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Effects of heterogeneous habitat use by cattle on nutrient availability and litter decomposition in soils of an Alpine pasture

Sabine Güsewell[1,2], Peter L. Jewell[1] & Peter J. Edwards[1]
[1]*Geobotanisches Institut ETH Zürich, Zürichbergstrasse 38, CH-8044 Zürich, Switzerland.* [2]*Corresponding author**

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Abstract

Grazing by free-ranging cattle on Alpine pastures in southern Switzerland creates sharp contrasts in plant species composition between small 'camp areas', which are grazed intensely and receive most cattle excreta, and surrounding pasture dominated by *Nardus stricta,* which is only lightly grazed. We hypothesised that these contrasts are maintained by positive feedbacks related to nutrient availability in soil, in that (a) plant material with rapid decomposition and nutrient release decomposes in camp areas and (b) litter decomposition is further stimulated by enhanced nutrient availability in soil. We compared nutrient availability at three camp areas with that in surrounding *Nardus* vegetation and investigated how the decomposition of plant material from both vegetation types responds to nutrient availability in soil, both in the field (during 14 weeks) and in the laboratory (during 4, 10, and 16 weeks). At all three field sites P availability was significantly enhanced in camp areas, whereas differences in N availability were inconsistent among the three sites. Laboratory incubations indicated that microbial activity after the addition of labile C (cellulose) was limited by P availability in the *Nardus* vegetation but not in camp areas. The camp-area plant substrate decomposed much faster (81.5% vs. 27.1% ash-free dry mass loss in the field) and released more N and P than the *Nardus* substrate, which tended to immobilise soil nutrients. However, the decomposition rate of neither substrate was influenced by nutrient availability in soil, both in the field (comparing camp areas and *Nardus* vegetation) and in the laboratory (comparing incubations with and without N or P fertilisation). We conclude that the contrasting quality of plant substrates contributes to the greater nutrient availability in camp areas (feedback a) but that the latter does not influence the decomposition of *in situ* plant material (feedback b) because the latter is not nutrient-limited.

Introduction

Grazing herbivores can considerably modify the productivity of the vegetation and the availability of nutrients in the soil of their pastures (Milchunas and Lauenroth, 1993). Grazing affects plant species composition (Proulx and Mazumder, 1998; Wilson and Agnew, 1992), morphological and physiological traits of plants (Holland et al., 1996; McIntire and Hik, 2002), inputs of organic matter to the soil (Smit and Kooijman, 2001; Tracy and Frank, 1998), and physical, chemical and biological properties of the soil (Frank et al., 2000; Haynes and Williams, 1999; Kooijman and Smit, 2001). Both increased and decreased nutrient availability may result from these influences, depending on their relative importance and on the factors limiting primary production in a particular ecosystem. For example, grazers often reduce the quantity but improve the quality of organic matter inputs to the soil (Frank et al., 2000; Olofsson and Oksanen, 2002). This can increase nitrogen mineralisation if the latter is controlled by the intensity of microbial activity (Hamilton and Frank, 2001; Tracy and Frank, 1998), or reduce N mineralisation if the amount of

*FAX No: +41–1–632 1215.
E-mail: guesewell@geobot.umnw.ethz.ch

organic matter in the soil is determining (e.g. Kooijman and Smit, 2001; van Wijnen et al., 1999). In some studies, litter quality decreased under grazing because of a lower proportion of root litter and a higher proportion of litter from species with high lignin content (Ritchie et al., 1998; Smit and Kooijman, 2001). Overall, grazers tend to increase rates of nutrient cycling and nutrient availability in rather nutrient-rich systems and to decrease them in nutrient-poor systems (de Mazancourt et al., 1998; Frank et al., 2002; Ritchie et al., 1998). Grazer activity might therefore strengthen landscape-level gradients in nutrient availability (Frank and Groffman, 1998; Tracy and Frank, 1998) .

The effects of grazers on productivity and nutrient availability have mostly been studied through the comparison of grazed with ungrazed areas or of areas grazed at differing stocking rates. These studies, as well as simulation models based on them (e.g. Seagle et al., 1992), are concerned with the combined effects of defoliation, trampling and excretion. A typical feature of grazer activity, however, is spatial heterogeneity (McIntire and Hik, 2002; Olofsson and Oksanen, 2002). Animals tend to graze on areas with the most nutritious plant cover whereas they select particular landscape features for resting and ruminating (Pratt et al., 1986). These 'camp areas' receive a large proportion of animal excreta (Gander et al., 2003; Haynes and Williams, 1999). Spatial segregation of grazing and excretion may result in a considerable redistribution of nutrients within the pasture, and over the long term, create a heterogeneous pattern of nutrient availability in soil (Haynes and Williams, 1999). In response to nutrient availability and to differential grazing pressure, different types of vegetation may develop within heterogeneously used pastures (Austrheim and Eriksson, 2001; Olofsson and Oksanen, 2002); this in turn influences the subsequent behaviour of the gazers in a way that tends to reinforce the existing patterns (Olofsson and Oksanen, 2002), leading to what has been called a 'herbivore-mediated positive-feedback switch' (Wilson and Agnew, 1992).

Alpine pastures in southern Switzerland have been grazed by domestic livestock, especially cattle and goats, for hundreds of years (Bätzing, 2003). In the past they were managed carefully to ensure a homogeneous utilisation of the grazing area, but this management was increasingly abandoned during the 19th and 20th centuries, so that animals could range freely on large grazing areas and develop characteristic spatial patterns of habitat use, which result in contrasting vegetation types. Most of the area is grazed but hardly used for resting, e.g. because of a steep slopes; on the nutrient-poor, acidic soils of the southern Swiss Alps, extensive grazing promotes the dominance of the rather unpalatable tussock grass *Nardus stricta* (Jewell, 2002). Only a small fraction of the pastures is used for resting; these camp areas bear more nutrient-demanding, trampling-resistant and grazing-tolerant graminoid species such as *Festuca rubra*, *Agrostis tenuis*, *Carex leporina* or *Poa annua*.

In the present study we investigated whether soil chemistry and the rates of litter decomposition differ between camp areas and the surrounding *Nardus* vegetation in such a way that they contribute to the 'switch' that has created and maintained the contrasting vegetation types (Wilson and Agnew, 1992). We expected decomposition and nutrient mineralisation to be faster in camp areas than in the *Nardus* vegetation due to (a) a higher quality of the plant material and (b) a stimulation of microbes by enhanced nutrient availability in soil. Both would promote the more nutrient-demanding species of camp areas at the expense of *Nardus stricta*. In the surrounding pasture, decomposition and nutrient mineralisation would be slow due to poor litter quality and low nutrient availability in soil (Bloemhof and Berendse, 1995; Parton et al., 1987), strengthening the nutrient-poor conditions under which slow-growing species such as *Nardus stricta* compete best (cf. Berendse, 1994).

