Exploring the potential for improved internal nutrient cycling in dairy farming systems, using an eco-mathematical model

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Abstract

Nutrient management at Dutch dairy farms is changing rapidly from strong reliance on external inputs to more prudent utilization of internal resources. This paper explores opportunities and constraints arising from this shift towards eco-technological management. A mathematical model of inorganic and organic nitrogen (N) flows in a dairy farming system was formulated based on ecological concepts, integrating processes of nutrient input, recycling, immobilization and mineralization. Recycling is defined as the mineralization of N within the year of its incorporation into herbage, which occurs through release from faeces, animal urine and non-harvested biomass. We simulated changes in inorganic and organic N per hectare, and the consequent emission (E), mineralization (M_S) and recycling (R) of N for different initial amounts of inorganic and organic N. Results demonstrate that in the long term, the system evolves to equilibrium amounts of inorganic and organic N, which are strongly determined by the imposed management practices, such as fertilizer input and grassland management. In the short term, moving away from the equilibrium is possible for particular initial amounts of inorganic and organic N. In the equilibrium state, E was reduced by lowering inorganic fertilizer input rate, increasing grassland productivity and improving animal N conversion efficiency, i.e., only by production-related parameters. Only in the short term E was affected by adjustments in quality-related parameters: lower N content, lower digestibility of herbage, reduced degradability of non-harvested biomass and faeces, and parameters determining the functioning of soil biota (degradation rate, efficiency, C/N ratio). Quality-related parameters had no effect on internal nutrient cycling in the equilibrium state, because adjustments in M_S were completely compensated by changes in R. A comparison of farming systems demonstrated that farming systems can be designed in such a way that improvement of internal nutrient cycling supports the same production with lower inputs and lower emissions.

Additional keywords: nitrogen, soil, grassland, nutrient use efficiency, emission, mineralization, modelling

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Introduction

Nitrogen (N) in agro-ecosystems is present both in inorganic forms and as part of organic compounds. Inorganic N compounds are incorporated in organic compounds during plant growth and by micro-organisms in or associated with the soil: the soil biota. Farm animals and soil biota convert these organic compounds, thus liberating the N in inorganic form. Primary production in natural ecosystems is highly dependent on such cycling and re-use of N and other nutrients (Delwiche, 1970; Chapin, 1980). In intensive farming systems developed in temperate regions like Western Europe, substantial imports of inorganic fertilizers, manure and feed have reduced the importance of N cycling. In these farming systems often more nutrients are imported than required to replenish nutrients in exported products (Van Keulen *et al.*, 1996).

The adverse effects of intensive agricultural practices on agro-ecosystem functioning in temperate regions are widely acknowledged (e.g. Williams, 1995; Jarvis *et al.*, 1996; Vitousek *et al.*, 1997; Van Keulen *et al.*, 2000; Jenkinson, 2001; Watson & Foy, 2001). Increased nutrient loads lead to uncontrollable losses to the environment and changes in ecosystem species composition. In response to these problems substantial efforts have been initiated to increase nutrient use efficiency. In the Netherlands several large research programmes aiming at quantification of nutrient flows on dairy and mixed farms have yielded valuable information on management alternatives that rely less on external resources (e.g. Oomen *et al.*, 1998; Hilhorst *et al.*, 2001). These programmes should provide options for farm managers to comply with the nutrient input restrictions implemented in the mineral accounting system (MINAS) that will be established in the Netherlands from 2003 onwards (Henkens & Van Keulen, 2001).

In the VEL & VANLA Nutrient Management Project, strategic adjustment of farm management is based on three categories of management changes that are hypothesized to act synergistically in increasing nutrient use efficiency (Van Bruchem *et al.*, 1999a, b), in particular for N (Table 1). The first category aims to enhance fertilizer use efficiency by reduction of inorganic fertilizer inputs and improved utilization of slurry manure. The second category addresses feeding rations with more structural

Table 1. The three VEL & VANLA strategies to improve farm N use efficiency and their relation with parameters in the model. + and – indicate the desired direction of the strategy concerned.

Strategy	Parameters[1]										
	Production related				Quality related						
	i	$u_{\mathrm{MAX,H}}$	ρ	φ_{P}	α	d_{H}	k_{F}	k_{B}	k_{D}	ε	q_{M}
Improve fertilizer utilization	–	+	+								
Adjust animal ration				+	–	–	–	–			
Stimulate soil biota									+	+	–

[1] For abbreviations see Table 2.

components and a higher C/N ratio, which in terms of nutrient use efficiency is expected to result in (1) higher animal nutrient use efficiency, (2) reduction of losses from animal excreta due to lower inorganic N content, and (3) build-up of soil organic N through manure with higher C/N ratio, which ultimately increases the N supplying capacity of the soil. The third category of management changes aims at stimulating soil biota and modifying the mineralization/immobilization turnover, to increase N supply for plant growth from the soil organic N pool. Methods used are application of manure with a higher C/N ratio, minimization of use of heavy machinery, surface application of slurry manure rather than injection to minimize sward damage and deterioration of soil structure, and application of soil and manure additives such as Effective Microbes® and Euromestmix®. Overall, these changes constitute a movement from increasing inputs to increasing utilization of internal resources in farming systems, also denoted as a shift from technological to eco-technological management (cf. Altieri, 1991; Bawden, 1991; Thompson & Nardone, 1999).

If a reduction in the dependence of external resources is being pursued – while aiming at maintaining productivity – various adjustments in the dynamics of nutrient cycling within the system are required. Nutrients should be retained longer within the system, but not solely immobilized in stable pools that are not prone to emission. To support agro-ecosystem functioning and agricultural productivity, sufficient quantities of nutrients in inorganic form should be available at appropriate moments for incorporation into organic structures, particularly through plant growth. Thus, nutrients should be frequently transferred between inorganic and organic pools, and the proportion of nutrients cycling within the system should be high. To assess the nutrient cycling capacity of dairy farming systems we propose to use a combination of indicators to yield the required quantitative insight into the characteristics of agro-ecosystem nutrient dynamics (Finn, 1980). Relevant indicators include (1) the residence time of a nutrient in the system, (2) the intensity of use of the nutrient as reflected in the number of components it forms part of whilst in the system, (3) total system through-flow, and (4) the proportion of nutrient throughflow that can be attributed to cycling (Finn, 1976, 1980; DeAngelis, 1992). The resulting cycling indicators can be used to devise changes in management of agro-ecosystems if they are related to both environmental objectives (e.g. emission reduction) and controllable aspects of flows within systems (Bailey, 2000), as elaborated in this paper.

Nitrogen cycling is affected by interactions between different components of the system, resulting in complex behaviour at the system level. Moreover, time coefficients of some of the processes affecting soil organic N pools are large and consequences of changes in management strategy may become apparent only after a long time. In this paper we describe a model and use indicators to quantify nutrient cycling in a dairy farming system. Purpose of the model is to structure thinking about consequences of strategic choices as a complement to the empirical and experimental work in the VEL & VANLA project. In the model, essential interactions between inorganic and organic forms of N in the system are represented, based on ecological concepts of nutrient cycling. The model is used to examine strengths and weaknesses of the VEL & VANLA strategies. After describing the conceptual framework, model behaviour is first evaluated for a simplified farming system with no import or export of feed, followed by a full

model analysis. To identify relevant parameters that contribute to reduction in emission and to increasing soil organic N mineralization, the sensitivity of these variables to changes in parameter values is determined. Equilibrium states are calculated for two commercial and two experimental farms to illustrate the differences in internal nutrient cycling between farming systems.

Materials and methods

Conceptual framework

Inorganic N is taken up from the soil and incorporated in organic compounds during plant growth. Nitrogen incorporated in these organic compounds is released as inorganic N after conversion by farm animals and soil biota. In our concept, *available inorganic N* is defined as cumulative inorganic N present in the soil solution throughout one year. This definition corresponds with the concepts of 'inorganic' or 'leachable' N pools as proposed by Scholefield *et al.* (1991) and Di & Cameron (2000), respectively. *Recycling* refers to the N that is incorporated in organic compounds in plants and converted to available inorganic N within one year. Nitrogen that is not recycled within one year remains in the soil organic matter pool, and may be released as inorganic N in subsequent years. We summarized these dynamics in a model that describes the
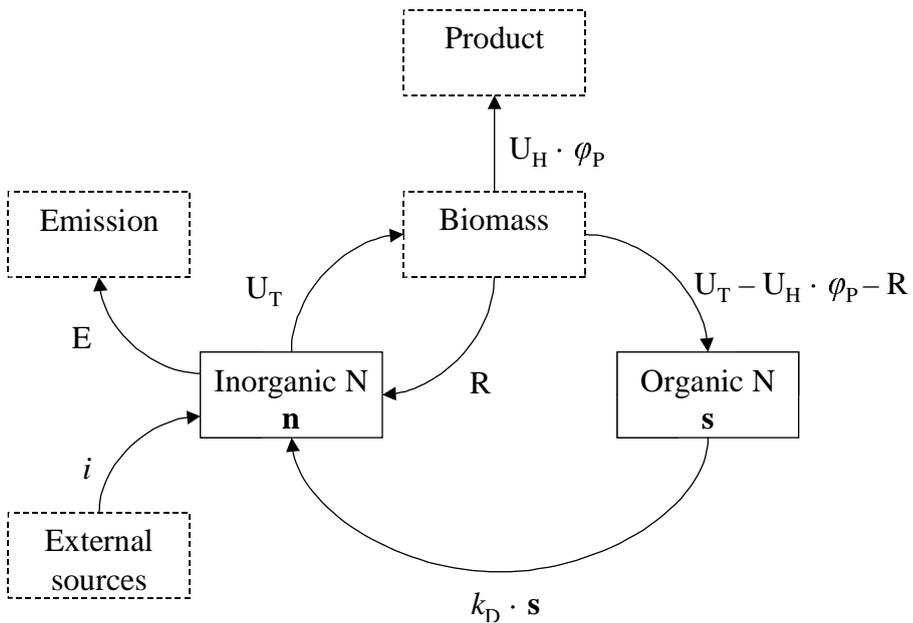
Figure 1. Schematic representation of the model. Solid boxes indicate modelled state variables, and arrows denote flows of nitrogen. For further explanation see text.

