RESEARCH ARTICLE

Nitrogen Depletion and Redistribution by Free-Ranging Cattle in the Restoration Process of Mosaic Landscapes: The Role of Foraging Strategy and Habitat Proportion

Jan Van Uytvanck,[1,2,3] Tanja Milotic,[1] and Maurice Hoffmann[1,2]

Abstract

In a mosaic landscape in N-Belgium (W-Europe), consisting of forest, grassland, and wooded pasture on former agricultural land, we assessed nitrogen redistribution by free-ranging cattle (± 0.2 animal units ha^{-1} yr^{-1}). We examined if the spatial redistribution of nitrogen among habitats by cattle could restore nutrient-poor conditions in preferred foraging habitats, and conversely whether such translocation could lead to extreme eutrophication in preferred resting habitats. We used nitrogen content of different diet classes, habitat use, foraging and defecation behavior, weight gain, and nitrogen losses in the actual situation to explore four different habitat proportion scenarios and two different foraging strategies to calculate a net nitrogen balance per habitat. An atmospheric deposition of 30 kg N ha^{-1} yr^{-1} with varying interception factors according to the habitat types was included in an integrated nitrogen balance. All scenarios showed a net nitrogen transport from grassland and wooded pasture to forest habitat. We found that nitrogen redistribution strongly depends on habitat proportion. Nitrogen losses from preferred grassland habitat can be high, given its proportion is small. Depletion is only to be expected at excretion-free areas and probably is of minor importance to trigger the establishment of woody species. In general, nitrogen transported by cattle was much lower than input by atmospheric deposition, but grazing can compensate for high N inputs in excretion-free areas and maintain grassland types that support critical loads of 20–25 kg N ha^{-1} yr^{-1}. In none of the scenarios, N transport by cattle resulted in the exceeding of critical nitrogen loads to vulnerable forest ground vegetation.

Key words: atmospheric deposition, critical nitrogen loads, grazing management, habitat and diet selection, large herbivores.

Introduction

The use of free-ranging large herbivores (cattle, horses, and sheep) as a tool for conservation management in Europe is increasing (WallisDeVries et al. 1998). Targeted grazing with wild or livestock species can play a key role in restoring the functioning of ecological processes in a wide range of landscapes, habitats (including former agricultural land), communities, and species (Holl & Smith 2007). The creation of open nutrient-poor habitats by large herbivores, as part of shifting successional mosaics or the restoration of highly productive sites (e.g., heavily fertilized agricultural land), is important conservation items (Bakker & Berendse 1999; Pywell et al. 2007; Prach & Hobbs 2008). For conservation managers, a prediction of the magnitude and the direction of nutrient redistribution (e.g., nitrogen) by large introduced herbivores in a certain area is important. This knowledge may help determining stocking rate, herbivore species, area, and nature of different habitat types to include (or exclude) for grazing. For instance, horizontal nutrient transport by free-ranging cattle may affect vulnerable vegetation types such as forest ground flora. The aim of this paper is: (1) to assess to which extent nitrogen redistribution by free-ranging cattle in a nutrient-rich mosaic landscape results in the creation of nitrogen-poorer conditions or, alternatively, in the eutrophication of habitats and (2) to assess the role of habitat proportion and foraging strategy of cattle on nitrogen redistribution.

Selective foraging, habitat use, and migration influence nutrient distribution: e.g., nutrient depletion in heathland (Bokdam 2003) and semiarid savanna (Augustine et al. 2003), and nutrient redistribution in riparian systems (Jacobs et al. 2007) and humid grasslands (Moe & Wegge 2008). Bokdam (2001) found clear indications that in nutrient-limited

ecosystems, cattle grazing caused alternating dwarf shrub-grassland transitions as a result of alternating lawn depletion and increased nutrient availability after dwarf shrub mortality. Mechanisms determining succession patterns in low-intensity grazed, nutrient-rich areas refer to associational resistance (Van Uytvanck et al. 2008*b*) as a driving force, but little is known about underlying processes such as nutrient redistribution by free-ranging cattle.

Effects of cattle grazing on nitrogen flows are variable, complex, and sometimes opposed in time (seasonal differences) and space (Bailey et al. 1996). They are induced by diet choice, intake rate, body retention, excretion, nitrogen losses from excreta, and habitat use. Indirectly, grazing affects primary production, litter production, and the relative availability of forage species and habitats (Semmartin et al. 2008; van Langevelde et al. 2008). Habitat use and foraging of free-ranging cattle and other large herbivores play a crucial role in understanding nitrogen flows in an area, because they link all above-mentioned factors. The foraging pattern may result from decisions made by the animals at different spatial and temporal scales (Bailey et al. 1996). Noncognitive mechanisms act at smaller spatial scales: foraging velocity decreases and intake rate increases in areas of abundant and high-quality forage. Cognitive mechanisms include selection of feeding sites, based on spatial memory, to improve foraging efficiency. The ability to distinguish and to remember (the quality of) different feeding sites enables decision-making on a larger spatial scale. Both mechanisms refer to matching behavior. Matching is an aggregate response pattern that has been observed in several species, among which cattle: the preference for plant communities is related to relative quantities of preferred species and nutrient abundance (Senft et al. 1987*a*). However, as a consequence of searching and recognition costs and other advantages (e.g., shelter and water) certain habitats offer, that the foraging pattern will not be a straightforward response to resource distribution (WallisDeVries & Daleboudt 1994). Cognitive and noncognitive selection mechanisms do not exclude each other but they may interact in a different way with habitat proportion. The use of spatial and temporal memory may increase or decrease foraging in a particular habitat, though its proportion is small or large, respectively.

The magnitude of nitrogen redistribution and potential depletion in grazed areas needs assessment within the larger scope of air-borne nitrogen pollution, which has caused the deterioration of many sensitive ecosystems (Sala et al. 2000). Critical loads (Achermann & Bobbink 2003) are often exceeded (Neirynck et al. 2007), and restoration management measures for a wide range of ecosystems in Europe will be required to mitigate or compensate the negative impact of high deposition. In low productive systems, Kooijman and Smit (2001) found that grazing by large herbivores reduced nitrogen availability and compensated for high-atmospheric nitrogen deposition. However, very little data are available on the interaction of free-ranging cattle on nitrogen redistribution and atmospheric deposition in predominantly nutrient-rich mosaic landscapes.