To test this hypothesis, we studied nutrient availability as well as the decomposition of plant substrates from a camp area and from *Nardus* vegetation along transects from the centre of camp areas to the surrounding *Nardus*-dominated pasture. We further carried out three laboratory experiments to understand which factors determine the patterns of decomposition at our field sites. We investigated how the decomposition of our two plant substrates responds to N and P enrichment, whether soil microbes from camp areas and *Nardus* vegetation differ in their ability to decompose cellulose, and if so, whether differences in soil nutrient availability can account for the difference.

Materials and methods

Study area

The field sites were part of 'Alpe Nisciora', an alpine pasture (1400–1900 m a.s.l.) on the north-eastern flank of Mount Gradiccioli in the southern part of the Swiss

Alps (46.49°N and 8.76°E). The climate is insubrian, with hot summers, mild winters, and high precipitation all year. During the growing season, the mean temperature at 1600 m a.s.l. is approximately 13 ˚C, and the mean monthly precipitation 300 mm, most of which falls in short spells of heavy rain (Berry, 2000). The bedrock is a mixed biotite plagioclase gneiss (Reinhard et al., 1962). The soils are silty and mainly of the 'cryptopodzol' type with extremely low pH, high aluminium content, and the accumulation of humic acids in the topsoil (Blaser et al., 1997). The system has been grazed during the summer for many centuries, as indicated by ruins of former stables and stone walls. The number of grazing animals decreased steadily during the 20th century, until Scottish Highland cattle were introduced in 1994 for meat production. Since the pasture has been grazed for approximately 100 days per year (June-September) by some 40 cows and their calves, except for 1999, when it was not grazed. In some years, the pasture was subdivided by a fence into two paddocks, which were grazed in turns; in other years animals ranged freely over the entire area (Jewell, 2002).

More than three quarters of Alpe Nisciora are a species-poor pasture dominated by *Nardus stricta*, or a mixture of *Nardus* and heathland in the steepest parts of the slope. Camp areas are mainly found around present or former utility buildings and on flat areas, often at the top of small ridges (Jewell 2002). While the *Nardus* pasture is rather homogeneous across Alpe Nisciora, camp areas are more varied both in plant species composition and in soil chemistry (pH and total P concentration). For the present study, three camp areas were selected at different elevations and topographic situations (Table 1). At sites A and C, the camp area was dominated by *Agrostis capillaris* and *Carex leporina*, and at site B, which was slightly wetter and less acidic due to groundwater seepage, the camp area was dominated by *Poa annua*. All camp areas were surrounded by almost monospecific, homogeneous *Nardus stricta*-dominated grassland.

Nutrient concentrations in plant biomass and soil

Because no detailed measurements of site conditions were carried out in 1999, when the decomposition experiments were done (see below), plant and soil samples were collected for chemical analysis in summer 2003. Given the long-term grazing management of Alpe Nisciora, we assume that patterns of nutrient availability in 2003 were similar to those in 1999. Sampling was carried out in the centre of camp areas and at the end points of the horizontal transects (= six stations).

Three biomass samples were collected at each station on 18 July 2003. As camp areas had already been heavily grazed, we also sampled grazed micro-sites at the end points of the transects, so that differences in biomass nutrient concentrations were likely to reflect site conditions rather than the age of tissues. Accordingly, the sampled area had to small (25×25 cm^2). Plant material was dried at 75 °C and ground to pass a 1-mm sieve. Total nitrogen and phosphorus were extracted using a modified Kjeldahl method (1 h digestion at 420 °C with 98% H_2SO_4 and a copper sulphate-titanium oxide catalyst). Concentrations of N and P in digests were determined colorimetrically on a flow injection analyser (FIA, TECATOR, Höganäs, Sweden).

Four soil cores (8 cm diameter, 10 cm depth) were collected at each station on 19 September 2003. After removing the litter layer and the upper cm of soil (mixed with cattle dung in most soil cores from camp areas) as well as stones and large plant roots, the soil was passed through a 1-mm sieve. Subsamples were used to determine the water content (drying at 105 °C), the pH (in a 1:2.5 mixture with deionised water), the total C and N concentrations (CNS-2000 analyser, LECO, St. Joseph, MI, USA), and the total P concentration (modified Kjeldahl method and FIA analysis as described above). To determine mineral N concentrations, 5-g subsamples of fresh soil were extracted for 1 h with 50 mL of 6% KCl solution, and extracts were analysed for ammonium- and nitrate-N on the FIA. To determine phosphate concentrations, 3-g subsamples of fresh soil were extracted for 1 h with 50 mL of deionised water, and extracts were analysed for phosphate-P on the FIA.

For all variables, differences among sites and positions (camp area vs. *Nardus* pasture) were analysed with two-way Anova, after log-transformation of the data if necessary to obtain normally distributed residuals and homogenous variances.

Nitrogen mineralisation and litter decomposition

On 30 June 1999, two transects were set out on each of the three sites, one across slope ('horizontal') and one down slope ('vertical'). Each transect ran from the centre of the camp area into the surrounding *Nardetum* and consisted of 5 stations, of which the first (central) one was common to both transects. Stations were 10 m

Table 1. Effects of cattle on soil nutrients on an alpine pasture: density of cattle dung pats (end of the grazing season in 1998; from Jewell 2002), nutrient concentrations in plant biomass (July 2003), and topsoil chemistry (1–10 cm soil depth, September 2003) at the centre of camp areas and in surrounding *Nardus*-dominated vegetation at each of three field sites. Nutrient data are means of three (plants) or four (soil) samples. For each site, symbols after the data from camp areas indicate significant differences to the *Nardus* vegetation (*t*-test; ***, $P < 0.001$; **, $P < 0.01$; * $P < 0.05$; °, $P < 0.1$; no symbol, $P > 0.1$). The average standard error (*SE*) of the six means is given in the last column as an overall measure of variability

	Site A		Site B		Site C		
	Camp	*Nardus*	Camp	*Nardus*	Camp	*Nardus*	*SE*
Altitude (m a.s.l.)	1650 m		1610 m		1460 m		
Topographic position	Ridge		Slope		Slope bottom		
Dung pats (m^{-2})	0.11	0.01	0.03	0.01	0.08	0.02	
Plant N concentration (mg/g)	19.7	18.5	26.8	21.0	23.5	19.6	1.72
Plant P concentration (mg/g)	1.8*	1.1	3.6**	1.6	3.1*	1.4	0.19
Plant N/P ratio	10.7**	16.6	7.5**	13.3	7.8**	14.0	0.71
Total soil C (%)	10.8*	15.7	9.5°	11.8	12.5°	10.0	0.78
Total soil N (mg/g)	10.0°	12.6	8.7	9.4	10.6*	8.8	0.06
Total soil P (mg/g)	2.3*	2.2	1.9	2.1	2.2***	1.4	0.07
Soil C:N ratio	10.9*	12.4	10.8***	12.6	11.8	11.3	0.30
Phosphate-P (mg/kg)	3.3*	1.9	1.9	1.5	4.3	3.2	0.90
Nitrate-N (mg/kg)	20.4*	5.8	22.7*	7.7	19.1	26.2	8.48
Ammonium-N (mg/kg)	57.4*	21.4	44.9*	15.6	27.7	36.7	12.29
Soil pH (H_2O)	4.6	4.4	4.9**	4.4	4.3*	4.6	0.09

apart on all vertical transects and on the horizontal transect of site A, but 3 and 6 m apart on the horizontal transects of sites B and C, respectively, because of the smaller width of the camp area. At each station a trench 1 m long and 10 cm deep was dug. Four bags containing ion exchange resin (IER) and eight litter bags (4 × 2 substrates) were inserted horizontally at 5 cm depth in small slits made in the side wall of each trench, so that the three types of bags alternated and were 5–10 cm apart from each other. The turf was then carefully replaced so that the trench was completely closed again.