relations between the amounts of inorganic and organic N present in the top 20 cm of the soil at a time scale of one year (Figure 1; Equations[1] 1a and 1b).

$$\frac{d\mathbf{n}}{dt} = i - k_\mathrm{w}\mathbf{n} + R + k_\mathrm{D}\mathbf{s} \tag{1a}$$

$$\frac{d\mathbf{s}}{dt} = G - R - k_\mathrm{D}\mathbf{s} \tag{1b}$$

where
$\mathbf{n}$ = available inorganic N (kg ha^{-1}),
$\mathbf{s}$ = organic N (kg ha^{-1}),
i = supply of inorganic N inputs from external sources (kg ha^{-1} year^{-1}),
k_W = the relative withdrawal rate of inorganic N by emission or uptake (year^{-1}),
R = the rate of recycling of available inorganic N (kg ha^{-1} year^{-1}),
k_D = the relative transformation rate of organic to inorganic N (year^{-1}),
G = the rate of N uptake in plant biomass, corrected for export in animal products (kg ha^{-1} year^{-1}).

Changes in the inorganic N pool (Equation 1a) are the result of supply from external sources, uptake into biomass, emission from the system, and mineralization of organic N from a fast and a slow pool. The parameter i represents inputs of inorganic N from external sources, such as inorganic fertilizers, atmospheric deposition or
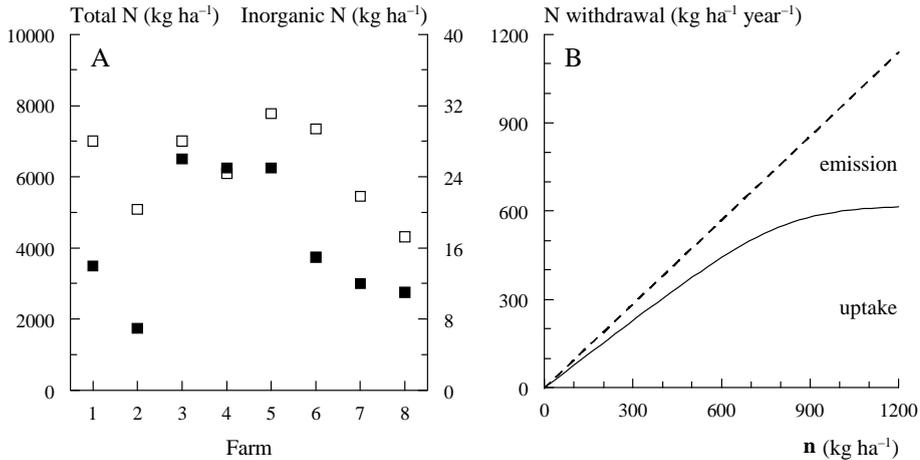
Figure 2. A: Amounts of total (□) and inorganic N (■) on conventionally managed fields of 8 farms in the VEL & VANLA region, sampled (0–20 cm) in January 2000. B: Total N withdrawal ($k_\mathrm{W} \cdot \mathbf{n}$, broken line) and uptake in total plant biomass (U_T, solid line).

[1] Throughout this paper a bold lower case letter indicates a state variable. Model parameters are denoted in italics, with capital subscript if appropriate. Process rates are indicated with capitals.

symbiotic N fixation. A proportion of available inorganic N is lost by uptake into biomass and emission through volatilization, leaching, denitrification and runoff, resulting in a relative rate of decrease k_W. The low concentrations of inorganic N in the soil solution *in situ* in winter (Figure 2A) suggest that total loss on an annual basis is substantial. For the sandy soils of the VEL & VANLA region we estimate the proportion of inorganic N lost over a period of one year to be 0.95. This holds for temperate regions where winter precipitation exceeds evapotranspiration resulting in complete loss of nitrate N (Scholefield *et al.*, 1991). Only small residues of inorganic N in ammonia persist in winter when not subject to nitrification (Whitehead, 1995). The partitioning of inorganic N over emission and uptake is given in Equation 2. This relationship, in which E is the balancing term, is illustrated in Figure 2B.

$$E = k_W \, \mathbf{n} - U_T \tag{2}$$

where
E = the rate of N emission (kg ha^{-1} year^{-1}),
U_T = the rate of N uptake in total plant biomass (kg ha^{-1} year^{-1}).
    Due to mineralization, part of the N incorporated in plant biomass is returned within one year as inorganic N. This recycling rate (R, kg ha^{-1} year^{-1}) is highly amenable to strategic management, and will be described in the next section. Recycling constitutes a loss for the organic N pool (Equation 1b) as it draws upon G, the rate of N uptake in plant biomass corrected for removal of N from the system in animal products (Equation 3):

$$G = U_T - U_H \, \varphi_P \tag{3}$$

where
U_H = the rate of N uptake in harvested plant biomass (kg ha^{-1} year^{-1}),
φ_P = the fraction of harvested N that is converted to animal products.
    Mineralization of organic N, assumed to occur at a constant relative rate k_D ($M_S = k_D\mathbf{s}$), results in an increase in the inorganic N pool (Equation 1a) at the expense of the organic N pool (Equation 1b). In an equilibrium state the amount of available inorganic N can be calculated as $\mathbf{n} = (i + M_S + R)/k_W$ or $\mathbf{n} = (E + U_T)/k_W$. Figure 1 gives a graphical representation of the conceptual framework defined by Equations 1–3.

Quantification of recycling

The concept of nutrient recycling was inspired by studies of remediation strategies for eutrophic lakes by Scheffer *et al.* (1993) and Carpenter *et al.* (1999). We modelled the rate of recycling by combining relations that describe N uptake in plant biomass, N utilization by farm animals and release of inorganic N by mineralization, either by ruminants or by soil biota.

Plant biomass production

The relation between N uptake and biomass production is inferred from the three-quadrant analysis for agricultural crops (De Wit, 1953; Ten Berge *et al.*, 2000). While this approach usually starts with the amount of fertilizer applied, we related N uptake and biomass production to **n**, the amount of available inorganic N in the soil. We used adjusted expo-linear equations (Goudriaan & Monteith, 1990) to subsequently describe N uptake (quadrant IV) and biomass production (quadrant I). These equations proved to result in accurate fits of data for several datasets of DM yield and N uptake (e.g. Richards, 1977; Snijders *et al.*, 1987; Baan Hofman, 1988; results not presented). Farm animals can only harvest part of the total amount of plant biomass produced, the remainder staying behind in the field as organic material. Therefore, we distinguished total and harvested amounts of N (U_T and U_H) and total and harvested biomass (Y_T and Y_H), which resulted in four equations. The following equation shows the general form of the expo-linear equation:

$$Z = z_{max} - \frac{\rho.}{\lambda} \ln(1 + e^{-\lambda.(x - z_{max}/\rho)}) \tag{4}$$

where

Z = the dependent variable, representing U_T, Y_T, U_H or Y_H (kg ha^{-1} year^{-1}),
x = the independent variable, representing **n**, U_T, or U_H (kg ha^{-1} year^{-1}),
z_{max} = maximum value of Z, representing $\mu_{MAX,T}$, $\gamma_{MAX,T}$, $u_{MAX,H}$ or $\gamma_{MAX,H}$ (kg ha^{-1} year^{-1}),
$\rho.$ = initial response of Z to x, representing ρ_U and ρ_Y (kg kg^{-1} ha^{-1} year^{-1}),
$\lambda.$ = the decline of the response of Z to x, representing λ_U and λ_Y (kg^{-1}).
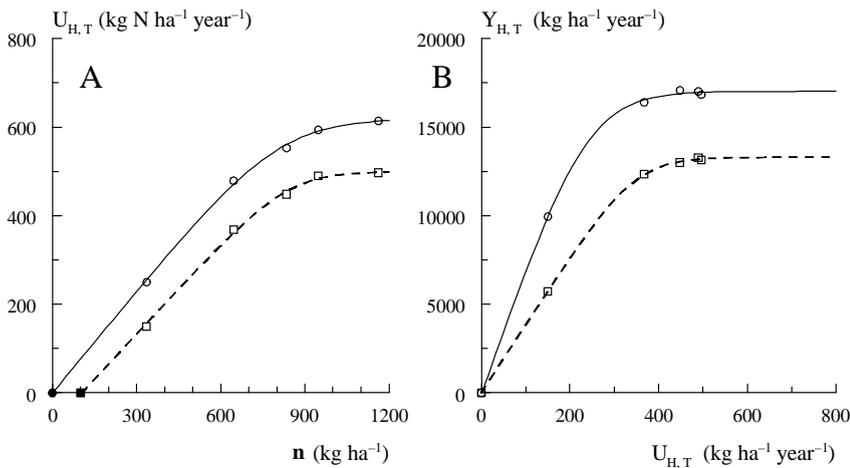
Figure 3. Relation between inorganic N availability (**n**) and N uptake (U_T and U_H) (A), and between N uptake and DM yield (Y_T and Y_H) (B) for total (U_T and Y_T, solid line) and harvestable (U_H and Y_H, broken line) biomass. Lines are fitted and solid points in A are calculated by extrapolation of fitted curves to the intersection with the x-axis. For derivation see Appendix 1; original data from Lantinga *et al.* (1999).