In this paper, we test the hypothesis that a net nitrogen transport occurs from preferred grazing habitat (grassland) to less preferred habitats (forest and wooded pasture), having lower nutritional value, but showing a relatively higher occupancy. Second, we simulate the impact of different habitat proportion scenarios (equal proportion, grassland dominance, forest dominance, and wooded pasture dominance) on nitrogen redistribution among these habitats. We hypothesize that nitrogen depletion is possible to occur in excretion-free areas of preferred foraging habitat with a more pronounced effect when the preferred habitat proportion is small. Further, we explore the effects of two different foraging strategies, related to noncognitive and cognitive foraging mechanisms, respectively. In the former, we assume that the observed foraging pattern corresponds with the velocity of cattle which transit a certain habitat: slower movement through areas of greater nutrient abundance, and therefore dependent on the present habitat proportion. In the latter strategy, we assume that the observed pattern corresponds with a strong selection, based on the qualities of a habitat, and therefore independent of its proportion. We hypothesize that by using the latter strategy, higher nitrogen losses will be found. In these scenarios, we assess the chances for restoration of nutrient-poor conditions or the risks of habitat eutrophication over time by calculating the seasonal and yearly proportion of excretion-free area per habitat. Finally, we assess the relative impact of nitrogen redistribution by cattle in an environment with a high-atmospheric nitrogen input. Results are discussed in the framework of succession in grazed mosaics and the restoration of low productive grasslands versus the danger of increased nitrogen input on vulnerable forest ground vegetations.

Methods

Study Site

The study was carried out in the nature reserve Bos t' Ename (lat $50°86'$N, long $3°65'$E; ±100 ha) in N-Belgium (Fig. 1). The climate is temperate; annual precipitation is ±700 mm. The study site is a mosaic of forest, grassland, and developing wooded pasture on sandy loam soils. The forests mainly consist of *Carpinion* and smaller parts of *Alno-Padion* vegetation. In both forest types, vast areas with species-rich ground flora (with abundant *Anemone nemorosa*, *Hyacinthoides nonscripta*, *Primula elatior*, and *Vinca minor*) are present. Grasslands are moist to wet and composed of moderate nutrient-rich (*Molinio-Arrhenatheretea*) to nutrient-rich vegetation types (dominated by *Poa trivialis* or *Lolium perenne*). The developing mid-successional wooded pastures are situated on former agricultural land. *Salix caprea*, often heavily grazed, is the dominant tree species. Saplings and juvenile trees of *Betula pendula*, *Fraxinus excelsior*, *Quercus robur*, and *Alnus glutinosa* occur frequently; scrub patches of *Rubus sp.*, *Prunus spinosa*, *Crataegus monogyna*, and *Rosa canina* occur occasionally. The ground flora in the wooded pastures consists of a mix of short and tall grassland and ruderal forb patches. Given the temperate climate, the moist and loamy soils, and the
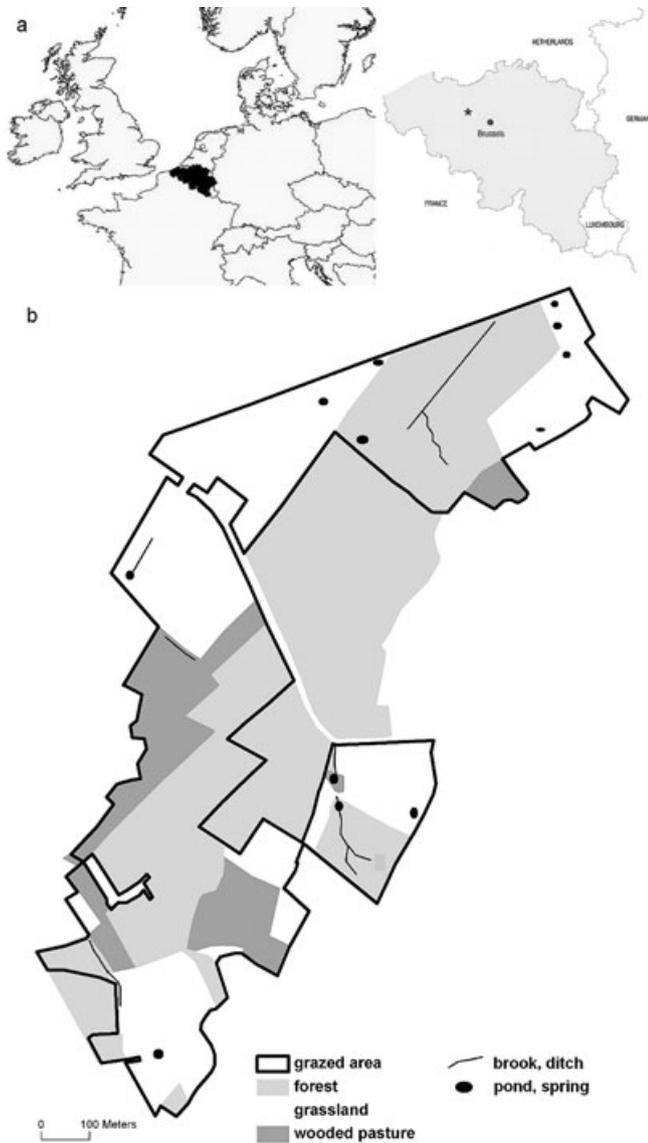
Figure 1. Study site Bos t' Ename. (a) Location in Europe and Belgium (asterisk); (b) map of the grazed landscape mosaic, distinguishing three global habitat types and water supply sites.

negligible presence of *Leguminosae* (*Trifolium repens* occurring occasionally and locally in grassland habitat), we assumed nitrogen leaching and biological fixation to be very low in all vegetation types.

In Bos t' Ename, cattle have free access to forest (25.16 ha), adjacent grassland (27.16 ha), and developing wooded pasture (9.92 ha) since 2004. Small dust roads and paths lacking vegetation are found in forest (0.35 ha) and wooded pasture (0.15 ha). Drinking water sites (ditches, brooks, ponds, and springs) are available throughout the year and spread over the whole area (Fig. 1). A small herd of the hardy "white-red cattle breed of East-Flanders" was introduced in the area for year-round grazing. This herd consisted of 11 animals: one bull, five cows, two heifers, and three calves.

Mean individual live weight (LW) was 516 ($\pm$219) kg. Though herd size tends to a minimum, grazing pressure is rather high ($\pm$9,000 kg/km^2), exceeding grazing pressure in most natural ecosystems (WallisDeVries et al. 1998).

Nitrogen Intake by Free-Ranging Cattle and Net N Balance Per Habitat

We studied the role of free-ranging cattle in the process of nitrogen redistribution using field observations, measurements, and literature data. We assessed seasonal nitrogen (N) intake by grazing and included body retention, excretion, and volatilization to calculate a net N balance per habitat per hectare. We presented consecutive steps in Fig. 2 and explained them below (numbers between brackets correspond with numbers in Fig. 2).

Field Observations: Seasonal Foraging (1) and Occupancy Pattern (2), Seasonal Diet (3), and Number of Urinations and Defecations.

We assessed habitat use (foraging and occupancy) and diet using direct observations on time budget in the field. In 2005–2006, we conducted 36 observation sessions spread over 1 year: nine per season (spring = March–May; summer = June–August; autumn = September–November; and winter = December–February). Observation sessions lasted 5 hours and were conducted in the morning (6–11 a.m.), afternoon (11–16 p.m.), or evening (16–21 p.m.). In each season, we conducted three morning, three afternoon, and three evening sessions. We used an instantaneous sampling method (Lamoot et al. 2005). We recorded position, habitat, behavior, diet, and drinking every 15 minutes for all animals of the herd. All individuals were used to the presence of people and could be approached easily (within a 2 m range) without apparent impact on their behavior.