Ion exchange resin (IER) bags (3 cm × 3 cm) were made from polyamide fabric (60 μm mesh; Sefar, Hausen, Switzerland), and filled with 1.5 ± 0.4 g of a mixture of Dowex-1 (nitrate exchanger) and Dowex-50 (ammonium exchanger) at a ratio of 1:0.72 (as recommended by Arnone, 1997). After 40 days in the field, the IER bags were removed, air-dried and stored dry until their contents were analysed. The air-dry IER was then weighed and washed three times with 5 mL 0.1-N HCl; the combined extracts were made up to 50 mL and analysed colorimetrically for ammonium (NH_4) and nitrate (NO_3) concentration on an auto-analyser (Tecator, Höganäs, SE).

Litter bags were prepared with plant material (bulk samples of above-ground phytomass) collected from *Nardus*-dominated vegetation and from a camp area (different from the three study sites) in May 1999, briefly after snow melt. The material from the *Nardus* vegetation was almost entirely composed of the dead leaves of *Nardus stricta*, whereas the material from the camp area consisted of a mixture of grass species, of which *Agrostis capillaris* was the most abundant; it was an approximately 1:1 mixture of living and dead leaves. These two types of plant material are hereafter referred to as the *Nardus* and camp-area substrates. Subsamples of the substrates were dried at 70 °C and ground in a ball mill to a fine powder for chemical analyses. Initial C, N and P concentrations were determined as described above for soil samples. Mass loss on ignition (4 h at 550 °C) was used to determine initial ash content. Lignin content was derived from the C concentration of the insoluble residue remaining after extraction with methanol and chloroform at 25 °C and hydrolysis in HCl 10% at 100 °C. This method (Poorter and de Jong, 1999) assumes that the residue consists almost entirely of lignin (64% C), cellulose (42% C), protein and ash; the lignin content is therefore linearly related to the residue C concentra-

Table 2. Chemical properties of the two substrate types used in incubations (mean ± *SD*)

	Camp area	*Nardus*
C (mg/g)	451.4 ± 2.3	461.7 ± 4.7
N (mg/g)	33.4 ± 0.3	9.4 ± 0.3
P (mg/g)	3.15 ± 0.01	0.62 ± 0.02
C/N	13.3 ± 0.4	35.0 ± 1.1
N/P	10.6 ± 0.2	15.2 ± 0.6
Lignin (mg/g)	21.6 ± 2.3	25.6 ± 4.6
Soluble phenolics (mg/g)	24.5 ± 2.8	8.5 ($n = 1$)
Ash (mg/g)	5.5 ± 0.8	9.3 ± 0.6
Potential leaching (% dry mass)[a]	33.0 ± 0.1	9.0 ± 0.5
Saturated water content (% of DM)[a]	440 ± 16	269 ± 3

[a]After two days of gentle shaking in deionised water.

tion after accounting for protein content (derived from the residue N concentration) and ash content (ignition at 550 °C). Saturated water content and potential leaching were determined by gently shaking 200 mg of substrate in 150 mL of deionised water for 48 h. Saturated water content was determined from the difference between fresh and dry mass after shaking, and potential leaching from the difference in dry mass before and after shaking. The results of these analyses are shown in Table 2.

After air-drying for two weeks, subsamples of the substrates (3.00 ± 0.01 g of air-dry material) were packed into litter bags (7 cm × 10 cm) made of polyamide net (1 mm mesh) and sewn with a polyester thread. Three subsamples of each substrate were dried at 70 °C to determine their dry matter content (94% for both), and thus the initial dry mass (2.82 g per litter bag). After 14 weeks (6.10.1999), the bags were carefully dug out, taken to the laboratory and stored frozen until further processing. The content of each bag was cleaned of extraneous material with tweezers (in deionised water over a 250-μm sieve to facilitate the separation of materials), dried for 24 h at 70 °C and weighed. Samples from the first and last stations of all transects were analysed for ash content through burning at 550 °C. As final ash content varied little among these samples (it was 6–8% for the *Nardus* substrate and 7–10% for the camp-area substrate), the mean initial and final ash content of each substrate was used to convert data on dry mass loss into data on organic matter loss, recognizing that some of this loss was due to leaching and fractionation of material in the field or during the final processing of the material.

To test how the amount of mineral N adsorbed to IER (log-transformed sum of ammonium- and nitrate-N) and the mass loss of either substrate changed along the transects, analyses of covariance were performed on means of the four replicates per station ($n = 27$ stations) with the factors Site, Position and Site*Position. The covariate Position was an integer from 0 (centre) to 4 (end of gradient), regardless of the actual distances between sampling stations, as the latter had been adapted on each transect to the extension of the camp area. Since Site*Position interactions were significant for three of the four variables, we tested for changes in relation to position for each transect separately with linear regression. All analyses were done with the statistical package JMP, version 3.2.2 (SAS Institute 1993–2000).

Laboratory incubations

Laboratory experiments were carried out to test whether nutrient enrichment in camp areas could potentially stimulate decomposition, as needed for our second hypothetical feedback mechanism to operate. Several factors might prevent this feedback: (1) substrate quality might be such that its decomposition is not nutrient-limited (Bloemhof and Berendse, 1995; Bosatta and Ågren, 1991); (2) differences in nutrient availability between camp areas and surrounding soils might be too marginal for an effect on decomposition; (3) microbial respiration might not respond or respond negatively to nutrient enrichment (Ågren et al., 2001); (4) drought or low temperature might inhibit decomposition more than nutrients (Bryant et al., 1998). We examined the role of the first three factors through laboratory incubations at 22 °C with substrates kept moist at all times to avoid any influence of the fourth factor, which we considered unlikely to be relevant under the mild and moist Insubrian climate.