Table 2. Description and values of model parameters relating to systems ecology and systems management.

Parameter	Value	Unit	Description	Source
Ecological				
$u_{MAX,H}$	500	kg ha^{-1} year^{-1}	maximum N uptake in harvested biomass	
$\rho_{U,H}$	0.6790	kg kg^{-1}	initial response of N uptake in harvested biomass	
$\rho_{U,T}$	0.7683	kg kg^{-1}	initial response of N uptake in total biomass	Baan Hofman, 1988
$\alpha_{MIN,H}$	0.02607	kg kg^{-1}	minimum N content in harvested biomass	Hansson & Pettersson, 1989
$\alpha_{MIN,T}$	0.01365	kg kg^{-1}	minimum N content in total biomass	Whitehead *et al.*, 1990
$\alpha_{MAX,H}$	0.03762	kg kg^{-1}	maximum N content in harvested biomass	Lantinga & Deenen, 1999
$\alpha_{MAX,T}$	0.03641	kg kg^{-1}	maximum N content in total biomass	
h_N	0.807	–	harvested N as a proportion of total N uptake	
k_F	0.40	year^{-1}	fractional degradation rate of faeces organic matter	
k_B	0.70	year^{-1}	fractional degradation rate of unharvested biomass	
q_M	8.0	–	C/N ratio of soil biota	Janssen, 1996
ε	0.30	kg kg^{-1}	efficiency of biomass conversion by soil biota	
k_D	0.03	year^{-1}	fractional degradation rate of soil organic N	estimate
k_W	0.95	year^{-1}	fractional rate of inorganic N withdrawal	
Management				
i	150	kg ha^{-1} year^{-1}	rate of inorganic N supply (deposition, fertilizers)	
d_H	0.75	kg kg^{-1}	dry matter digestibility of harvested biomass	
φ_P	0.23	–	proportion ingested N converted to animal products	
c	0.405	kg kg^{-1}	carbon content of plant biomass dry matter	
p_H	12,500	kg ha^{-1} year^{-1}	annual milk production per hectare grassland	
p_A	8000	kg year^{-1}	annual milk production per cow	
r	0.30	–	replacement rate of milk cows	
σ	0.75	–	minimum self supply rate in quantitative analysis	
σ	1.00	–	minimum self supply rate in qualitative analysis	

According to the expo-linear equation, the initial response of N uptake to available inorganic N and of biomass production to N uptake is linear, with an initial slope ρ. This initial slope declines with a rate depending on λ until the maximum z_{MAX} is reached. An example of the relations for N uptake and biomass production, for both total and harvested amounts, is shown in Figure 3. The derivations of the relationships between N availablity, N uptake and DM yield are given in Appendix 1.

Some model parameters were derived from the fitted expo-linear curves. The ratio between $u_{MAX,H}$ and $u_{MAX,T}$ is denoted h_N: the fraction of harvested N in biomass. Maximum N content in biomass is calculated as $\alpha_{MAX,\bullet}=u_{MAX,\bullet}/y_{MAX,\bullet}$. The minimum N content in herbage is calculated from the initial response of plant biomass yield to N uptake: $\alpha_{MIN,\bullet}=1/\rho_Y$. The resulting fitted and derived values of parameters used in the model are listed in Table 2.

Symbiotic N fixation by Rhizobium bacteria associated with white clover in mixed swards was linearly related to available inorganic N, based on data of Ledgard *et al.* (1999). N fixed by white clover was considered as an inorganic input, and thus modelled as an additional component of *i*.

Animal production and nitrogen utilization

Nitrogen in harvested biomass is fed to ruminants, either through grazing or by indoor feeding of cut herbage. The composition of the animal ration was tuned to animal requirements for protein, which were calculated with equations used by Aarts *et al.* (1999b). Excess feed was removed from the system and shortages of protein were supplemented by feed imports to maintain the desired level of milk production per ha (p_H) and per animal (p_A) with a replacement rate (*r*) for milk cows of 0.30 per year (see Table 2). For simplicity, it was assumed that the N content and digestibility of the supplementary feeds were constant at 35 g kg^{-1} and 0.825 kg kg^{-1}, respectively. The energy content (net energy for lactation, expressed in MJ kg^{-1}) of the harvested biomass grown at the farm and of the supplement was calculated from their digestibility and N content (Anon., 2000). The maximum proportion of allowed supplementary feed in the ration was controlled by the minimum self-supply rate σ. Where applicable, the amounts of biomass DM and N and digestibility were corrected for feed imports, yielding adjusted variables Y_H' and U_H' and parameter d_H'.

Ruminants convert consumed N to milk or meat with production efficiency φ_P, and N that is not utilized for production is excreted in faeces and urine. The distribution of N output between products, faeces and urine for milking cows is linearly related to φ_P,
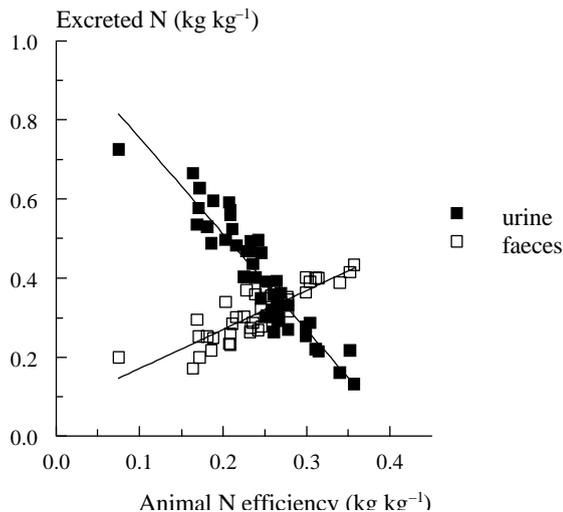
Figure 4. Relation between animal efficiency and the proportion of N excreted in faeces and urine. Data from Castillo *et al.* (2001a, b) and Valk (2002) in experiments with dairy cows with average dry matter intake of 16–20 kg day^{-1} and milk production of 20–25 kg day^{-1}.

as demonstrated in Figure 4 derived from data of Valk (2002) and Castillo *et al.* (2001a, b) resulting in a relationship that is similar to that given by Kemp *et al.* (1979). Nitrogen in faeces is assumed to be present completely in organic form, while N is excreted in urine in inorganic or readily mineralizable forms (Whitehead, 1995; Bussink & Oenema, 1998). Thus, ruminant inorganic N excretion can be calculated as:

$$M_U = U_H' \, \varphi_U \tag{5}$$

where
M_U = inorganic N excretion in urine by ruminants (kg N ha^{-1} year^{-1}),
φ_U = the fraction of ingested N excreted in urine.

Mineralization by soil biota
Organic structures containing N in unharvested biomass and in faeces are subject to degradation by fauna and micro-organisms in or associated with the soil: the soil biota (Brussaard, 1998). Depending on the C/N ratio of the decomposed substrate (q_B and q_F for non-harvested biomass and faeces, respectively) and of the soil biota (q_M), N is either mineralized or immobilized in the degradation process. Mineralization occurs when during a degradation step more N is released than is required for soil biota growth. N is immobilized from inorganic sources in the soil if the amount of released N is insufficient for soil biota growth (Janssen, 1996). This is quantified in Equation 6, where positive and negative values of M_B and M_F indicate mineralization and immobilization, respectively.

$$M_B = \frac{k_B \, c \, (Y_T - Y_H)}{1 - \varepsilon} \left(\frac{1}{q_B} - \frac{\varepsilon}{q_M} \right), \quad q_B = \frac{c \, (Y_T - Y_H)}{U_{T-} U_H} \tag{6a}$$

$$M_F = \frac{k_F \, c \, Y_H \, (1 - d_H)}{1 - \varepsilon} \left(\frac{1}{q_F} - \frac{\varepsilon}{q_M} \right), \quad q_F = \frac{c \, (Y_H \, (1 - d_H)}{U_{H-} \varphi_F} \tag{6b}$$

where
M_B = N mineralization by soil biota for unharvested biomass (kg N ha^{-1} year^{-1}),
M_F = N mineralization by soil biota for faeces (kg N ha^{-1} year^{-1}),
$k_{\bullet}$ = fractional degradation rate for faeces (k_F) or unharvested biomass (k_B) (year^{-1}),
$q_{\bullet}$ = the C/N ratio for unharvested biomass (q_B), faeces (q_F) and soil biota (q_M),
d_H = dry matter digestibility of harvested biomass (kg DM per kg DM),
ε = the conversion efficiency of carbon by soil biota (kg carbon in soil biota per kg carbon in DM),
c = the amount of carbon per unit plant biomass (kg carbon per kg DM),
φ_F = the fraction of ingested N excreted in faeces.
    Carbon content of dry matter (c, 0.405 kg kg^{-1}) is calculated assuming ash content in dry matter of 0.10 kg kg^{-1} and carbon content in organic matter of 0.45 kg kg^{-1}. The conversion efficiency ε denotes the part of the converted matter used for assimilation in microbial tissue, thus $1-\varepsilon$ is the dissimilated fraction used for oxidation to gain energy. Since dry matter in faeces has been subject to fermentation and digestion in

the gastro-intestinal tract of the ruminant, it is considered the less degradable fraction of biomass. Therefore, the fractional degradation rate is probably lower for faeces dry matter than for non-harvested biomass (Whitehead, 1995). This is also in line with the differences in the humification coefficients for young roots and leaves and for animal manure, as indicated by Janssen (1996).