We distinguished four habitat types: forest, grassland, wooded pasture, and "other habitat" (dust roads, paths, and ponds situated in the three former habitats). We determined seasonal habitat preference using Jacobs' (1974) index of selection. We divided diet in four classes that were easily distinguishable during field observations: grasses, herbs, grasses–herbs mix, and woody vegetation. Time budget (%) of habitat use, foraging, and diet of all individuals was pooled and averaged per season.

Diet Nitrogen Content (4).

During 1 year, we took biomass samples each month in one permanent quadrate (PQ, 20 m x 20 m) per habitat type. Each time, we took four random samples of 0.25 m^2 per PQ, avoiding re-sampling of previous sampled cells. We subdivided samples in monocotyledons (grasses, sedges, and rushes), dicotyledons (herbs), mosses, woody vegetation, and litter. For these classes, we determined nitrogen content monthly. We excluded mosses and litter for further calculations because we had no observations of cattle foraging on these classes in our study site. We determined crude protein concentration after a drying period of 48 hours (65 $\pm$ 2°C), using the Kjeldahl method. We calculated nitrogen content per season (i), habitat (j),
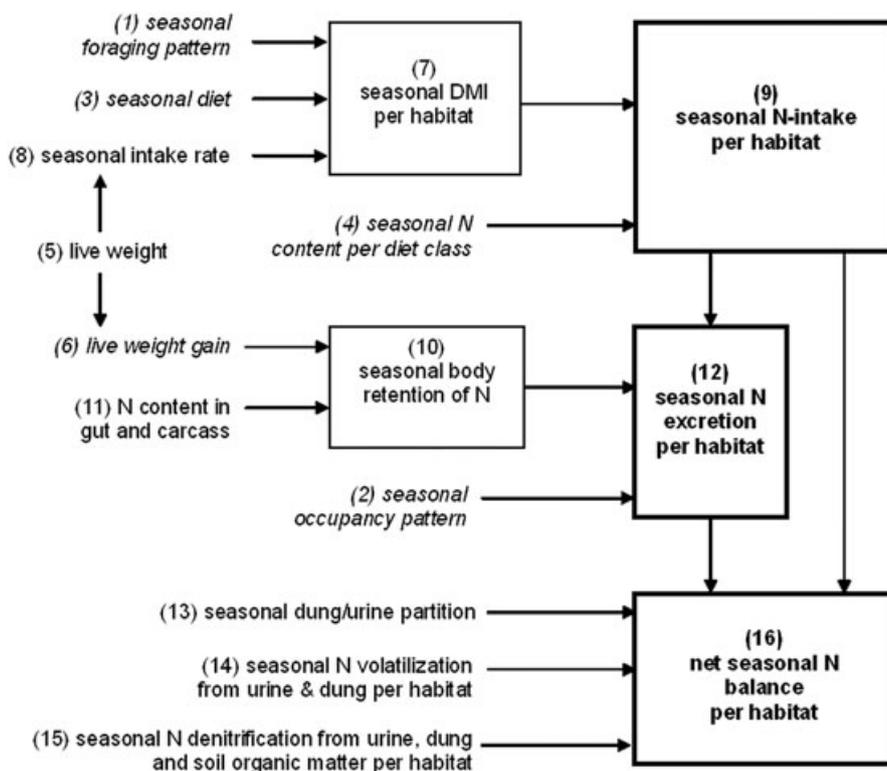
Figure 2. Nitrogen flows determining N intake by cattle and net N balance in a grazed mosaic landscape. Calculated results (in boxes, bold ones presented in figures) are based on field data of the study site (italics) and literature data (regular font).

and diet class (k) $(= \%N_{i,j,k})$ using Bradstreet's (1965) formula:

$$\%N_{i,j,k} = \%\text{crude protein} \times 6.25^{-1}$$

We pooled and averaged data per season. For the classes, grasses, herbs, grasses–herbs mix, and wood, we used the data on nitrogen content of monocotyledons, dicotyledons, average of both former classes, and woody vegetation, respectively.

LW (5) and LW Gain (6). We measured LW of all animals of the herd in winter, before and after 1 year grazing. LW gain per season was estimated: spring: +35%; summer: +40%; autumn: +25%; and winter: ±0%. These estimates were based on growth curves for the breed (Butaye & De Baerdemaecker 1972). Body mass losses in winter are reported for cattle and wild herbivores in natural environments, but highly depend on site and severity of winter season (WallisDeVries 1992). For the nutrient-rich study site and the mild winter of 2005–2006, we assumed a stand still in LW gain.

Dry Matter Intake (7). For cattle, Van Dyne et al. (1980) found a daily dry matter intake (dDMI) (8) of 0.021 kg kg^{-1} LW (confirmed by WallisDeVries 1994). For the herd in Bos t' Ename, this meant an average DMI of 4,391 kg per animal per year (i.e., 48,310 kg for the whole herd). We differentiated dDMI per season: 0.030 and 0.015 kg kg^{-1}LW for summer and winter, respectively (Senft et al. 1987*b*;

Bokdam 2003); intermediate values for spring and autumn: 0.023 and 0.017 kg kg^{-1} LW, respectively, allowing us to calculate the seasonal DMI for the herd (DMI$_{\text{herd},i}$).

$$\begin{aligned} \text{DMI}_{\text{herd},i}(\text{kg season}_i^{-1}) &= 91.25(\text{day season}_i^{-1}) \\ &\times \text{dDMI}_i(\text{kg day}^{-1} \text{ kg}^{-1}\text{LW}^{-1}) \\ &\times \text{LW}_{\text{herd},i}(\text{kg LW}) \end{aligned}$$

We used foraging time (%) to calculate seasonal DMI per habitat for the herd (DMI$_{\text{herd},i,j}$)

$$\begin{aligned} \text{DMI}_{\text{herd},i,j}&(\text{kg season}_i^{-1}\text{habitat}_j^{-1}) \\ &= \text{DMI}_{\text{herd},i}(\text{kg season}_i^{-1}) \times \text{foraging time}(\%\text{habitat}_j^{-1}) \end{aligned}$$

We used seasonal foraging time (%) on different diet classes to calculate the seasonal DMI of the herd for each diet class per habitat (DMI$_{\text{herd},i,j,k}$). We assumed a constant intake rate for all diet classes. For woody vegetation, this is probably an overestimation.

$$\begin{aligned} \text{DMI}_{\text{herd},i,j,k}&(\text{kg season}_i^{-1}\text{habitat}_j^{-1}\text{dietclass}_k^{-1}) \\ &= \text{DMI}_{\text{herd},i,j}(\text{kg season}_i^{-1}) \\ &\times \text{foraging time}_k(\%\text{dietclass}_k^{-1}) \end{aligned}$$

Nitrogen Intake (9). Using the measured seasonal N concentrations in the diet, we calculated N intake per season, habitat,

and diet class ($Nintake_{i,j,k}$). We further calculated total seasonal nitrogen intake per habitat ($Nintake_{i,j}$).