The role of substrate quality was tested by incubating 150 mg subsamples of our two plant substrates as well as cellulose (filter paper LS14, Schleicher & Schuell, Dassel, Germany) in Petri dishes (6 cm diameter) on a polyethylene mesh (300 μm) over 18 ± 0.5 g of quartz sand (method adapted from Wardle et al., 1998). Cellulose was incubated in addition to plant litter because it is a nutrient-free, labile source of carbon. Quartz sand is the main constituent of the soil matrix at our study sites; its use in the Petri dishes ensured that plant substrates were the only nutrient source for microbes in the control treatment. For microbial inoculation, substrates were wetted with 8 mL of soil

extracts prepared by making a slurry of 0.5 kg fresh soil from the field site (mixture of soil subsamples from the six stations) and 2 l of water, which was repeatedly mixed during 12 h and then passed through a 0.5-mm sieve. Four nutrient treatments (control, +N, +P, +N&P) were created by adding or not adding 10 mg N (as NH_4NO_3) and 2 mg P (as KH_2PO_4) to the extracts. Petri dishes were incubated in cardboard boxes at 22 °C. The material was sprinkled periodically with deionised water to keep it moist and to simulate leaching that would be associated with rainfall in the field. After four weeks of incubation, the remaining material was dried for 24 h at 70 °C and weighed. The effects of nutrient treatments on percentage mass loss were analysed with one-way ANOVA followed by pairwise treatment comparisons with Tukey HSD tests. The importance of variation in soil conditions was tested by incubating cellulose (filter paper disks) in Petri dishes on the 24 soil samples analysed for soil chemistry (see above). The decomposition of labile carbon sources has often been used to assess the nutrient limitation of soil microbes; we used cellulose rather than glucose or soft wood because cellulose is the main component of our plant substrates (Roberts and Rowland, 1998), and its decomposition has proved to correlate well with the quality and decomposition of *in situ* plant material in other studies (Fox and van Cleve, 1983; Kurka et al., 2000). The procedure was as described above, except that Petri dishes were filled with 10 g of fresh, sieved soil, which was moistened with 10 mL of deionised water or nutrient solutions (same treatments as above). The mass loss of cellulose was determined after four weeks of incubation. The effects of nutrient treatments on mass loss were analysed with one-way ANOVA for each of the six sampling stations, followed by pairwise treatment comparisons with Tukey HSD tests. Differences among sampling stations were analysed with two-way ANOVA (factors site and Position) for each nutrient treatment. Mass loss was correlated with the log-transformed mineral N and phosphate-P concentrations in soil.

The role of soil microbial composition was tested by repeating experiment 1 (incubation of the plant substrates on sand) using a different microbial inoculum: soil surface water from a wet lowland meadow, which contained some species from Alpe Nisciora while being more nutrient- and base-rich (pH 7.5). Four replicates for each combination of substrate type and nutrient treatment were harvested after 4, 10 and 16 weeks, respectively (to see whether effects change over time), and weighed after 24 h drying at

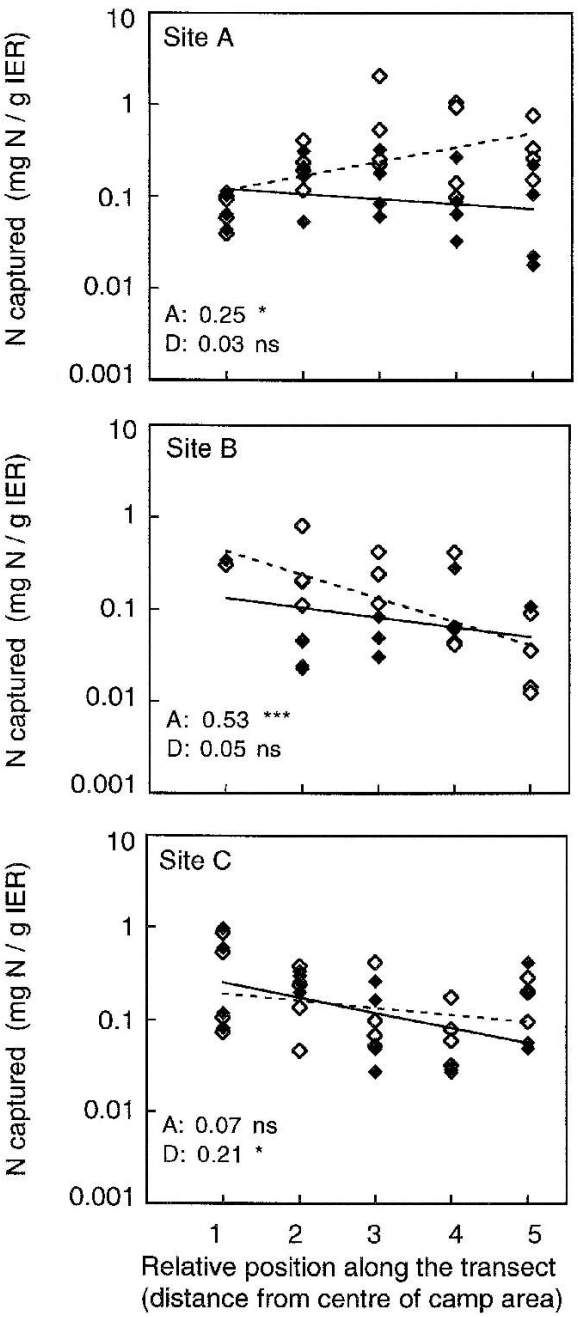

Figure 1. Changes in the amount of mineral N (sum of ammonium- and nitrate-N, logarithmic scale) captured in 40 days (30.6.1999–10.7.1999) by ion exchange resins along gradients from the centre of camp areas to the surrounding *Nardus stricta* vegetation. At each of three sites, one transect ran across slope (open symbols) and one ran down slope (closed symbols). Coefficients of determination from linear regression and their significance as well as regression lines are indicated for both transects (A = across slope, broken line; D = down slope, full line; ***, $P < 0.001$; **, $P < 0.01$; * $P < 0.05$; °, $P < 0.1$; no symbol, $P > 0.1$).

70 °C. The effects of nutrients on the percentage dry mass loss at each date were analysed with one-way ANOVA. After 4 and 10 weeks, the N and P concentrations of the residues were determined (Kjeldahl method as described above) to calculate the changes in their N and P contents (residual mass × N or P concentration).

Results

Nutrient availability

Camp areas had higher P concentrations in plant biomass and generally higher P (total and phosphate-P) concentrations in soil than the surrounding *Nardus* pasture (Table 1). In contrast, plant N concentrations were not enhanced in camp areas, which caused plant N:P ratios to be lower in camp areas than in *Nardus* vegetation. At the two upper sites, total C and N concentrations in soil were lower in camp areas than in *Nardus* vegetation, yet lower C/N ratios and higher ammonium and nitrate concentrations indicated a greater availability of N. At the lowest site, the pattern was reversed, with higher total C, N and P concentrations in the camp area, no difference in C/N ratios, and lower ammonium and nitrate concentrations (Table 1). Analyses of variance indicated significant differences between camp areas and *Nardus* vegetation for all variables except total soil N; in addition, significant position-by-site interactions for total soil nutrients and pH reflected the contrasting patterns at site C compared to A and B (Table 3a).

Nitrogen was mostly captured by ion exchange resins as ammonium-N, with on average only 8.9% of it being in the form of nitrate. The total amount of mineral N captured by the IER in six weeks did not differ among the three sites nor did it change significantly along transects from the centre of camp areas to the surrounding pasture (Table 3b). Along individual transects there was generally a weak decreasing tendency, but on one transect at site A, IER-N tended to be lower in the camp area than around it (Figure 1).