Calculation of recycling
Equations 4, 5 and 6 can be combined to quantify N recycling as a function of inorganic N availability (Equation 7).

$$R = M_U + M_B + M_F \qquad\qquad (7)$$

In Figure 5, the recycling rate described by Equation 7 is compared with the net rate of N uptake in plant biomass G (Equation 3), using the parameter values of Table 2. The net rate of N uptake in plant biomass G is largely determined by the gross uptake rate U_T, since φ_P in the second term of Equation 3, which corrects for N exported in milk and meat, generally ranges between 0.15 and 0.30. Therefore, G has a nearly expo-linear shape. The recycling function R has a sigmoid shape (Figure 5), which can be explained by a shift in the contribution of ruminants and soil biota to mineralization of organically bound N. At low levels of available N, the amount of herbage above the cutting or grazing height is limited and a large fraction of N is accumulated in non-harvested roots and stubble. Under these conditions, most of the mineralization originates from soil biota feeding on decaying roots and stubble. At higher levels of available inorganic N, the amount of harvested biomass is greater and the propor-
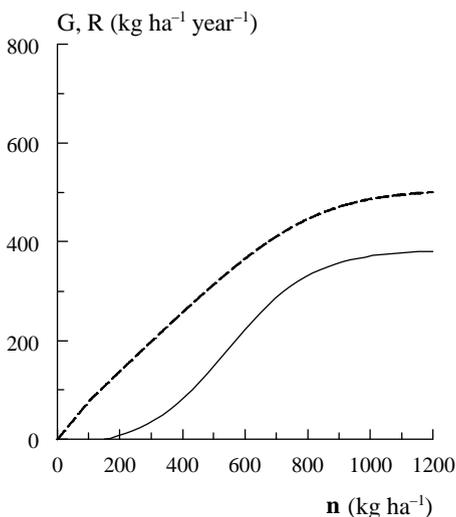
Figure 5. Nitrogen uptake corrected for export in animal products (G, broken line) and recycling (R, solid line), both as a function of inorganic N availability (**n**). Parameter values are listed in Table 2.

tion of N recycled by ruminants increases. The increase in ruminant-based mineralization is accompanied by an increase in the total rate of recycling because excretion of inorganic N in urine is a faster process than release by successive generations of micro-organisms. The recycling rate finally levels off because at high levels of available inorganic N, the crop no longer takes up all inorganic N.

Relation between VEL & VANLA strategies and model parameters

The VEL & VANLA Nutrient Management Project strategies to improve nutrient use efficiency can be related to parameters in the model (Table 1). Parameters were grouped in two categories (1) production-related parameters that determine grassland and animal production, and (2) quality-related parameters that affect the composition and degradability of organic substances and functioning of soil biota. In Table 1, for each model parameter the direction of change required towards the VEL & VANLA goals is indicated.

Cycling indicators

Flow metrics are introduced as indicators of the degree of nutrient cycling within the system, following Finn (1976; 1980). The method of calculation of the cycling indicators is described in Appendix 2. To assess cycling, all conversions between inorganic and organic forms of N are accounted for, so that the organic N compartment comprises not only soil organic N (**s**) but also N in biomass that is recycled within the year of incorporation (see Appendix 2).

For a 2-compartment model the cycling indicators can be calculated analytically, as derived by Bailey (2000). Total system throughflow (TST) is defined as the sum of all compartmental throughflows and is used to calculate path length (PL) and cycling index (CI). TST measures the total flow activity of the nutrients within the system. A flow of nutrient into the system may partly leave the system immediately from the first compartment, a portion may flow through the other compartment and a portion may cycle through both compartments many times before leaving the system (Finn, 1978). PL is the average number of compartments through which a nutrient passes after inflow, before it leaves the system. PL can be simply calculated as the ratio between TST and the sum of inflows. Cycling index CI is defined as the fraction of TST that is cycled. CI can vary from 0 to 1, 0 implying a throughflow system and 1 indicating a closed system (Finn, 1980). In contrast with CI, the values of TST and PL are sensitive to the number of compartments identified in the system (Finn, 1976). However, in a 2-compartment system as proposed here, PL and CI are highly correlated. In addition to the indicators adopted from flow metrics, in the equilibrium state the residence time (T_{RES}) of nutrients within the system can be calculated as the ratio of total stock (**n** + **s**) and the sum of exports (or imports) (DeAngelis, 1992).

Analysis of nitrogen dynamics

Equations 1–7 were implemented in a computer programme that enabled continuous simulation of inorganic and organic N pools in a dairy farming system. Numerical integration was performed with a self-adjusting time step algorithm. Model parameters (Table 2) were chosen such as to represent a current Dutch intensive dairy farm-

ing system on sandy soils. Only the grassland part of the farm was modelled. Therefore, slurry manure applied to other crops was considered as an export.

The following steps were taken to analyse the model.

– *Phase plane analysis* of the system of **n** and **s**. A simplified version of the model excluding imports and export of feeds ($\sigma = 1$) was used to evaluate trajectories from 8 initial conditions. This analysis is comparable to the analysis of two species interactions, between preys and predators (Rosenzweig & MacArthur, 1963; Vandermeer, 1973) or producers and grazers (Noy-Meir, 1975; Van De Koppel *et al.*, 1996; Illius & O'Connor, 1999; Loladze *et al.*, 2000).

– *Full model analysis* for the study of the time course of several model variables after starting the simulations from two extreme initial conditions, allowing import and export of feeds where necessary to meet feeding requirements ($\sigma < 1$).

– *Sensitivity analysis* of model parameters to evaluate the effects of changes in the direction as desired according to the VEL & VANLA strategy (see explanation below).

– *Farming systems comparison* of four contrasting farms (see explanation below).

Sensitivity analysis

Effects of changing a selected set of parameters by 10% in the direction corresponding to the VEL & VANLA strategies were evaluated in terms of average N emissions (E) and soil N mineralization (M_S) during the first 50 years. Simulation started from two extreme points in the phase plane with low inorganic N and high organic N (high **n**, low **s**) and high inorganic N and low organic N (low **n**, high **s**), respectively. To evaluate effects on efficiency of internal N use in the long term, sensitivity of total system throughflow (TST), residence time (T_{RES}), path length (PL) and cycling index (CI) was determined in the equilibrium state. The four parameters $\alpha_{..}$ that represent minimum and maximum N contents in biomass were varied jointly, and will be referred to as α. The selected parameters and the desired direction of change within the different strategies are listed in Table 1.

Farming systems comparison

To evaluate the long-term effects of differences in management practices in existing farming systems on equilibrium conditions, a preliminary comparison was made of two representative commercial farms and two experimental farms in the Netherlands. Commercial farms C1 and C2 represented a typical average farm on sandy soils in the mid 1990s and a current farm in the VEL & VANLA region, respectively, while the experimental farms were characterized as focusing on technological and agronomic innovations (E1) and on improved feeding strategy and use of white clover (E2), albeit on highly different soils (see also Aarts, 2000 and Hilhorst *et al.*, 2001 for C1 and E1; Oomen *et al.*, 1998 and Van Bruchem *et al.*, 1999a for E2). Parameter values for each farming system are listed in Table 4. Only the grassland parts of the four farms were considered in the simulations. Other roughages grown at the farm, such as maize, were modelled as feed imports, and slurry manure used on these crops as being exported. The value of $u_{MAX,H}$ for commercial farms was estimated to be lower than for experimental farms, which is in line with differences in grassland DM and N produc-

Table 3. Individual, summed and combined relative effects (% of original value) after a 10% change in selected parameters corresponding to the strategy of the VEL & VANLA Nutrient Management Project on N emission (E) and soil N mineralization (M_S), total residence time (T_{RES}), total system throughflow (TST), path length (PL) and cycling index (CI). Effects of changes in production per ha and per animal (p_H and p_A) are evaluated too. Effects are averaged over a 50-year period from starting point ($\mathbf{n}_o$, $\mathbf{s}_o$) = 300, 9000 (a) and from ($\mathbf{n}_o$, $\mathbf{s}_o$) = 900, 3000 (b) or evaluated for the equilibrium state.