$$Nintake_{i,j,k} (\text{kg N season}_i^{-1} \text{habitat}_j^{-1} \text{diet class}_k^{-1})$$
$$= DMI_{herd,i,j,k} (\text{kg season}_i^{-1} \text{habitat}_j^{-1} \text{dietclass}_k^{-1}) \times \%N_{i,j,k}$$

$$Nintake_{i,j} (\text{kg N season}_i^{-1} \text{habitat}_j^{-1})$$
$$= \sum_{k=1}^{n} Nintake_{i,j,k} (\text{kg N season}_i^{-1} \text{habitat}_j^{-1} \text{dietclass}_k^{-1})$$

Body Retention (10). Body retention is the N incorporated in the yearly LW gain. LW gain is the sum of carcass LW increment (85%) and gut fill increment (15%, Agricultural Research Council 1980, in WallisDeVries et al. 1998). We assumed N concentrations (11) in the carcass and in the gut as 2.56 and 0.52%, respectively (Bokdam 2003). We used the seasonal LW gain of the herd to calculate the seasonal body retention of nitrogen ($BR_{herd,i}$).

$$BR_{herd,i} = 2.56\% \times 85\% \times LWgain_{herd,i} + 0.52\%$$
$$\times 15\% \times LWgain_{herd,i}$$

Nitrogen Excretion ($Nexcr_i$) (12).

$$Nexcr_i (\text{kg N season}_i^{-1}) = Nintake_i (\text{kg N season}_i^{-1})$$
$$- BR_{herd,i} (\text{kg N season}_i^{-1})$$

We further incorporated the seasonal occupancy time (Occuptime) (2) of cattle to calculate excretion distribution among different habitats ($Nexcr_{i,j}$).

$$Nexcr_{i,j} (\text{kg N season}_i^{-1} \text{habitat}_j^{-1})$$
$$= Nexcr_i (\text{kg N season}_i^{-1}) \times Occuptime_{i,j} (\%\text{habitat}_j^{-1})$$

Gaseous Nitrogen Losses from Excreta and Soil Organic Matter (13–14–15). Ammonia volatilization from urine patches usually ranges from 10 to 40% of the total N in urine (Ruess & McNaughton 1988). Losses from fine textured soils are lower than those from coarse textured soils (Schimel et al. 1986). Volatilization is positively related to soil humidity (Milchunas et al. 1988) and negatively related to soil cation-exchange capacity, plant biomass concentration. Volatilization is higher in summer than in winter (Ruess & McNaughton 1988; Frank & Zhang 1997). Given the fine textured soils with a comparable humidity in all habitats of the study site and the volatilization percentages in the above-mentioned studies, we estimated seasonal nitrogen volatilization (14) from urine patches ($Nvolu_i$): 5–15% (summer = 15%; autumn and spring = 10%; and winter = 5%). We incorporated the partition (13) of N in urine and dung, respectively, to estimate N loss by volatilization per season and habitat ($Nlossvolu_{i,j}$). We assumed that the partition of total N in excreta was 50–70% in urine and 30–50% in dung, varying among seasons (N percentage in urine [Nu_i]: summer = 70%; autumn and spring

= 60%; winter = 50%; Senft et al. 1987b; Frank et al. 1994; Bokdam 2003).

$$Nlossvolu_{i,j} (\text{kg N season}_i^{-1} \text{habitat}_j^{-1})$$
$$= Nvol_i (\%) \times Nu_i (\%) \times Nexcr_{i,j} (\text{kg N season}_i^{-1} \text{habitat}_j^{-1})$$

Ammonia volatilization from dung (14) is much lower than those from urine, but may be of ecological importance (Saarijärvi et al. 2006). We estimated N volatilization from dung ($Nvold_i$) was 3% for all seasons (percentages in literature range from 0.5 to 8%, Sugimoto & Ball 1992a; Jørgensen & Jensen 1997; Saarijärvi et al. 2006). Seasonal N percentage in dung (Nd_i) − 100 Nu_i.

$$Nlossvold_{i,j} (\text{kg N season}_i^{-1} habitat_j^{-1})$$
$$= Nvold_i (\%) \times Nd_i (\%) \times Nexcr_{i,j} (kg N season_i^{-1} habitat_j^{-1})$$

Further, we incorporated N losses from urine, dung, and soil organic matter due to denitrification (N_2O emission) (15). Most literature describes intensively used pastures, but it is known that reduced exploitation (e.g., in grazed nature reserves) decreases denitrification (Loiseau et al. 2005). Therefore, our assumptions of N losses are rather conservative. The literature does not provide a consistent seasonal pattern for N_2O emission. It seems rather dependent on soil moisture and rainfall (van Groenigen et al. 2005a). Therefore, we used equal denitrification rates for all seasons. We assumed that the N_2O emission from urine ($Nlossdenu_{i,j}$) was 0.5% and from dung 1.0% ($Nlossdend_{i,j}$) (ranges 0.05–0.9 and 0.33–4.0, respectively, Sugimoto & Ball 1992b; van Groenigen et al. 2005a; Wachendorf et al. 2008).

$$Nlossdenu_{i,j} (\text{kg N season}_i^{-1} \text{habitat}_j^{-1})$$
$$= 0.5 (\%) \times Nu_i (\%) \times Nexcr_{i,j} (\text{kg N season}_i^{-1} \text{habitat}_j^{-1})$$

$$Nlossdend_{i,j} (\text{kg N season}_i^{-1} \text{habitat}_j^{-1})$$
$$= 1.0 (\%) \times Nd_i (\%) \times Nexcr_{i,j} (\text{kg N season}_i^{-1} \text{habitat}_j^{-1})$$

We assumed that background N_2O emission from soil organic matter ($Nlossdens_j$) was 1.5 kg N_2O-N ha^{-1} yr^{-1} for wooded pasture and forest habitat, 2.5 kg N_2O-N ha^{-1} yr^{-1} for grassland, and 5 kg N_2O-N ha^{-1} yr^{-1} for other habitats (mostly compacted soils of paths) (van Groenigen et al. 2005b; Saggar et al. 2008).

