICHNESS

The positive effect on species richness was explained by cattle-mediated seed dispersal, release from competitive exclusion by suppression of taller dominants and by increased spatial heterogeneity (Bullock & Pakeman 1997; Olff & Ritchie 1998). The nitrophilous herbs (see the Appendix; e.g. *Poa annua* L. and *Stellaria media* (L.) Villa) occurred mainly on (old) dung patches. The increased frequency of non-nitrophilous herbs (see the Appendix; e.g. *Carex pilulifera* L. and *Potentilla erecta* (L.) Räuschel) was explained by improved germination conditions for seeds from the seed bank and the seed rain. The stabilization of the species richness (Figs 6 and 7) on a relatively low level may have been the result of the low pH and a

failing long-distance dispersal (Bakker & Berendse 1999).

Proulx & Mazumber (1998) suggested reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. We found positive effects of grazing in grass heaths on poor and rich soils (Fig. 6). The decline of the species richness during the second 5 years in the most nutrient-poor *Calluna* habitats may support Proulx & Mazumber's (1998) theory. The decline was explained by outshading of the small light-demanding heathland species by the closing *Calluna* canopy.

MOSAIC CYCLES

Cattle grazing generated shifting grass–heather mosaics in more or less homogeneous *Calluna* heaths (Fig. 1b,c) and grass heaths (Fig. 1d,g) on soils of intermediate fertility. No mosaics developed in the nutrient-poor turf-stripped pioneer *Calluna* heath and in the nutrient-rich *Deschampsia* heath on plaggen soil (Fig. 1a,e). Diemont & Heil (1984) concluded that the sustained grass dominance in eutrophicated (non-grazed) Dutch heathlands conflicted with cyclic succession of the four classic *Calluna* stages (Watt 1955; Barclay-Estrup & Gimingham 1969) and with the *Calluna*–moss–grass cycle in fixed drifting sand (Stoutjesdijk 1959). In the Wolfhezerheide, free-ranging cattle could change the linear heather–grass transition into a heather–grass–heather cycle because invading trees were removed. Without tree removal, a heather–forest–grass–heather cycle would have been generated. Grazing acted as the driving force for the cycling in two ways: (i) by inducing the invasion of grass in degenerating forest and heather; and (ii) by inducing the invasion of *Calluna* and other unpalatable woody pioneers in the grass lawn after a period of exploitation and nutrient depletion.

NUTRIENT-MEDIATED EFFECTS

Despite the obvious light-mediated effect of grazing on the grass invasion in ageing *Calluna* and the recovery of *Calluna* in grass heath, we may not conclude that grazing diminished the importance of nutrients for the heather–grass balance.

The nutrient requirements of *Deschampsia* and *Calluna* were apparently met in all open habitats of the study area, except in the turf-stripped *Calluna* heath. Here, nitrogen deficiency probably excluded *Deschampsia* (Table 2 and Fig. 1a). This result agrees with the relatively high nitrogen demand (Aerts 1993a,b; Alonso & Hartley 1998) and low phosphorus requirement (Bokdam & Wallis de Vries 1992) of this grass species. The shade-tolerant *Deschampsia* was only locally restricted by shading (Fig. 1f,h).

Calluna was indirectly limited by nutrients. The relatively high nutrient availability allowed the grasses to inhibit the germination and seedling survival of *Calluna* in the grass heaths. By short-cropped lawns and gaps, cattle eliminated the nutrient-based competitive advantage of the established *Deschampsia* over the establishing *Calluna*. The grass sward on the plaggen soil with grass litter may have been more resistant to trampling, gap creation and nutrient depletion than the grass sward on the podzolic soils with *Calluna* litter. The rich *Calluna* recruitment on the turf-stripped plots on plaggen soil emphasized the essential role of gaps. Ten years of nutrient depletion in a *Deschampsia* heath at Hoog Buurlo (the Netherlands) by hay making ('defoliation without treading gaps') did not result in any *Calluna* recovery, despite a rich seed bank (Diemont & Lindhorst Homan 1989).