Parameter[1]	Direction of change	First 50 years				Equilibrium					
		E		M_S		E	M_S	T_{RES}	TST	PL	CI
		a	b	a	b						
ρ	+	−23.0	−31.3	−3.5	−6.4	−30.7	−9.7	11.7	1.6	24.2	9.1
φ_P	+	−8.3	−9.6	1.2	2.0	−7.7	3.5	7.5	−6.5	−2.0	−1.1
$u_{MAX,H}$	+	−7.7	−7.2	5.3	9.4	−3.9	13.3	14.8	0.9	3.3	1.5
i	−	−4.5	−5.2	1.1	2.0	−3.9	3.0	4.9	−1.7	0.7	0.2
α	−	−1.7	−2.5	2.9	7.6	0.0	8.4	7.6	0.0	0.0	0.0
q_M	−	−1.7	−2.3	3.0	6.6	0.0	8.0	7.2	0.0	0.0	0.0
k_B	−	−1.2	−1.1	2.2	2.9	0.0	4.6	4.1	0.0	0.0	0.0
ε	+	−1.1	−1.8	1.8	5.4	0.0	6.0	5.4	0.0	0.0	0.0
k_F	−	−0.6	−0.2	1.2	0.3	0.0	1.4	1.3	0.0	0.0	0.0
d_H	−	−0.5	−0.5	0.9	1.5	0.0	2.1	1.9	0.0	0.0	0.0
k_D	+	2.9	2.2	3.7	4.0	0.0	0.0	−8.2	0.0	0.0	0.0
Summed		−47.5	−59.5	19.8	35.4	−46.2	40.6	58.3	−5.6	26.1	9.7
Combined		−47.1	−54.7	23.9	43.5	−45.1	47.7	78.1	−5.3	29.2	10.3
p_H	−	−6.6	−7.6	0.0	0.2	−6.5	0.8	8.9	−6.3	1.8	0.9
p_A	+	−0.4	−0.5	−0.6	−0.9	−0.8	−1.2	−0.3	−0.7	0.2	0.1

[1] For abbreviations see Table 2.

tivity between commercial farms and trials (Lantinga & Groot, 1996). Different values for ρ_U were motivated by differences in agronomic methods: in comparison with C1 the other farms employed low-emission application techniques, and at E1 a 'siesta' grazing system reducing the number of urine patches in the field was used. In farming systems C2 and E2 roughage of lower digestibility and higher cell wall content was fed to the animals, reflected in lower d_H and k_F. Inorganic fertilizer levels differed greatly between farming systems, and in E2 nitrogen deposition rates were lower than on the other farms (35 versus 49 kg ha⁻¹ year⁻¹). In E2, large proportions of white clover in swards were promoted as an additional source of N.

Results

Phase plane analysis

The phase plane for the simplified system without import or export of feeds is shown in Figure 6A. In any point of the phase plane the rates of change in the amounts of available inorganic N (**n**) and organically bound N (**s**), i.e. d**n**/dt and d**s**/dt, can be calculated using Equation 1. The system is attracted to values of **n** and **s** where the state variables are in steady state, thus d**n**/dt = 0 and d**s**/dt = 0. Isoclines are lines in the phase plane that connect the points where rates of change in **n** and **s** are zero (Figure 6A). The isoclines of the two state variables divide the phase plane into four regions where rates of change in **n** and **s** are non-zero. The direction of change, either increasing or decreasing, changes for a dynamic variable when the isocline is crossed as indicated by the arrows in Figure 6A.

Eventually, the whole system evolves to a steady state where both dynamic variables are constant. This equilibrium is the intersection of the isoclines for **n** and **s** in the phase plane (**n***, **s***). The path the system will follow to an equilibrium point is illustrated by the simulated trajectories for different starting points in Figure 6B. The system is strongly attracted to the **n**-isocline, as changes in **n** are rapid, while build-up and depletion of **s** are slow processes. We illustrate the dynamics of **n** and **s** for two trajectories in Figure 6B with extreme starting points but the same management and
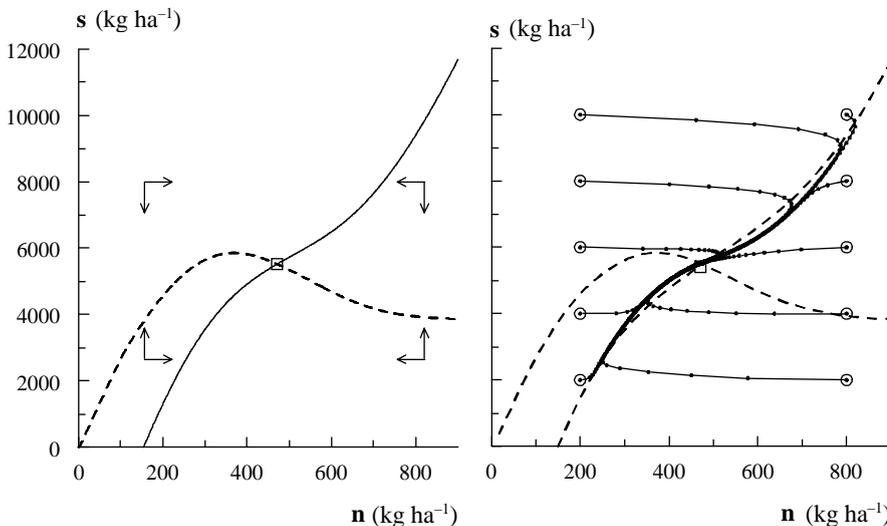
Figure 6. Phase plane for the interaction between available inorganic N (**n**) and organic N (**s**). A: Isoclines of zero change in available inorganic N (d**n**/dt = 0, solid line) and organic N (d**s**/dt = 0, broken line) and their intersection (□). The arrows indicate the vector analysis in the four regions of the graph, where →: d**n**/dt > 0, ←: d**n**/dt < 0, ↑ : d**s**/dt > 0 and ↓ : d**s**/dt < 0. B: Simulated trajectories of consecutive time steps (●) through the phase plane to the equilibrium (□) from different starting points (◉). The broken lines indicate the isoclines for **n** and **s**. For parameter values see Table 2.

thus reaching the same equilibrium. The trajectory from starting point $(\mathbf{n}_o, \mathbf{s}_o) = (800, 2000)$ may be considered as the result of extensification of farming on intensively utilized, recently sown grassland on a sandy soil. The trajectory shows the subsequent phases of investment and return. Initially, from t = 0 to 6 years, $\mathbf{s}$ builds up slowly, while inorganic N availability is reduced from 800 kg ha^{-1} to about 300 kg ha^{-1}. Thereafter $\mathbf{n}$ and $\mathbf{s}$ both increase slowly towards the equilibrium point. In contrast, when starting from $(\mathbf{n}_o, \mathbf{s}_o) = (200, 10000)$ under the stipulated management the organic N stock can be exploited for about 6 years, leading to a slow decline of $\mathbf{s}$ and to high availability of inorganic N, before a maximum level of $\mathbf{n}$ is reached. Thereafter, depletion of $\mathbf{s}$ continues and also $\mathbf{n}$ declines. Thus, the trajectories demonstrate that adjustments of management aimed at reaching a particular equilibrium state may initially result in undesired changes (i.e., movement away from the equilibrium) before the equilibrium is eventually approached.

Full model analysis

Time courses of model variables from initial conditions $(\mathbf{n}_o, \mathbf{s}_o) = (900, 3000)$ and $(\mathbf{n}_o, \mathbf{s}_o) = (300, 9000)$ in Figure 7 demonstrate rapid changes during the first years followed by more gradual progress towards equilibrium values. In the selected cases, the direction of change in the first few years was opposite to the direction of change in the subsequent period. This is consistent with the findings in the qualitative analysis (Figure 6B). Starting conditions with low $\mathbf{n}$ and high $\mathbf{s}$ resulted in rapid increase of $\mathbf{n}$ due to mineralization of the large $\mathbf{s}$ pool (Figures 7A and 7B), which also led to increased emission rates E (Figures 7C and 7E), while $\mathbf{s}$ and mineralization rate M_S gradually declined (Figures 7B and 7D). During the period between 3 and 30 years of simulation when N availability is high, excess amounts of roughage were produced on farm (increasing U_H) and these were partly exported (Figures 7F and 7G). Consequently, the farm N surplus declined and farm efficiency increased (Figures 7H and 7I). Conversely, after starting with initially high $\mathbf{n}$ and a small $\mathbf{s}$ pool, $\mathbf{n}$ was rapidly depleted, and increased only with the gradually increasing $\mathbf{s}$. Therefore, during the first 10 years of simulation, harvestable N in biomass grown at the farm was not sufficient, so that increasing amounts of feed were imported and farm surplus enhanced, while efficiency declined (Figure 7). In practice, on most farms not only feed imports and exports but also the amount of applied fertilizer N will be adjusted to compensate for low N availability for crop growth. Nevertheless, these trends illustrate the dependency of farm performance on the amount of soil organic N in terms of N surplus and efficiency.