Total seasonal gaseous nitrogen loss (Nlossg) from the system was than calculated as:

$$Nlossgas_{i,j} (\text{kg N season}_i^{-1} \text{habitat}_j^{-1})$$
$$= Nlossvolu_{i,j} + Nlossvold_{i,j} + Nlossdenu_{i,j}$$
$$+ Nlossdend_{i,j} + \frac{1}{4} Nlossdens_j$$

Net N Balance (16). We used the previous calculated seasonal intake, seasonal excretion, and seasonal gaseous nitrogen losses per habitat to calculate the net N balance:

$$NetNbalance_{i,j} (\text{kg N season}_i^{-1} \text{habitat}_j^{-1})$$
$$= Nintake_{i,j} - Nexcr_{i,j} + Nlossgas_{i,j}$$
$$(\text{kg N season}_i^{-1} \text{habitat}_j^{-1})$$

Habitat Proportion Scenarios and Foraging Strategy Scenarios

In addition to the actual situation in Bos t' Ename, we assessed N flows in four extra scenarios with variable habitat proportions, that is, with woodland–grassland–wooded pasture proportions of 33.3–33.3–33.3% (equal proportions), 60–20–20% (forest dominance), 20–60–20% (grassland dominance), and 20–20–60% (wooded pasture dominance), respectively. For each habitat proportion scenario, we calculated two subscenarios representing different foraging strategies (see Introduction). In the first subscenario, we assumed that a noncognitive foraging pattern will be related to habitat proportion. We changed time budget of foraging and occupancy relatively to the proportion of the habitats in accordance with the observed pattern in the real situation. In the second subscenario, the foraging pattern is independent of habitat proportion: time budget of foraging and occupancy in different habitat proportion scenarios remained the same as in the observed situation at the study site.

Excretion-Free Areas

We counted urination and defecation events in six observation sessions. On average 12.0 ($\pm$2.4) urinations and 11.8 ($\pm$2.9) defecations per cow per day were counted. This corresponds with Afzal and Adams (1992), reporting 10.7 $\pm$ 0.36 and 10.9 $\pm$ 1.8 dung and urination patches, respectively, per cow per day. Affected areas of 0.04 m^2 (Afzal & Adams 1992; own observations) for dung and 0.4 m^2 for urine patches (averaging Afzal & Adams 1992; Bokdam 2003) were assumed. We calculated total area of seasonally excretion-free habitat at the study site and in all habitat proportion scenarios using affected area, occupancy time, and habitat surface.

Integrated Nitrogen Balance (at Ground Level)

We included atmospheric N deposition to study the relative importance of nitrogen redistribution by free-ranging cattle.

The OPS model (van Jaarsveld 2004) provided modeled deposition data (resolution = 1 km^2) for Flanders (N-Belgium). For Bos t' Ename, total N deposition was 30 kg N ha^{-1} yr^{-1}, which is at present the average deposition level in Flanders and in two nearby and comparable deciduous forest sites (Flemish Level II sites of the European ICP-forests network, EC-UN/ECE 1996; Genouw et al. 2005). We corrected N deposition with an interception factor (IF) based on vegetation roughness (Fowler et al. 1999 : IF = 1.5, 0.6, and 1.1 for forest, grassland, and wooded pasture, respectively). Further, for forest habitat, we corrected real throughfall at ground level with a factor of 0.7 (data Level II sites).

Results

Nitrogen Intake by Free-Ranging Cattle

Foraging and Occupancy Pattern of Free-Ranging Cattle.
Except for winter, grassland habitat was the most important habitat for both occupancy (60.17%) and foraging (63.10%), and grassland and wooded pasture were strongly preferred and preferred forage habitats, respectively (Fig. 3b). Forest is used in all seasons, but only in wintertime it is a substantial forage habitat (Fig. 3a). Throughout the year, 1.62% of the time budget was spent on non-foraging sites (roads and paths used for resting: 87.40%; ponds for drinking: 12.60%).

Diet and Diet Nitrogen Content. Overall, grasses were the major food source. Woody vegetation became an important food source during winter (>20% of the foraging time, mostly *Rubus sp*.) and summer (mostly young tree shoots and leaves; Fig. 4b). N concentrations in forage range from 0.97 to 2.03% and were highest in spring for all diet classes (Fig. 4a). After spring, concentrations decreased gradually with the lowest concentrations in winter. Herbs had the highest nitrogen concentration; woody vegetation had the lowest concentration, showing a sharp decline in autumn and winter.
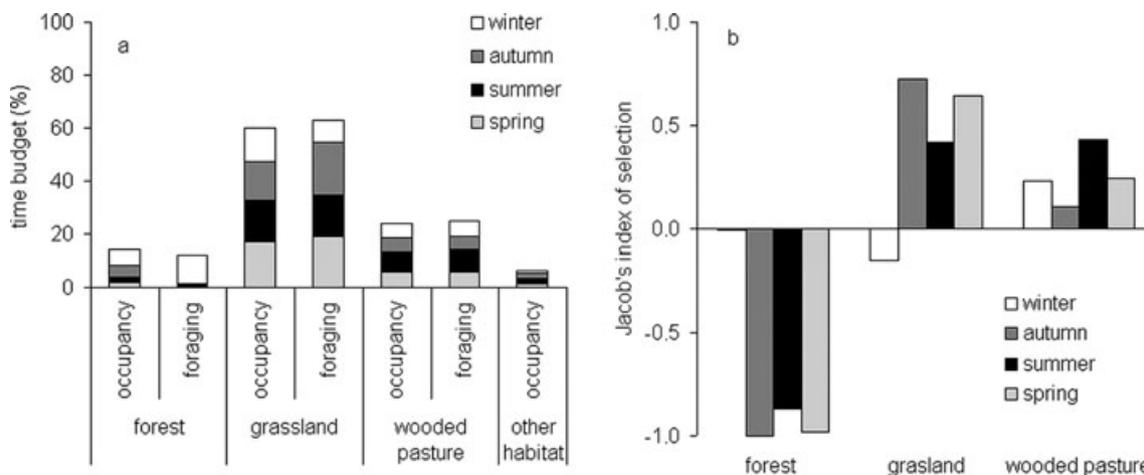

Figure 3. Habitat use (occupancy) and foraging pattern of free-ranging cattle in four habitat types in Bos t' Ename. (a) Seasonal variation in time budget (other habitat: roads, paths, and ponds; (b) seasonal variation in habitat preference for foraging, using Jacob's index of selection. No selection: $-0.08 <$ index <0.08; avoidance: $-0.4 <$ index < -0.08; strong avoidance: index < -0.4; preference: $0.08 <$ index <0.4; strong preference: index >0.4.
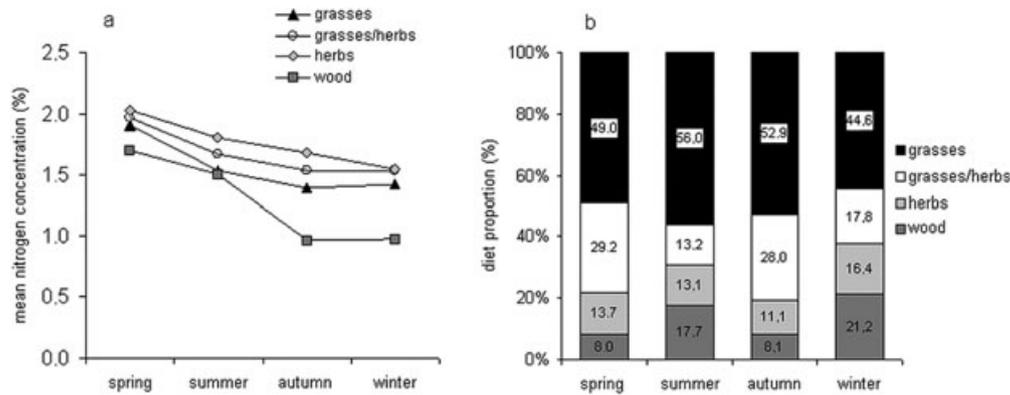
Figure 4. (a) Seasonal variation in nitrogen concentration in four diet classes; (b) seasonal variation in diet of free-ranging cattle in Bos t' Ename.