Decomposition

The camp-area substrate had higher N and P concentrations and lower C/N ratio, N/P ratio, lignin concentration and ash content than the *Nardus* substrate. The camp-area substrate also contained more soluble phenolics; a greater fraction of it was leachable, and its saturated water content was higher (Table 2).

In the field experiment, the camp-area substrate lost on average 81.5%, and the *Nardus* substrate 27.1% of its organic (ash-free) mass in 14 weeks. Mass loss did not change consistently along the transects, but it differed among sites, and changes along transects differed among sites as well (Table 3b): on some transects mass loss increased with distance from the centre of camp areas, on others it decreased, but any of these trends were very weak (Figure 2). Mass loss did not correlate with the amount of N captured by ion exchange resins across the 27 sampling stations (Pearson's $r = 0.04$ for the camp-area substrate and 0.20 for the *Nardus* substrate, $P > 0.05$)

In the first laboratory experiment, nutrient addition did not accelerate the decomposition of either the camp-area or the *Nardus* substrate over sand inoculated with microbes from the field sites (Anova, $P > 0.05$; Figure 3a). In contrast, cellulose (filter paper) decomposed much faster when N and P were added (29% mass loss) than without nutrient addition (2%) or with addition of N or P alone (Anova, $P < 0.001$; Figure 3a).

In the second laboratory experiment, cellulose that was incubated without nutrient addition lost a greater fraction of its initial mass over soils from the camp area stations than over soils from the *Nardus* stations at sites A and B; there was no difference with soils from site C (Figure 3b, Table 3c). The addition of N tended to reduce the mass loss but did not remove the difference between camp area and *Nardus* soils (Figure 3b, Table 3c). The addition of P tended to reduce cellulose mass loss on soils from camp area stations but to increase it on soils from *Nardus* stations; as a result, camp area and *Nardus* soils did not differ (Figure 3b, Table 3c). Finally, the addition of both N and P enhanced cellulose mass loss, but more so on soils from *Nardus* stations, so that camp area and *Nardus* stations did not differ (Figure 3b, Table 3c). Cellulose decomposition correlated positively with the mineral N concentration of soil samples when either no nutrients or P alone was added to the Petri dishes (Table 4). After addition of N, cellulose decomposition correlated with the phosphate-P concentration; after addition of both N and P, cellulose decomposition was independent of mineral nutrient concentrations in soil (Table 4).

In the third laboratory experiment, the mass loss of both substrates after four weeks (Figure 4) was similar to that in the first experiment (Figure 3a), but in this case nutrient addition slightly accelerated decomposition in the initial phase: After four weeks

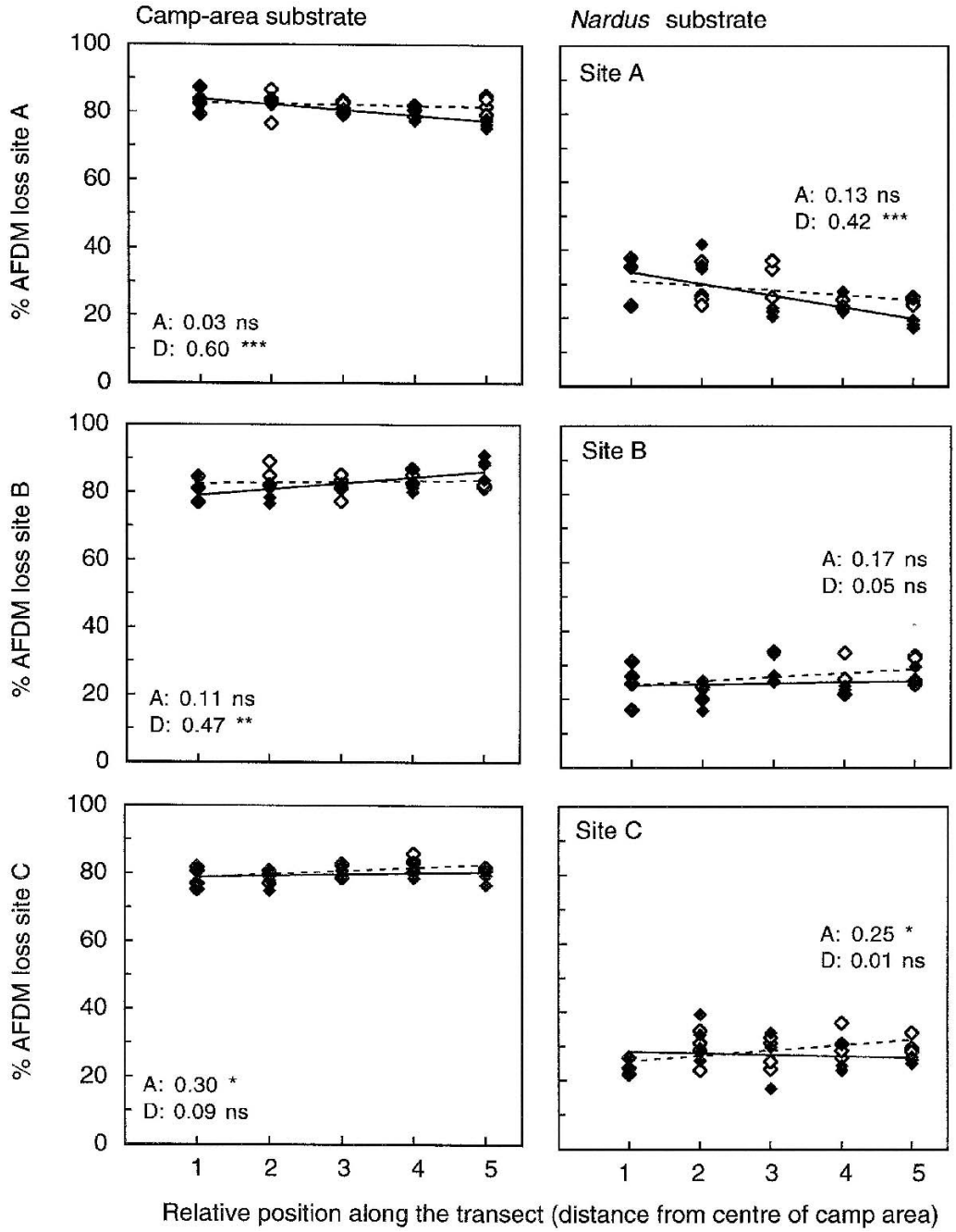

Figure 2. Changes in the mass loss of two plant substrates (from a camp area and from *Nardus* vegetation) after 14 weeks (30.6.1999–6.10.1999) of decomposition in litter bags along gradients from the centre of camp areas to the surrounding *Nardus stricta* vegetation. See Figure 1 for symbols and lines.