Sensitivity analysis

Averaged over the first 50 years, increasing the initial response of N uptake in biomass (ρ_U) by 10% resulted in the largest reduction of emission rate E from 23 to 34%, depending on initial conditions (Table 4). Increasing maximum N uptake in harvested biomass ($u_{MAX,H}$) and increasing animal efficiency (φ_P) resulted in approximately proportional decreases in E. Decreasing fertilizer N input by 10% resulted in about 5%
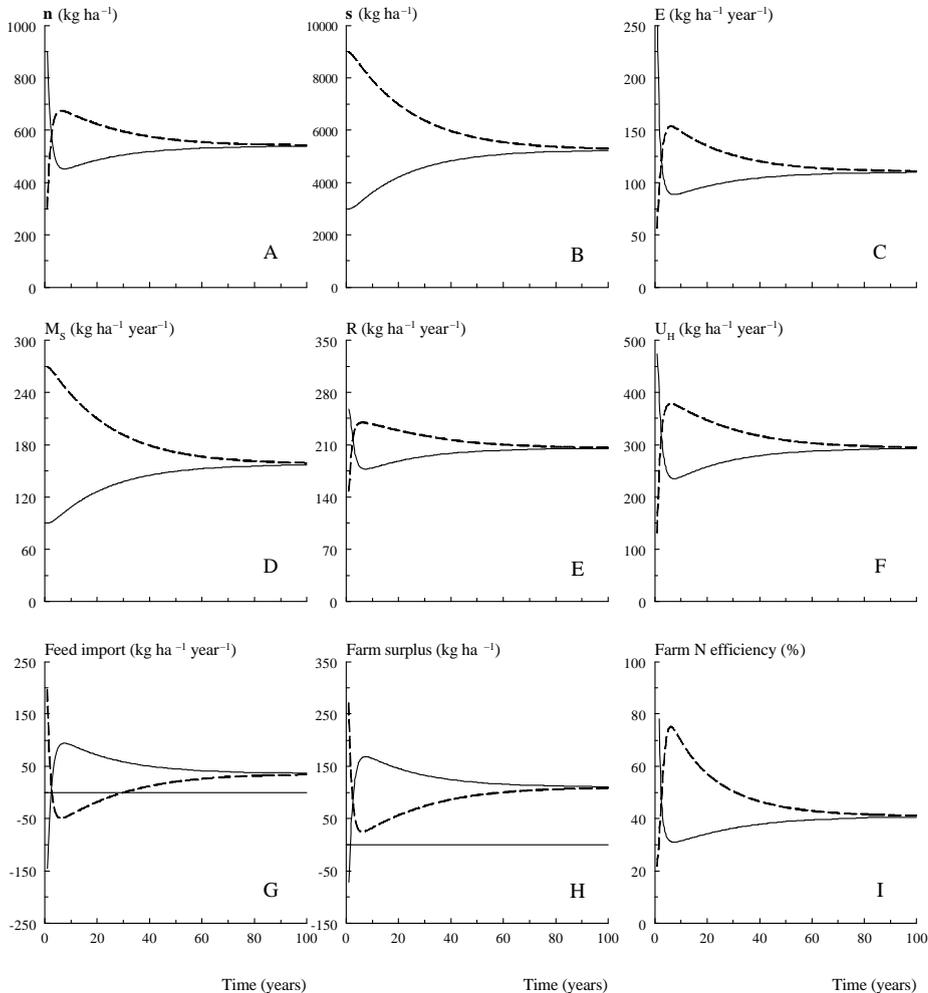
Figure 7. System characteristics during simulations starting from two extreme starting points: (n_o, s_o) = (300, 9000), broken lines and (n_o, s_o) = (900, 3000), solid lines. A: Inorganic nitrogen (n). B: Organic nitrogen (s). C: N emission (E). D: Nitrogen mineralization of s (M_S). E: Nitrogen recycling (R). F: Nitrogen uptake in harvestable biomass (U_H). G: Feed import. H: Farm surplus, calculated as the difference between N inputs (in fertilizers, deposition, fixation and supplementary feed) and outputs (in products, excess feed and slurry). I: Farm N use efficiency, defined as outputs over inputs. Parameter values are listed in Table 2.

reduction in E. Varying other management-related parameters had little influence on E over the first 50 years.

Mineralization (M_S) over the first 50 years was affected most by changes in N content in biomass (α) as well as changes in k_D, ε and q_M, which directly affect decomposition of organic matter. Generally, the proposed direction of change of a manage-
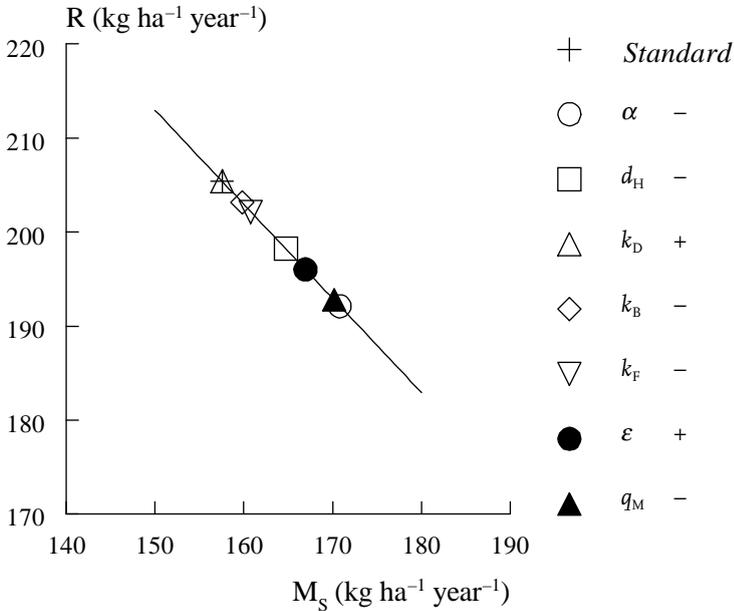
Figure 8. Relation between N recycling (R) and mineralization of **s** (M_S) in the standard situation (parameters in Table 2) and after 10% changes in various quality-related parameters in the indicated direction (+ or −).

ment-related parameter reduced E and enhanced M_S, although to highly different extents. Only if k_D, the relative rate of soil organic matter transformation, was increased the increase of M_S was associated with a short-term increase in E. In the equilibrium state, emission E was affected only, but substantially, by i, $u_{MAX,H}$, ρ_U and φ_P. Other parameters had no effect on E, indicating that they do not affect the flow of N through the system in the equilibrium state. The absence of effects on TST, PL and CI confirmed this conclusion. In contrast, changes in most management-related parameters did have an effect on the equilibrium values of both M_S and T_{RES}. The lack of effect of N on E and flow characteristics is explained by Figure 8, which demonstrates the complete compensation of changes in mineralization M_S by recycling R. Obviously, this compensation is a feature of the equilibrium but does not appear in the short term due to differences in rate of adaptation of **n** and **s**.

Comparison of the summation of effects in E and M_S ('summed' in Table 3) with the result of simultaneous change of all management-related parameters in one model evaluation ('combined' in Table 3) did not reveal consistent and major differences that pointed to synergistic effects.

A 10% decline in the milk production per ha (p_H) or 10% higher production per animal (p_A), resulted in a lower N yield in milk and meat of 68 and 75 kg ha⁻¹, respectively, compared with 77 kg ha⁻¹ in the standard situation. The simulations indicated that these measures are beneficial for emission reduction, both in the short and in the long term, but also reduce M_S (Table 2).

Table 4. Nitrogen performance for the grassland part of two commercial (C1 and C2) and two experimental farms (E1 and E2) in the Netherlands. Parameters describing the farming systems and simulation results in the equilibrium state: balance sheets, inorganic and organic N pools (**n** and **s**), N emission (E), recycling (R) and soil N mineralization (M_S), residence time (T_{RES}) and flow metrics (total system throughflow TST, path length PL and cycling index CI).

Characteristic	Unit	C1	C2	E1	E2
Process parameters[1]					
$u_{MAX,H}$	kg ha^{-1} year^{-1}	350	350	400	400
ρ_U	kg kg^{-1}	0.64	0.64	0.78	0.73
d_H	kg kg^{-1}	0.80	0.75	0.75	0.70
k_F	year^{-1}	0.45	0.40	0.45	0.35
φ_P	–	0.19	0.19	0.23	0.25
i[2]	kg ha^{-1} year^{-1}	350	200	150	35
p_H	kg ha^{-1} year^{-1}	15,850	12,500	22,000	17,500
p_A	kg ha^{-1} year^{-1}	7250	8000	8350	8000
r	–	0.45	0.35	0.30	0.30
Excreta to grass[3]	–	0.85	0.85	0.80	0.95
Clover	–	no	no	no	yes
System inputs					
Feeds	kg ha^{-1} year^{-1}	191	131	215	106
Fertilizer	kg ha^{-1} year^{-1}	305	155	100	0
Fixation	kg ha^{-1} year^{-1}	0	0	0	96
Deposition	kg ha^{-1} year^{-1}	45	45	50	35
Total	kg ha^{-1} year^{-1}	541	331	365	237
System outputs					
Products	kg ha^{-1} year^{-1}	100	77	133	106
Slurry manure	kg ha^{-1} year^{-1}	64	49	89	16
Total	kg ha^{-1} year^{-1}	164	126	222	122
Farm surplus	kg ha^{-1} year^{-1}	370	187	129	113
Farm efficiency	%	31	38	61	51
Simulated variables					
n	kg ha^{-1}	829	582	626	555
s	kg ha^{-1}	3305	3390	3694	4413
E	kg ha^{-1} year^{-1}	376	205	144	115
M_S	kg ha^{-1} year^{-1}	99	102	111	132
R	kg ha^{-1} year^{-1}	338	251	334	264
T_{RES}	year	7.6	12.0	11.8	21.0
TST	kg ha^{-1} year^{-1}	1390	1031	1261	1046
PL	–	2.57	3.12	3.45	4.41
CI	–	38.0	46.4	50.6	59.8

[1] For abbreviations see Table 2.