LW, LW Gain, and Body Retention. Initial individual LW ranged from ±150 (calves) to ±700 kg (bull). Initial total LW of the herd was 5,675 kg. Total LW gain for the whole herd was 1,341 kg/year (mean per animal: 121.9 ± 135.9 kg). LW gain in spring was +469 kg; in summer +536 kg; in autumn +335 kg; and in winter 0 kg. Body retention comprised 30.20 kg N for the whole herd, that is, 3.74% of N intake.

Nitrogen Intake. Nitrogen intake in grassland and wooded pasture was comparable: -19.9 and -22.2 kg N ha^{-1} yr^{-1}, respectively, and mainly realized in spring and summer. In forest, nitrogen intake is almost negligible (-2.3 kg N ha^{-1} yr^{-1}) and almost completely confined to wintertime (Fig. 5).

Nitrogen Excretion. On average, N excretion was 92.5% of total N intake. The redistribution pattern was strongly related to the N intake pattern (Fig. 5), except for forest (excretion evenly spread throughout the year) and non-foraging habitats, which received 24.7 kg N ha^{-1} yr^{-1}.

Gaseaous N Losses. Volatilization from urine patches and denitrification from soil organic matter contribute the most to gaseous N losses. Gaseous losses are generally low (maximum loss: -4.0 kg N ha^{-1} yr^{-1} for all habitats, except for non-foraging habitat: -7.3 kg N ha^{-1} yr^{-1}) (Fig. 5).

Net Nitrogen Balance. We found a negative N balance (i.e., N losses) per hectare in grassland and wooded pasture (-6.9 and -6.2 kg N ha^{-1} yr^{-1}, respectively; Fig. 5). In grassland, all seasons, except for winter, evenly contributed to this negative balance. In wooded pasture, mainly summer contributed to N losses. In forest and non-foraging habitats, a net nitrogen input of 0.3 and 17.4 kg N ha^{-1} yr^{-1}, respectively, was calculated.

Habitat Proportion and Foraging Strategy. N intake strongly depended on habitat type and habitat proportion (Fig. 6). In forest, N intake was small in all scenarios (maximum: -4.5 kg N ha^{-1} yr^{-1}). In grassland, yearly N intake ranged from -14.5 to -43.4 kg N ha^{-1} yr^{-1}. The highest intake was found when grassland habitat proportion was small (20%). In general, N intake in grassland was higher in scenarios with a foraging strategy that was independent on habitat proportion. In wooded pasture, N intake ranged from -5.7 to -27.3 kg N ha^{-1} yr^{-1}. N intake was highest in the forest dominance scenario. For wooded pastures, in general, we found a higher intake in scenarios with a foraging strategy that was dependent on habitat proportion.

Yearly differences between habitats and scenarios were much smaller for the net N balance (range: -12.2 to 1.9 kg N ha^{-1} yr^{-1}). A small yearly net N input was found in forest habitat (<2.0 kg N ha^{-1} yr^{-1}). Nitrogen losses and inputs are most balanced in the grassland dominance scenario (range: -5.9 to 1.9 kg N ha^{-1} yr^{-1}). The highest N losses were found in grassland (-12.2 kg N ha^{-1} yr^{-1}), given its proportion was small and foraging strategy was independent on habitat proportion. N losses in wooded pasture were lower than or equal to those in grassland (-7.8 to -2.7 kg N ha^{-1} yr^{-1}).

Excretion-Free Areas

At the study site, we found high percentages of yearly excretion-free area for all habitats: forest, 98.8%; grassland, 95.3%; wooded pasture, 94.7%; and other habitat, 93.1% (Table 1). For all habitats and in all proportion scenarios, yearly excretion-free areas comprised more than 89.8% of the total surface (Table 1). Percentages given are minimal values, assuming no overlap in excretion patches, which is a conservative assumption.

Integrated Nitrogen Balance

With an atmospheric N input of 30 kg N ha^{-1} yr^{-1}, we found an average net N input for almost all habitat types and scenarios (Table 1). Only in grassland habitat, we found net N losses in excretion-free areas: a small loss in the actual situation (-1.9 kg N ha^{-1} yr^{-1}) and a considerable loss (-27.9 kg N ha^{-1} yr^{-1}) in habitat proportion scenarios with a relatively small grassland proportion (Table 1).
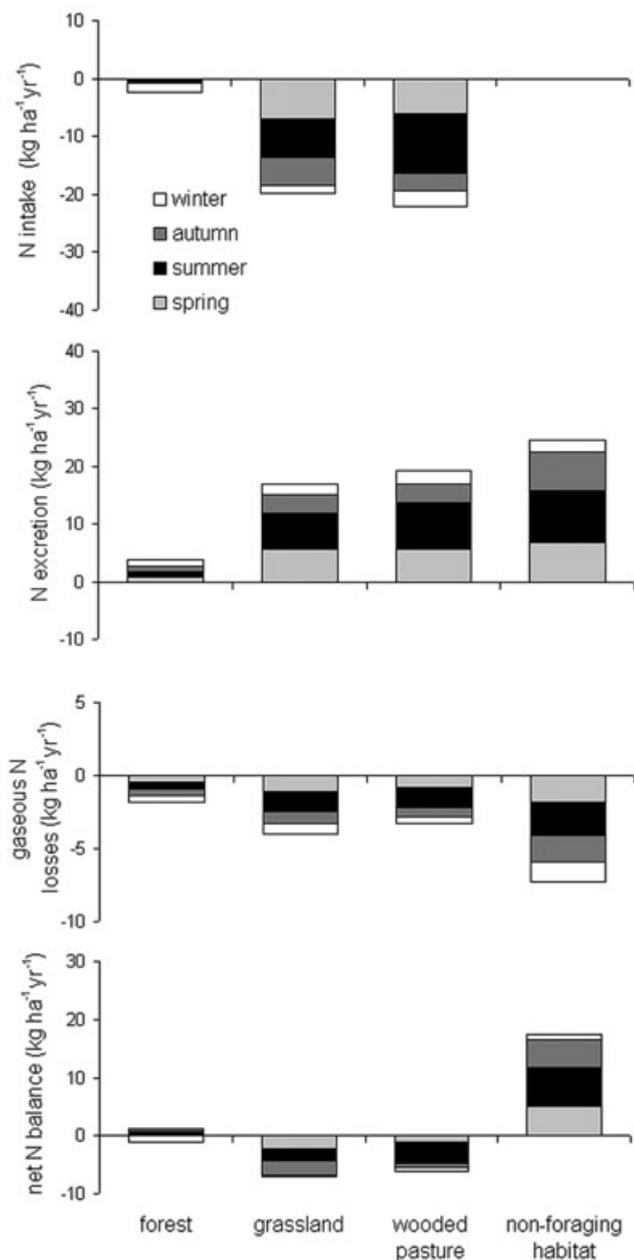
Figure 5. N intake, excretion, gaseous losses, and net N balance as a result of cattle effects in three foraging habitats and in non-foraging (forest) habitats in Bos t' Ename (negative values indicate N losses from the habitat, positive values indicate N input in a habitat).