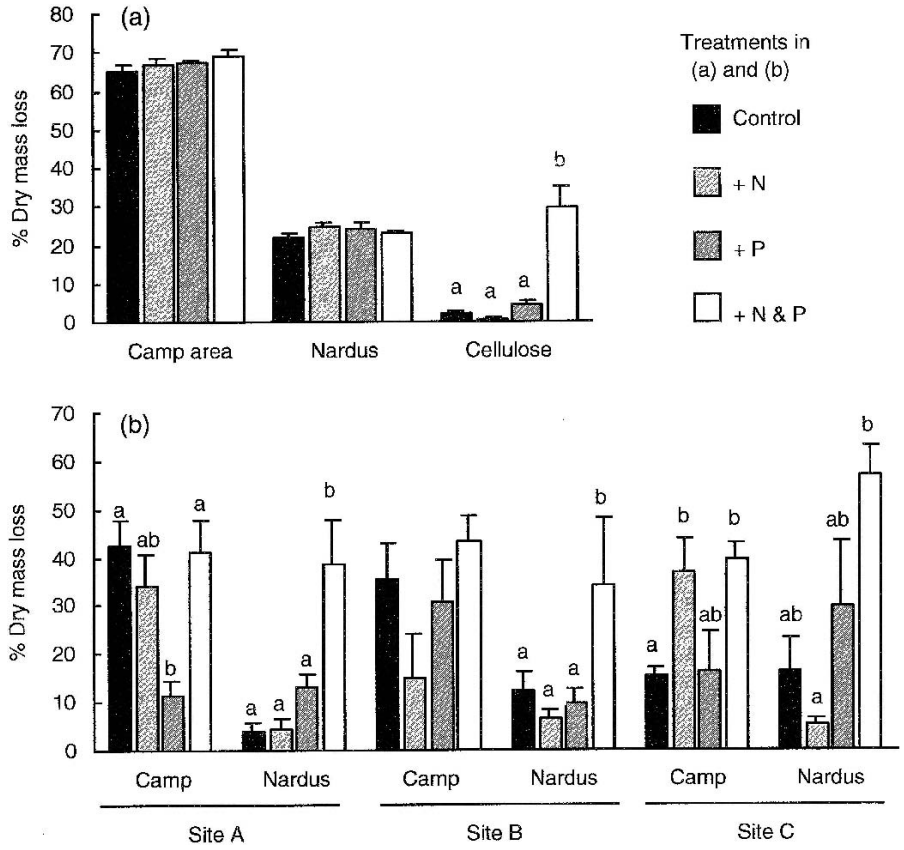

Figure 3. Mass loss after four weeks of decomposition of (a) the two plant substrates and cellulose (filter paper) when incubated over sand and (b) cellulose when incubated over soil from six sampling stations (cf. Table 1). All incubations were carried out in the laboratory at 22 °C, without or with nutrient addition (N or P or both). Data are means ± SE, $n = 4$. Significant differences among treatment means (Tukey HSD test, $P < 0.05$) are indicated by letters, separately for each substrate in (a) and for each soil type in (b).

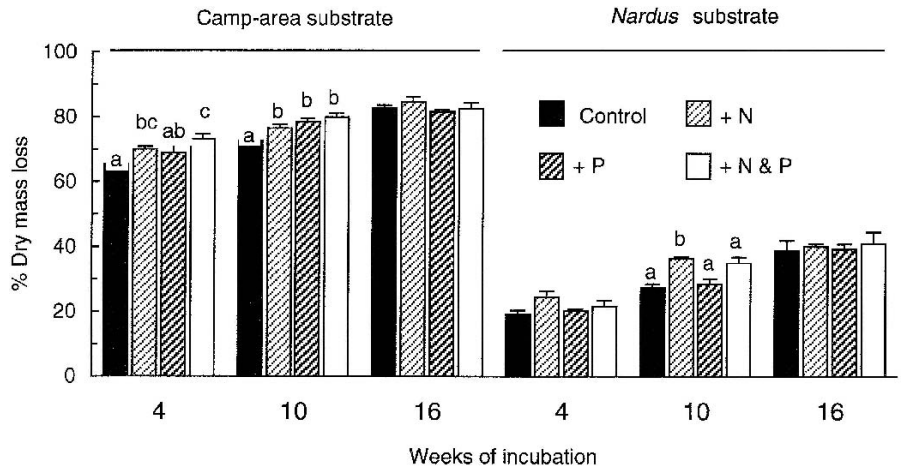

Figure 4. Mass loss after 4, 10 and 16 weeks of decomposition (means ± SE, $n = 4$) for two plant substrates incubated at 22 °C in Petri dishes over sand inoculated with water from a wet grassland, without or with nutrient addition (N or P or both). Significant differences among treatment means (Tukey HSD test, $P < 0.05$) are indicated by letters, separately for each substrate and decomposition period.

Table 3. Significance of differences in ecosystem properties between camp areas and surrounding *Nardus* pasture ('position'), of differences among the three field sites, and of the interaction, tested (a) for nutrient concentrations in plant biomass and soils from six sampling stations (cf. Table 1) with two-way analysis of variance, (b) for changes in decomposition and in N capture by ion exchange resins along transects from camp areas into surrounding pasture (cf. Figures 1 and 2) with analysis of covariance, and (c) for the mass loss of cellulose incubated over soils from six sampling stations with four different nutrient treatments (cf. Figure 3b) using two-way analysis of variance. Figures in the Table are *F*-ratios and the significance of effects (***, $P < 0.001$; **, $P < 0.01$; *$P < 0.05$; °, $P < 0.1$; no symbol, $P > 0.1$)

	Factor tested		
	Position (Camp vs. *Nardus*)	Site (A.B.C)	Site * Position
(a) Nutrient concentrations in plant biomass and soils			
Plant N concentration (mg/g)	3.59°	2.57	0.48
Plant P concentration (mg/g)	77.77***	16.15***	1.81
Plant N/P ratio	115.81***	14.04**	1.08
Total soil C (%)	4.57*	4.75*	8.53**
Total soil N (mg/g)	1.04	6.71**	5.94*
Total soil P (mg/g)	12.94***	16.20***	27.89***
Soil C:N ratio	12.57**	0.14	7.17**
Phosphate-P (mg/g)	3.25°	4.80*	0.18
Nitrate-N (mg/g)	5.34*	2.17	2.90°
Ammonium-N (mg/g)	4.63*	0.37	2.54
Soil pH (H_2O)	3.37°	3.30°	9.68**
(b) Decomposition and N captured by IER along transects			
Mineral N captured by IER	1.81	0.10	0.82
Mass loss camp-area substrate	0.92	3.58*	4.69*
Mass loss *Nardus* substrate	0.48	3.43°	4.02*
(c) Cellulose decomposition on soil samples			
Control treatment	24.64***	1.71	7.42**
N addition	24.79***	2.02	2.71°
P addition	0.11	1.07	2.70°
N & P addition	0.11	0.79	1.45

of incubation, mass loss of the camp-area substrate in the N- and N&P-treatment significantly exceeded mass loss in the control treatment (Figure 4). After ten weeks of incubation, the mass loss of both substrates was enhanced by N addition (and by P addition witht the camp-area substrate). After 16 weeks, however, when mass loss was similar to that in the field incubations (cf. Figure 2), nutrient addition did no longer affect the decomposition of the two substrates (Figure 4).