[2] Excluding symbiotic N fixation by clover.

[3] Proportion of N in excreta deposited on or applied (slurry) to grassland.

Farming systems comparison

The farming systems comparison yielded strongly contrasting input-output relations per ha grassland (Table 4). Farm C1 had high inputs particularly in artificial fertilizer N to reach a moderate total system output of 164 kg N ha^{-1} year^{-1}, hence the high surplus and low efficiency. In comparison, for farm C2 the inputs of feeds and fertilizers were drastically reduced by 42%, while system outputs were only 23% lower, which resulted in more favourable figures for surplus and efficiency. From the balance sheets of experimental farms E1 and E2 two contrasting strategies became apparent: E1 maintained moderate input rates and had high productivity, whereas E2 was low in both input and output of the system. Both strategies led to improved performance in terms of surplus reduction and efficiency increase compared with the commercial farms C1 and C2.

Large differences between the farming systems were also observed for the simulated variables of process rates and cycling indicators (Table 3). In the equilibrium state, E equals the farm surplus by definition, so that farm C1 had by far the highest E. Farm C1 had the highest TST and the lowest values for T_{RES} and cycling indicators PL and CI. Farm C2 already showed considerable emission reduction, particularly by reducing flows, resulting in a 26% lower TST. For C2 the total $\mathbf{n} + \mathbf{s}$ pool size was reduced by only 8%, which, together with the lower inputs and outputs, explains the higher residence time T_{RES} of N compared with C1. In comparison with C2, E1 had the same residence time, but higher TST and total pool size, in particular in organic form. The better response to inorganic N availability ($u_{MAX,H}$ and ρ_U) resulted in lower emission and improved cycling indicators for E1. Experimental farm E2 reached the same production level as C2 with considerably lower inputs, by both higher grassland responses to $\mathbf{n}$ and improved cycling indicators. The reduction of E and the larger $\mathbf{s}$ pool resulted in enhancement of T_{RES} compared with C2.

The strategies that emerged from the balance sheet comparison for E1 and E2 were reflected in differences in the simulated variables (Table 4). The strategy of E1 (moderate input and high productivity) relied heavily on recycling of N (334 versus 264 kg ha^{-1} year^{-1}), which resulted in larger $\mathbf{n}$ and smaller $\mathbf{s}$ pools than for E2 (low input, low output) and conseqently in higher E despite the higher value for parameter ρ_U. As a result, the system with the highest farm efficiency (E1) differed from the system with the lowest emission rate (E2).

Discussion

Applicability of the model

We presented a whole-farm summary model focused on dynamics of inorganic and organic N, as an instrument to evaluate management strategies in terms of N emission and mineralization of soil organic N (M_S). We are not aware of any empirical data that would enable validation of the farm model over a substantial period of time. Therefore, model validity must be inferred from validity of its components as was

discussed in the Material and methods section, and plausibility of its results.

The simulated trajectories were characterized by rapid movement to the **n**-isocline and subsequent slow change towards the intersection with the **s**-isocline, i.e., the equilibrium. These dynamics are typical for a system describing combined slow (**s**) and fast (**n**) processes, as demonstrated by Rinaldi & Scheffer (2000) in a review of the dynamics of slow-fast systems. For most variables the equilibrium was not reached within the 100-year simulation period, which is in line with results of long-term experiments like for instance the Broadbalk Rothamsted experiments (Whitehead, 1995, p. 84). The calculated range of **n** between 200 and 1000 kg ha^{-1} corresponds with the range of annual inorganic N fluxes under contrasting management and fertilization intensities as calculated by Scholefield *et al.* (1991). The relationship between **n** and N emissions derived from the withdrawal curves presented in Figure 2B, corresponds with observations that N emission rates increase more than proportionally with increasing N application rates (Van Der Meer & Meeuwissen, 1989; Scholefield *et al.*, 1991) or with larger 'potentially leachable N' pools (Di & Cameron, 2000). Hence, the model gives plausible indications of the dynamics of inorganic and organic N in grasslands under dairy farming, as well as of the associated losses.

The presented approach constitutes a complement to studies that emphasize optimization of performance of farm system components, such as emission from stables or N leaching at given soil management, and studies that focus on empirical relations between production factors, such as fertilizer and outputs. It offers a quantitative framework for evaluating short and long-term effects of management interventions aimed at improving nutrient use efficiency. This framework supports formulation of scenarios describing future developments, rather than exact prediction (cf. Carpenter, 2002). Relevant trends identified by the model are that:
– the position of equilibria in the (**n**, **s**)-phase plane are greatly influenced by management practices, although to different extents (Tables 3 and 4). This offers opportunities for effectively and intentionally influencing future changes in nutrient cycling in agro-ecosystems, also when improved utilization of internal resources is being pursued;
– in the short term, effects of changes in management practices are highly dependent on the initial situation (Figure 6B);
– initially, the system can develop in an undesirable direction before approaching an equilibrium, for instance when emissions increase after large amounts of N are mineralized from soil organic N (Figures 6 and 7).

The summary approach used in the model to describe the response of grass growth to available N implies that the initial 'inefficiency' in N uptake $(1-\rho_U)$ represents aggregate losses from excreta deposited in the field or the stable, and from slurry manure storage and application, as well as the inability of the grass sward to capture available N from the soil. Hence, the model does not allow partitioning of emissions over leaching, run-off, volatilization and denitrification. While such detail is of interest for fine-tuning management strategies, our approach aimed at examining the relative importance of improving management of various components at whole-farm scale.

By definition, a model describes a limited part of reality in a simplified way. The current focus on inorganic and organic N flows, as well as the lack of ecological infor-

mation precluded inclusion of effects of management changes on system properties
such as:
– Soil structure. Stimulation of soil biota may result in improved soil structure, air
  and water-holding capacity and root growth (Brussaard, 1997, 1998; Neher, 1999);
– Physico-chemical properties of manure. Application of additives such as Euro-
  mestmix® to slurry manure may reduce odours and improve flow properties by
  preventing formation of crusts and sediments (Pain *et al.*, 1987);
– Animal health. Feeding rations with more structural components may contribute
  to improved animal health (Nørgaard *et al.*, 1999) and fertility (Laven & Drew,
  1999).
    These aspects are not accounted for in the model, but need to be considered at
least qualitatively in a whole systems view of dairy farm functioning and evaluation of
the effectiveness of VEL & VANLA strategies.

Strategies for reduction of emission and improvement of internal cycling

The production-related parameters listed in Table 1 affected N emission and the level
of internal N cycling in the equilibrium state. Quality-related parameters had no effect
on the levels of N emission and cycling, but influenced the pathway of N cycling by
altering the ratio between R and M_S. The consequences of these findings are discussed
below, followed by conclusions on eco-technological management.

Production-related parameters and internal cycling
The sensitivity analysis revealed that changes in parameters related to efficient grass-
land and animal production (lower i, higher $u_{MAX,H}$, ρ_U and φ_P) were most effective in
reducing emissions, in both the short and the long term (Table 3); this is in agreement
with the conclusions drawn by Kohn *et al.* (1997) based on a sensitivity analysis of N
management on dairy farms. As in the VEL & VANLA project, reduced fertilizer input
constitutes the first step to improving nutrient use efficiency in many on-farm proj-
ects, without or with only minimal reduction in grass biomass production (Van
Bruchem *et al.*, 1999a; Van Keulen *et al.*, 2000). However, our results show that if the
same production intensity per hectare and per animal is maintained, emission reduc-
tion and internal cycling will benefit more from reduction of losses from **n**, e.g. by
increasing ρ_U and $u_{MAX,H}$, than from reducing **n** by lowering i and increasing animal
efficiency φ_P.

    Possible ways to enhance ρ_U are reduction of grazing time and technical interven-
tions to minimize losses during handling of animal excreta and precision placement of
fertilizers (Frost, 1994; Misselbrook *et al.*, 1996; Bussink & Oenema, 1998; Chambers
et al., 2000; Van Alphen & Stoorvogel, 2000). Also more attention for grassland
management is required, aiming at maintaining a high sward density to ensure high
recovery of available N (Van Loo, 1993; Lantinga *et al.*, 1999). Improvement of the
botanical composition with high producing species and cultivars efficiently utilizing
available N by growing at low α (Baan Hofman, 1988) would further reduce the need
of high levels of available inorganic N and reduce the N content of harvested grass.