Discussion

Although our calculations are generally conservative, they clearly indicate a spatial N redistribution among different habitats. In general, free-ranging cattle cause N transport from grassland and wooded pasture to forest and non-foraging habitats as a result of seasonal differences in foraging, occupancy, diet, and diet N content. However, calculations indicate that the magnitude of redistribution strongly depends on proportional habitat availability. Variances are expected at two levels. First,

N intake will be influenced by both cognitive and noncognitive foraging mechanisms. We expect intermediate values of N intake, that is, between both extreme foraging strategies, to be more realistic. Our results may indicate the range of uncertainty caused by cattle foraging. Second, we assumed a constant intake rate for all diet classes. However, it is known that intake rates differ according to food type and season (Pastor & Cohen 1997; van Langevelde et al. 2008). As a result, weight (gain) may decrease in the dormant season (Wallis-DeVries et al. 1998). This may lead to an overestimation of N intake in autumn and winter and to an underestimation of intake in spring and summer. This may mask a more pronounced N flux to the forest. Further, our results show relative changes in the inorganic N pool of different habitats. Real nutrient availability for plants also depends on the amount and nature of litter (Wedin & Pastor 1993), N retention in aboveground woody biomass (Magill et al. 2000), the functioning of the decomposer trophic level, and feedback mechanisms of grazing on litter decomposition (Semmartin et al. 2008). All these factors influence the rate of N turnover in different seasons and habitats. They need further examination, but are beyond our current objectives.

We may expect N depletion of a habitat if the integrated balance shows yearly N losses. Different habitat proportion scenarios for the nutrient-rich study site show that depletion is possible in excretion-free patches in grassland and wooded pasture (i.e., in patches where N intake determines the net N balance completely), given that the proportion of these habitats is relatively small. The pattern is more pronounced for the preferred grassland habitat and with a foraging pattern that corresponds to a cognitive foraging mechanism of habitat selection. This is in line with the results of Moe and Wegge (2008) for deer, concentrating their grazing on small preferred patches, while depositing dung mostly elsewhere. Translocation of nutrients may be considerable when herbivores show so-called camping behavior (Güsewell et al. 2005) and it may be an efficient way to counteract soil nutrient enrichment on at least a part of the grassland area (Dahlin et al. 2005). Our own data showed that cattle often congregate in the forest, in non-foraging habitats such as roads and paths to rest and to a lesser extent at drinking sites (all with a relatively small surface) and as a consequence defecations are congregated as well. The importance of habitat proportion is related to the functional diversity of habitats and to the functional differences among plant species in nutrient uptake rates and herbivore preference (Pastor & Cohen 1997). These functional differences will strongly influence nutrient return. In our study, a relatively small proportion of preferred habitat in a nutrient-rich mosaic landscape seems to be of major importance to induce shifts in N transport and potential depletion. It may lead to high intake and a negative net N balance with N losses >40 kg N ha^{-1} yr^{-1}. van Langevelde et al. (2008) showed that grassland lawns, developed this way, can be maintained over longer periods. This is due to the limited ability to process information about food quality at the moment of foraging, reducing the consumer's ability to make diet choice decisions. This phenomenon may speed up depletion. Grazing may also
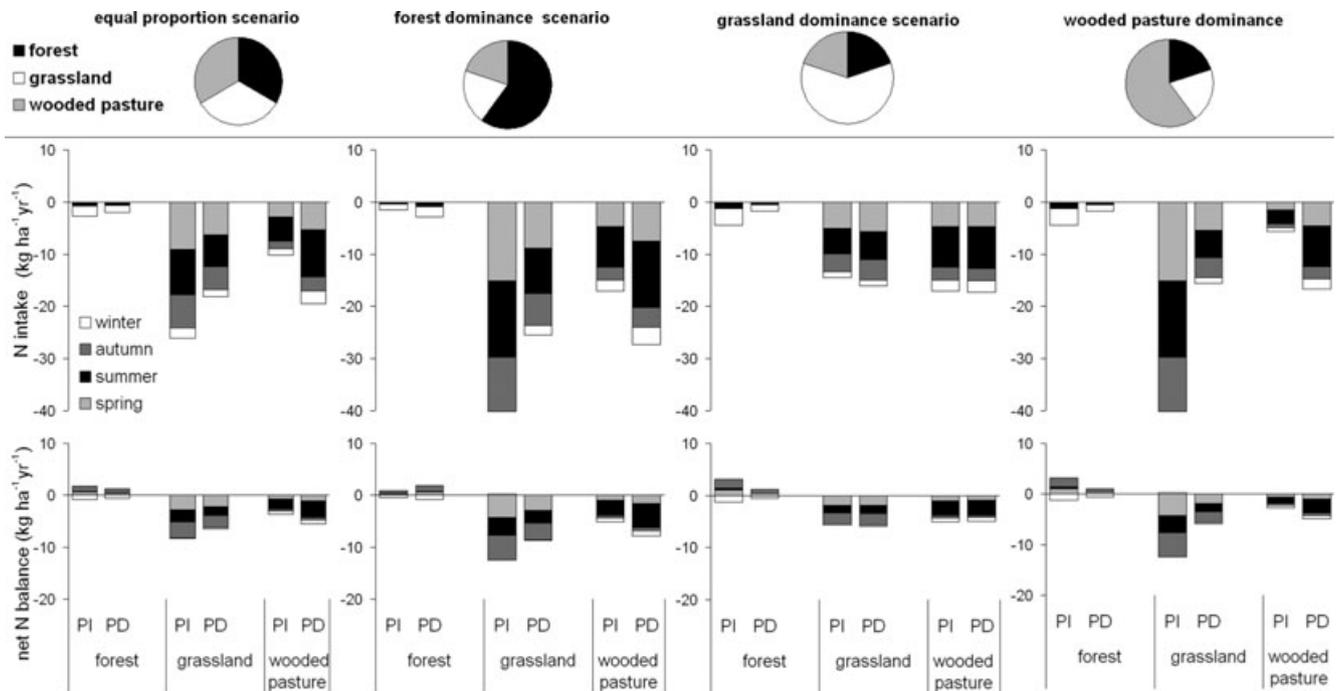
Figure 6. Seasonal and yearly N intake and net N balance in a mosaic landscape grazed by cattle in four habitat proportion and two foraging strategy scenarios. Proportion scenarios differ in the dominance of a particular habitat. Two contrasting foraging strategies (inside each diagram) were derived from the actual foraging pattern of the cattle herd at the study site Bos t' Ename. In a first strategy, foraging is based on cognitive mechanisms allowing habitat selection independent on habitat proportion (PI). In the second strategy, foraging is based on noncognitive mechanisms, dependent on habitat proportion (PD). (a) nitrogen intake by foraging cattle; (b) net N balance (including body retention, return by excretion, and N gaseous losses; positive values indicate a net N input, negative values indicate N losses per habitat).

cause over-compensatory growth of palatable species at fertile sites, resulting in the dominance of grasses (Hawkes & Sullivan 2001). Brathen et al. (2007) could not confirm this, but although productive and palatable plants were suppressed (reindeer grazing) at fertile sites, there was no evidence for a persistent loss of productivity.