The much faster decomposition of the camp-area substrate than of the *Nardus* substrate (Figure 4) was associated with a greater nutrient release: after ten weeks of incubation without added nutrients, the camp-area substrate had released 67% and 58% of its initial N and P content, respectively, compared to 25% N and 21% P released from the *Nardus* substrate. In the fertilised treatments, the *Nardus* substrate immobilised nutrients: after ten weeks of incubation with N&P added, its N and P contents were 13% and 17% greater than initially. In contrast, the N and P contents of the camp-area substrate were 81% and 31% smaller than initially, indicating that any nutrient immobilisation was rapidly offset by nutrient release.

Discussion

Our three field sites were characterised by sharp contrasts in plant species composition between the camp

Table 4. Correlations (Pearson's *r*) between the mass loss of cellulose incubated on soil samples from six sampling stations (cf. Figure 3b) and the concentrations of mineral N (ammonium + nitrate) and phosphate-P in these soils (cf. Table 1, $n = 4$ per station). Correlations were calculated for cellulose decomposition in Petri dishes without nutrient addition or with the addition of N or P (four treatments), but in all cases mass loss was correlated with nutrient availability in the unfertilised soil samples. The significance of correlations is indicated as: ***, $P < 0.001$; **, $P < 0.01$; * $P < 0.05$; °, $P < 0.1$; no symbol, $P > 0.1$

Treatment	Correlation of mass loss with	
	Mineral N	Phosphate-P
Control	0.51*	0.12
N addition	0.13	0.49*
P addition	0.71***	0.23
N & P addition	0.26	0.00

areas and the surrounding pasture dominated by *Nardus stricta*. We hypothesised that besides aggregated grazing and trampling by cattle (Wilson and Agnew, 1992), differences in nutrient availability also contributed to maintain the vegetation patterns. Our results showed that indeed, most indicators of nutrient availability differed significantly between camp areas and *Nardus* vegetation ('position' effects in Table 3). In particular, the phosphate concentration in soil and the P concentration of plant biomass were always higher in camp areas than in the *Nardus* vegetation. The lower biomass N:P ratios in camp areas (N:P < 11) suggested that plant growth was N-limited there but P-limited or co-limited in the *Nardus* grassland (N:P > 13, see Tessier and Raynal, 2003). The greater availability of P in camp areas indicated by these data must be due a faster P cycling (in soil or mediated by cattle grazing and defecation) given that total soil P hardly differed between camp areas and *Nardus* vegetation at sites A and B (cf. de Mazancourt et al., 1998).

However, significant site-by-position interactions (Table 3) also meant that several variables did not differ consistently between camp areas and *Nardus* pasture at the three study sites. Thus, patterns in N availability differed markedly between the two upper sites (A and B) and the lower one (C). At sites A and B, the soil C/N ratio was lower in camp areas than in the *Nardus* vegetation, indicating a higher quality of organic matter, and the mineral N concentration was much higher, suggesting a greater N availability. At the same time, the total N and C concentration in soil was lower in camp areas, reflecting a lower organic matter content. The results from site C were just opposite, with greater total N concentration but lower mineral N concentrations in the camp area.

While we investigated only three sites, such inconsistent patterns were also found in a broader survey of soil nutrients carried out in 1998 on Alpe Nisciora (Jewell, 2002): although total P concentration was on average higher and total N concentration lower in soils of camp areas than in those of *Nardus* vegetation, individual values varied substantially. Cattle thus appear to be only one of several factors determining soil nutrient concentrations on Alpe Nisciora. Besides possible pre-grazing differences in topography or underlying rock, soil erosion and run-off after heavy rainfall events certainly cause important re-distributions of nutrients (P.L.Jewell, pers observation). The Insubrian climate with its irregular precipitation, and the silty, poorly aggregated soils of the region promote soil run-off; in addition, cattle grazing certainly strengthened this tendency: the original forest vegetation was replaced by grassland, on which the trampling of cattle created unvegetated spots particularly susceptible to erosion (Ellenberg, 1996).

Some other results of our study may be related to the particular site conditions of Alpe Nisciora. The reduced soil organic matter content in camp areas of sites A and B may surprise given the high inputs of organic matter received by these areas with cattle dung. It also contrasts with the increased organic matter contents found by Haynes et Williams (1999) in camp areas on sheep pastures. On Alpe Nisciora, unlike the study sites of Haynes et Williams (1999), camp areas and surrounding pasture differed in plant species composition, and the surrounding pasture was only partly grazed. Thus, much of the herbage produced by *Nardus stricta* reached the soil *in situ* as litter instead of being transported to the camp areas as excreta. Given its relatively high lignin content and its slow decomposition, the litter of *Nardus* is likely to supply more recalcitrant organic matter to the soil than the combination of plant litter and cattle dung in camp areas. *Nardus stricta* also forms extended root systems with comparatively long-lived, slowly decomposing roots (van der Krift and Berendse, 2002), which may contribute to the long-term accumulation of C and N in soils equally or more than leaf litter (cf. Bryant et al., 1998). In contrast, grazing-tolerant species such as *Festuca rubra* (one of the dominants in camp ar-

eas) tend to reduce their root biomass in response to grazing (Guitian and Bardgett, 2000).

The effects of grazers on N mineralisation in soil often correlate positively with their effects on the soil organic matter content (Frank and Groffman, 1998; Haynes and Williams, 1999; Smit and Kooijman, 2001). In contrast, N availability in soils of Alpe Nisciora, as indicated by mineral N concentrations, was lower in the stations with greater organic matter content (*Nardus* pasture at sites A and B, camp area at site C). At the same time, the amounts of N captured by IER did not reflect these differences in N availability. The IER results seem to indicate that gross N mineralisation was similar at all stations, perhaps due to the relatively small differences in organic matter content, whereas mineral N concentrations indicate that net N mineralisation was reduced in soils with greater organic matter content, probably due to a stronger N immobilisation (Frank et al., 2000; Shariff et al., 1994). The high C/N ratio of the plant litter from *Nardus* vegetation (C/N = 35) relative to that of the soil (10–12) suggests that N is immobilised during the initial decomposition of this litter (Bloemhof and Berendse, 1995; Parton et al., 1987), as found in our third laboratory experiment. The particular soil chemistry of the acidic cryptopodzolic soils also tends to promote the immobilisation of N in soil organic matter (Blaser et al., 1997). For camp areas, the low C/N ratio of the camp-area substrate (13) suggests a release of N already during the initial stages of decomposition (Bloemhof and Berendse, 1995; Parton et al., 1987), in agreement with the results of our third laboratory experiment. The difference between the two substrates used in this study was exceptionaly high: new material collected from camp area C in May 2003 had lower nutrient concentrations due to a greater proportion of dead material (22.1 mg g^{-1} N, 1.22 mg g^{-1} P, C/N = 21), and its mass loss in 16 weeks was 63% (control treatment; S. Güsewell, unpublished data). This was less than the 83% mass loss obtained with the more nutrient-rich material from 1999 in our third laboratory experiment, but still clearly more than mass loss from the *Nardus* substrate.