There is growing evidence that soil fertility may also affect the disturbance risk and longevity of *Calluna*. The more intensive browsing of *Calluna* on the plaggen soil (compared with the podzolic soil; Fig. 5) might be attributed to three nutrient-mediated mechanisms: (i) a higher nutritional value of *Calluna*; (ii) a higher intrinsic palatability of *Calluna*; and (iii) a higher associational palatability, provided by a more productive and palatable grass matrix. Fertilization with a compound fertilizer including nitrogen and phosphorus induced higher nitrogen and lower lignin concentrations in *Calluna* shoots (Iason & Hester 1993). Brunsting & Heil (1985) found a positive effect of nitrogen availability on foliage nitrogen content and the performance of the heather beetles. *Calluna* plants growing near grass patches were more intensively used than individuals at larger distances (Clarke, Welch & Gordon 1995; Hester & Baillie 1998). High nitrogen availability may also increase the risk of damage by frost and drought for *Calluna* (Berdowski 1993). The findings emphasize that *Deschampsia* and *Calluna* are both affected by nutrients, but in different ways and directions. *Deschampsia* seems to be directly limited by nutrients as a resource for its performance. *Calluna* is affected indirectly and in the opposite direction by the same nutrients. High levels of nitrogen increased the competitive ability of competing grasses (Aerts 1993b) and its disturbance risk. The earlier grass invasion and failing *Calluna* recovery on the plaggen soil in our study area may ultimately be attributed to a higher soil fertility. It shows that the soil fertility pattern created by a medieval sedentary farming system may still control present day vegetation patterns.

The combination of a low phosphorus and high nitrogen availability attributes a limiting role to phosphorus for species with a relative high phosphorus requirement. Such species (e.g. bramble) might be expected to increase rapidly after phosphorus inputs (e.g. on dung patches).

A preliminary calculation revealed that the nutrient removal by defoliation exceeded the atmospheric inputs for potassium and phosphorus on intensively grazed grass lawn patches. Nitrogen inputs were nearly completely removed. As a consequence, lawn patches underwent phosphorus and potassium depletion until excreta replenished them. The calculated frequency of dung and urine deposition on these lawns was approximately once per 20–30 years, assuming no resting activities on the lawn (Bokdam 1989). This means that nutrient depletion may play a role in the establishment of *Calluna* in grass lawns.

At the scale of the whole grazed area, free-ranging cattle removed only a minor proportion of the atmospheric nutrient input. The animals excreted a major proportion of the ingested nutrients and redistributed a substantial amount from the grass lawns to the forest (J. Bokdam, unpublished data).

Calluna, pine and silver birch share many ecological traits as woody invaders in nutrient-poor grass heaths. They may be considered as a functional type (Smith, Shugart & Woodward 1997), a characterization that would broaden the scope of hypotheses, experiments and modelling from heathlands to other grazed ecosystems (Archer 1996; Putman 1996; Vera 1997; Bokdam 1998; Prins & Olff 1998; Olff *et al.* 1999; Ritchie & Olff 1999; Van Oene, Van Deursen & Berendse 1999).

MANAGEMENT IMPLICATIONS

Continued free-ranging cattle grazing will lead to a further eutrophication of the open heathland because of ongoing atmospheric inputs and because nutrient-rich forest patches will be converted into grassland. Cessation of tree removal would lead to the restoration of a half-open wood–pasture mosaic (Pott & Hüppe 1991) This process is accelerated by integrated grazing of heathlands, arable fields, improved grasslands and forest. Eutrophication may increase in the long term the grass proportion in the open heathland. A higher soil fertility will induce a higher grazing pressure in grass lawns. It may progressively hamper the invasion of woody pioneers of nutrient-poor environments (e.g. *Calluna*, pine and birch) and change the successional pathway from a grass–heather–pine–birch–oak route to a grass–bramble–oak–beech route (Bokdam 1998).

Replacement of the actual year-round grazing by summer grazing might increase the grass consumption and favour the heather proportion in the grass–heather mosaic.