The critical load for boreal and temperate forest ground flora is estimated at 10–15 kg N ha^{-1} yr^{-1} (Achermann & Bobbink 2003). The same load is critical for forest soil processes and biodiversity indicators such as lichens, algae, and mycorrhizae. Critical loads of 10–20(25) kg N ha^{-1} yr^{-1} were set for a broad range of species-rich grasslands and temperate heathlands (Achermann & Bobbink 2003). In our study, the relative influence of N transport by cattle on exceeding or declining beneath critical loads is largely scale dependent: that is, a small impact on the landscape and habitat level and a possible large impact on excretion-free areas. Although integrated N balances at ground level, under a high deposition of 30 kg N ha^{-1} yr^{-1}, on average show N surpluses, relatively high proportions of excretion-free areas remained present in all habitats (±90% per year). In these excretion-free areas of nutrient-rich grassland and wooded pasture, N intake by free-ranging cattle reduced net N input to an extent that critical loads of 20–25 kg N ha^{-1} yr^{-1} (Achermann & Bobbink 2003) were not exceeded in almost all scenarios. For low productive ecosystems, Kooijman and Smit (2001)

also found that grazing compensates for high-atmospheric N loads. However, in the productive, grazed (with 0.55 cattle per hectare) grasslands of the flooding pampa (Argentina), Chaneton et al. (1996) found N accumulation, even with very low atmospheric inputs (7.5 kg ha^{-1} yr^{-1}). This might be the case for a broad range of nutrient-rich grassland types where leaching is restricted (Dahlin et al. 2005). In these studies, however, no other habitats or mosaic landscapes were involved. N intake in excretion-free forest and N transport to forest at the habitat level were negligible compared with atmospheric input, whether moderate or high. Severe effects on vulnerable forest ground vegetation is only to be expected under excretion patches. N in urine patches of cattle may be equivalent to 1,000 kg N ha^{-1} yr^{-1} (Silva et al. 1999). In our study site, however, a maximum of 2.5% of the total forest area was affected per year.

Our data suggest that N redistribution by free-ranging cattle strongly depends on the proportional availability of different habitats. It is mainly in the highly preferred grassland habitat that N balances can be altered and N poor conditions can be restored. Given that potential N depletion is restricted to excretion-free grassland and wooded pasture patches when their habitat proportion is small (our results), attained dominance of grasses at fertile sites (Hawkes & Sullivan 2001) or persistence of productivity (Brathen et al. 2007), the restoration potential for oligotrophic grasslands is limited. Even so,

Table 1. Integrated N balance with an atmospheric input of 30 kg N ha^{-1} yr^{-1} and yearly proportion of excretion-free areas for the actual situation in Bos t' Ename and for different habitat proportion and foraging strategy scenarios.

		Integrated N Balance Entire Habitat (kg N ha^{-1}yr^{-1})		Integrated N Balance Excretion-Free Areas (kg N ha^{-1}yr^{-1})		Excretion-Free Area (% per year)	
Actual situation 40−44−16%	Forest	32.3		29.2		98.7	
	Grassland	11.1		−1.9		95.3	
	Wooded pasture	29.8		13.9		94.7	
Proportion scenarios		PI	PD	PI	PD	PI	PD
Equal proportion 33−33−33%	Forest	32.5	32.2	27.3	28.0	98.5	98.9
	Grassland	9.7	11.5	−10.5	−2.6	93.9	95.7
	Wooded pasture	32.4	30.5	24.3	15.1	97.6	95.4
Forest dominance 60−20−20%	Forest	31.9	32.5	28.5	27.0	99.2	98.5
	Grassland	5.8	9.3	−27.9	−10.0	89.8	94.1
	Wooded pasture	30.9	28.2	17.5	7.2	95.9	93.6
Grassland dominance 20−60−20%	Forest	33.4	32.1	26.7	27.2	97.6	99.0
	Grassland	12.3	12.1	1.0	−0.6	96.6	96.1
	Wooded pasture	30.9	31.1	17.5	17.3	95.9	95.8
Wooded pasture dominance 20−20−60%	Forest	33.4	32.1	25.5	28.3	97.6	99.0
	Grassland	5.9	12.2	−27.8	−0.1	89.8	96.3
	Wooded pasture	33.3	31.1	28.8	17.8	98.7	96.0

Average values are given for the entire habitat and for excretion-free areas. Negative values indicate a yearly net N loss. PI, proportion independent foraging strategy; PD, proportion dependent foraging strategy.

N depletion by grazing, as a trigger for the establishment of woody species, is not likely to be of major importance in nutrient-rich mosaic landscapes (cf the resource-mediated successional grazing cycle theory, Bokdam 2003). Woody species establishment rather seems dependent on the availability of microsites, created by disturbances or ecosystem dynamics (de Villalobos et al. 2005; Jentsch 2007; Van Uytvanck et al. 2008a). N redistribution by cattle in relation to the potential exceeding of critical N loads on vulnerable ground vegetations is almost negligible compared with atmospheric deposition. In grassland and wooded pastures, cattle grazing can compensate for high N inputs, maintaining grassland types that support N loads of 20−25 kg N ha^{-1} yr^{-1}.

Implications for Practice

- In grazed, nutrient-rich mosaic landscapes, which support a relatively high-grazing pressure (here ±9,000 kg km^{-2}yr^{-1}), proportional habitat availability has a considerable effect on N redistribution.
- The restoration potential for oligotrophic habitats, as a result of N transport and depletion by cattle, is limited. The proportion of grassland or wooded pasture habitat has to be small (<40%), compared with other, less used habitat types such as forest. Moreover, nutrient depletion is only to be expected in excretion-free areas under low atmospheric N input (less than ±20 kg N ha^{-1} yr^{-1}). N depletion as a trigger for the regeneration of woody species is of minor importance in grazed nutrient-rich ecosystems.

- In the preferred grazing habitats of mosaic landscapes, grazing can compensate for high-atmospheric N input and maintain grassland types that support N loads of 20−25 kg N ha^{-1} yr^{-1}.
- N transport in low-intensity grazed nutrient-rich mosaic landscapes does not lead to the eutrophication of vulnerable forest ground flora, given the proportion of forest habitat is not too small (minimum 25−30%). On this condition, only small areas that receive excreta (<3% per year) can be severely affected.

Acknowledgments

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