Cellulose decomposition in the second laboratory experiment showed that microbial activity is potentially higher in soils of camp areas than in those of the *Nardus* vegetation when labile carbon is supplied. This was likely due to the higher nutrient availability in camp areas given that cellulose decomposition (i) correlated positively with mineral N and P concentration in soils, (ii) was accelerated by fertilisation with N and P, and (iii) did not differ between soils from camp areas and those from *Nardus* vegetation when P was added. The effects of nutrient addition on cellulose decomposition suggest that microbial activity was limited by N in the camp area of site C, by P in the *Nardus* vegetation of sites A and C, and jointly by N and P in the *Nardus* vegetation of site B. Thus, P appeared to be more limiting for soil microbes in the *Nardus* vegetation than in camp areas, supporting the view that P limitation can also be relevant for soil processes in terrestrial ecosystems (Coûteaux et al., 1995).

While microbial activity on cellulose was potentially higher in soils of camp areas and could be stimulated by nutrient addition, this was not the case with the two plant substrates used in the field study: their decomposition did not decrease consistently from the centres of camp areas to the surrounding *Nardus* vegetation; it was uncorrelated to the amount of N adsorbed to the IER, and unaffected by nutrient addition in the first laboratory experiment. As the control treatment in the laboratory was a nutrient-free 'soil', nutrient immobilisation from the environment could not explain the absence of nutrient limitation (cf. Chauhan et al., 1981). The reason must be the refractory nature of material in the case of the *Nardus* substrate and high nutrient concentrations in the case of the camp-area substrate (Bloemhof and Berendse, 1995; Bosatta and Berendse, 1984; Cheshire and Chapmann, 1996; Hobbie, 2000).

In the third laboratory experiment, where plant substrates were inoculated with water from a wet grassland, there was a slight positive effect of fertilisation on decomposition, with a 7–9% greater mass loss after ten weeks of incubation in the N&P-treatment. Thus, the microbes from the more nutrient-rich wet grassland were slightly more responsive to nutrient addition than those from Alpe Nisciora, suggesting that the latter were more adapted to low-nutrient conditions. The same difference in responsiveness was found in the comparison of boreal forest soils (Vance and Chapin, 2001). However, even with the wet grassland microbes, the effects of nutrient addition on decomposition were marginal and disappeared after a few months, similar to patterns commonly found in field experiments (Berg et al., 1993; Coûteaux et al., 1995; Hobbie and Vitousek, 2000; Hunt et al., 1988).

We hypothesised initially that the 'switch' between the vegetation of camp areas and the surrounding *Nardus* pasture was not only maintained by the direct influence of grazers but also by soil processes, due to (a) differences in substrate quality and (b) effects

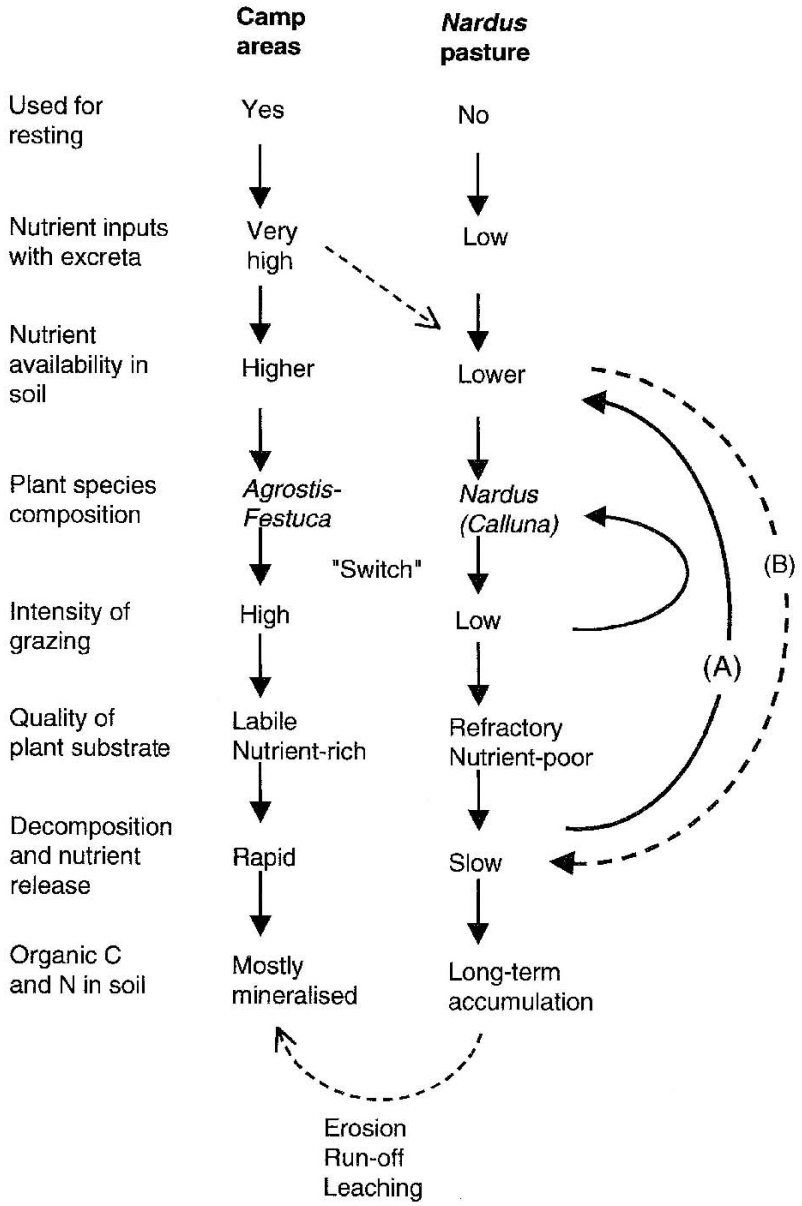

Figure 5. Flow diagram showing the contrasting effects of cattle use on plant species composition and nutrient availability in camp areas and in *Nardus* vegetation, including possible feedbacks. Various authors described a positive feedback caused by the selective feeding behaviour of cattle and plant responses to defoliation ('Switch' in figure, see Wilson and Agnew, 1992 and references therein). Based on the present study, we propose that feedback A (through changes in plant species composition and structure of the litter) was important, whereas feedback B (through effects of nutrient availability in soil on the decomposition of plant material) was unimportant. Differences in decomposition rates have implications for the accumulation of organic matter and nitrogen in soil but the latter are also influenced by other processes such as erosion, run-off or leaching (open arrows).

of nutrient enrichment by excreta on the decomposition process (Figure 5). Our field study confirmed that nutrient availability is generally enhanced in camp areas, and that differences in substrate quality could contribute to this by allowing a faster nutrient cycling in camp areas (feedback a). Our laboratory incubations showed that the resulting differences in nutrient availability could potentially influence the mineralisation of organic carbon in soil, but that they would not feed back on the decomposition of *in situ* plant material because the latter was not nutrient-limited. The same was shown by the decomposition experiments along gradients in the field. The second mechanism (feedback b) did therefore not operate on these Alpine pastures.

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