Replacement of free-ranging by traditional herding (with a daily return of the herd to the stable and a daily foraging time of about 8 h) would remove about 60% of the excreta, i.e. 40 kg nitrogen and 2·5 kg phosphorus per animal unit (or 8 kg N and 0·5 kg P ha^{-1}). Removal of the total actual atmospheric nitrogen input of the grazed area would

require the replacement of all forest and heather stands by intensively used grass lawns (J. Bokdam, unpublished data).

Multi-species grazing combining cattle with smaller herbivores (e.g. sheep, red deer and rabbits), might suppress shrubs and trees more effectively. Replacement of the large grazers by smaller ones may lead to dominance of coarse grasses (e.g. *Molinia* and *Calamagrostis epigejos* (L.) Roth) or other potential dominants that are unpalatable to smaller herbivores (J. Bokdam, personal observations)

We conclude that free-ranging grazing without additional management will generate dynamic tree–grass–heather mosaics in the long term. These wood–pasture mosaics are fundamentally different from the traditional heathlands in which trees and grasses were excluded by the land use. Free-ranging grazing combined with tree cutting appears to be a suitable management regime for the maintenance of open heathlands with dynamic grass–heather mosaics. Herding or a combination of free-ranging grazing with burning or turf stripping seems unavoidable if pure heather-dominated open heathlands are to be maintained under the present environmental conditions.

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Appendix

Frequency (%) of vascular plant species in the 17 grazed plots established in 1983 in open heathland, in 1983, 1988 and 1993. Nomenclature follows Van der Meijden (1990). The herbaceous species were arranged as nitrophilous and non-nitrophilous species according to their nitrogen indication value (I_N) of Ellenberg (1979) (1 = extreme nitrogen-poor environment; 9 = extreme nitrogen-rich environment; X = indifferent; ? = unknown).

Species (I_N-Ellenberg)	1983	1988	1993
Non-nitrophilous herbs (I_N-Ellenberg < 6 or X)			
Agrostis capillaris (3)	0	41	71
Carex pilulifera (5)	12	65	71
Cuscuta epithymum (2)	0	12	0
Danthonia decumbens (2)	0	18	18
Deschampsia flexuosa (3)	100	100	100
Festuca ovina (2)	0	0	12
Galium saxatile (3)	0	53	88
Hypochaeris radicata (3)	0	6	6
Juncus bufonius (X)	0	6	0
Juncus effusus (4)	0	6	0
Luzula multiflora (3)	0	0	6
Molinia caerulea (2)	18	41	41
Potentilla erecta (2)	0	18	24
Rumex acetosella (2)	0	18	53
Number of non-nitrophilous herb species	3	12	11
Nitrophilous herbs (I_N-Ellenberg >= 6)			
Cerastium fontanum (6)	0	0	6
Corydalis claviculata (?)	6	0	0
Poa annua (8)	0	6	0
Poa pratensis (6)	0	0	12
Sagina procumbens (6)	0	6	0
Stellaria media (8)	0	12	0
Number of nitrophilous herb species	1	3	2
Dwarf shrubs			
Calluna vulgaris (1)	53	95	100
Erica tetralix (2)	24	53	53
Genista anglica (2)	0	18	6
Vaccinium myrtillus (3)	0	6	6
Number of dwarf shrub species	2	4	4
Shrubs and trees			
Betula sp. (3)	29	71	71
Pinus syvestris (X)	35	71	35
Quercus robur (X)	35	18	29
Frangula alnus (X)	29	41	41
Rubus fruticosus (?)	0	18	48
Sorbus aucuparia (X)	0	23	6
Number of shrub and tree species	4	6	6
Total number of species	10	25	23

Species (I_N value) occurring in other years: *Epilobium* sp. (?), *Holcus lanatus* (4), *Holcus mollis* (3), *Luzula campestris* (2), *Spergularia rubra* (4), *Chamerion angustifolium* (8) *Lolium perenne* (7), *Polygonum persicaria* (7), *Senecio sylvaticus* (8), *Solanum nigrum* (8), *Prunus sertina* (?).