    The potential for improved internal nutrient cycling was demonstrated in the farm-

ing systems comparison (Table 4), in particular the contrast between farms C2 and E2. With the same total system throughflow (TST), the input for E2 was considerably lower and internal cycling higher, as reflected in higher values for T_{RES}, path length and cycling index. These farms had the same N output, although it should be noted that for C2 a larger proportion was exported in slurry manure. The contrast between E1 and E2 clearly indicated that the farming system with the highest input:output efficiency (E1) is not necessarily the lowest in N emission (E2), since emission is also dependent on the total volume of N flowing through the system.

Quality-related parameters and the ratio between recycling rate and mineralization
Changes in quality-related parameters determining herbage biomass and manure composition and degradability (lower α, d_H, k_F, k_B) and mineralization by soil biota (lower q_M, higher k_D and ε) affected N emission in the short, but not in the longer term. In the equilibrium state, changes in mineralization (M_S) by adjustments in these parameters were fully compensated by modifications in recycling rate R (Figure 8), so that also flow characteristics and thus internal nutrient cycling in the equilibrium were not affected by the quality-related parameters (Table 3). Selection of strategies and associated management practices to diminish N emissions from dairy farming systems requires awareness of this trade-off between the M_S and R pathways of mineralization, which offer different opportunities to manipulate ρ_U. Measures affecting the ratio between M_S and R should be tuned to:
– agronomic demands of optimal temporal distribution of N availability to match the requirements for grass growth and quality (i.e., protein content), and
– the expected relative ability to control the flows and reduce emissions from either of these sources of available N.

High recycling rates originate from rapid mineralization from organic N compounds and from high inorganic N content in slurry manure, enabling synchronization of supply of inorganic N when grass growth rates are expected to be high, particularly in spring. At the same time, high recycling rates are associated with currently acknowledged emission routes and environmental pollution, which may be partly reduced by fine-tuning, technical interventions, and improved grassland management (see above). In contrast, reduction of R and a shift to higher M_S can have several advantages. This strategy would especially decrease the N content of excreta and non-harvested biomass, which can potentially reduce (1) ammonia-N in excreta exposed to air after deposition and during storage and application of slurry manure (Hutchings *et al.*, 1996) and (2) local soil-N content after application of slurry manure, prone to leaching and denitrification losses (Thompson *et al.*, 1987). Furthermore, damage from shallow injection of (larger quantities of) slurry manure can be reduced, thereby maintaining more intact and dense grass swards and rooting systems (Rees *et al.*, 1993; Frost, 1994), by:
– the use of surface-application techniques, which would be justified if N in slurry manure is present in lower concentrations with a larger proportion in organic forms, especially in spring when high humidity and rainfall probability mitigate volatilization losses, and
– reduction of the number of slurry manure applications when N supply from the soil

increases, especially in late spring and summer.

An additional advantage of supply of N through M_S may be the release of inorganic N in the rooted soil profile, in the same environment where it is utilized, reducing the risk of losses if synchronized with plant requirement. These advantages of a shift to M_S were important for the selection of management practices in the VEL & VANLA Nutrient Management Project. However, increasing the dependency of the grassland production on M_S increases the dependency on physical conditions, in particular temperature and soil moisture, which govern the rates of biological processes and thereby the annual amount and the timing of organic matter degradation and N mineralization (Franzluebbers *et al.*, 1995; Goulding *et al.*, 2001). Since soil temperature lags behind air temperature, the activity of soil biota is not synchronized with crop growth. This can lead to available inorganic N deficits in spring and surpluses in autumn.

Conclusions on eco-technological management

The proposed cycling indicators support monitoring of the performance of farming systems that change into an eco-technological direction. Therefore, they may become a valuable extension of the traditional indicator set of farm surplus and farm N efficiency.

The simulation results clearly show that the VEL & VANLA strategies identified in Table 1 will result in N emission reduction due to adjustments in production-related parameters and a change in the ratio between R and M_S as a result of changes in quality-related parameters. The farming systems comparison (Table 4) demonstrated that a considerable shift in the ratio between R and M_S is attainable. The actual desirability of this shift depends on the expected opportunities of altering production-related parameters, in particular ρ_U. This in turn is dictated by many farm-specific circumstances, such as soil and crop characteristics, whole farm management (e.g. ration composition, grazing management) and technical means (e.g. stable type, slurry storage and application technique). Consequently, changes in current management should be considered for each farm separately and should primarily aim for possibilities to enhance ρ_U, to improve internal N cycling.

References

Aarts, H.F.M., 2000. Resource management in a 'De Marke' dairy farming system. PhD thesis Wageningen University, Wageningen, 222 pp.

Aarts, H.F.M., B. Habekotte, G.J. Hilhorst, G.J. Koskamp, F.C. Van Der Schans & C.K. De Vries, 1999a. Efficient resource management in dairy farming on sandy soil. *Netherlands Journal of Agricultural Science* 47: 153–167.

Aarts, H.F.M, B. Habekotte & H. Van Keulen, 1999b. Limits to intensity of milk production in sandy areas in The Netherlands. *Netherlands Journal of Agricultural Science* 47: 263–277.

Altieri, M.A., 1991. An agroecological analysis of the environmental degradation resulting from the structure of agriculture. In: P.B. Thompson & B. Stout (Eds), Beyond the Large Farm. Westview Press, Boulder, pp. 125–135.

Anonymous, 2000. Book of Tables on Animal Nutrition 2000. CVB Series No 24, Centraal Veevoeder-bureau (CVB), Lelystad, 110 pp. (In Dutch)

Baan Hofman, T., 1988. Effects of Nitrogen Application and Mowing Frequency on Dry Matter Yield of Perennial Ryegrass Cultivars differing in Persistence. Report No 86, Centrum voor Agro-biologisch Onderzoek (CABO), Wageningen, 27 pp. (In Dutch)

Bailey, R., 2000. Input-output modeling of material flows in industry. PhD thesis G.W. Woodruff School of Mechanical Engineering. Georgia Institute of Technology, Atlanta. <http://www.srl.gatech.edu/reid/rb_phd.html> Accessed: 25 February 2003.

Bawden, R.J., 1991. Systems thinking in practice in agriculture. *Journal of Dairy Science* 74: 2362–2373.

Brussaard, L., 1997. Interrelationships between soil structure, soil organisms, and plants in sustainable agriculture. In: L. Brussaard & R. Ferrera-Cerrato (Eds), Soil Ecology in Sustainable Agricultural Systems. Lewis Publishers, New York, pp. 1–14.

Brussaard, L., 1998. Soil fauna, guilds, functional groups and ecosystem processes. *Applied Soil Ecology* 9: 123–135.

Bussink, D.W. & O. Oenema, 1998. Ammonia volatilization from dairy farming systems in the temperate regions: a review. *Nutrient Cycling in Agroecosystems* 51: 19–33.

Carpenter, S.R., 2002. Ecological futures: building an ecology of the long now. *Ecology* 83: 2069–2083.

Carpenter, S.R., D. Ludwig & W.A. Brock, 1999. Management of eutrophication for lakes subject to potentially irreversible change. *Ecological Applications* 9: 751–771.

Castillo, A.R., E. Kebreab, D.E. Beever, J.H. Barbi, J.D. Sutton, H.C. Kirby & J. France, 2001a. The effect of energy supplementation on nitrogen utilization in lactating dairy cows fed grass silage diets. *Journal of Animal Science* 79: 240–246.

Castillo, A.R., E. Kebreab, D.E. Beever, J.H. Barbi, J.D. Sutton, H.C. Kirby & J. France, 2001b. The effect of protein supplementation on nitrogen utilization in lactating dairy cows fed grass silage diets. *Journal of Animal Science* 79: 247–253.

Chambers, B.J., K.A. Smith & B.F. Pain, 2000. Strategies to encourage better use of nitrogen in animal manures. *Soil Use and Management* 16: 157–161.

Chapin, F.S. III, 1980. The mineral nutrition of wild plants. *Annual Review of Ecological Systems* 11: 233–260.

DeAngelis, D.L., 1992. Dynamics of Nutrient Cycling and Food Webs. Population and Community Biology Series No 9. Chapman and Hall, London, 270 pp.

Delwiche, C.C., 1970. The nitrogen cycle. *Scientific American* 223: 137–146.

De Wit, C.T., 1953. A Physical Theory on Placement of Fertilisers. Verslagen Landbouwkundige Onderzoekingen 59.4. Government Printing Office, The Hague, 70 pp.

Di, H.J. & K.C. Cameron, 2000. Calculating nitrogen leaching losses and critical nitrogen application rates in dairy pasture systems using a semi-empirical model. *New Zealand Journal of Agricultural Research* 43: 139–147.

Finn, J.T., 1976. Measures of ecosystem structure and function derived from analysis of flows. *Journal of Theoretical Biology* 56: 363–380.

Finn, J.T., 1980. Flow analysis of models of the Hubbard Brook ecosystem. *Ecology* 61: 562–571.

Franzluebbers, A.J., F.M. Hons & D.A. Zuberer, 1995. Tillage-induced seasonal changes in soil physical properties affecting soil CO_2 evolution under intensive cropping. *Soil and Tillage Research* 34: 41–60.

Frost, J.P., 1994. Effects of spreading method, application rate and dilution on ammonia volatilization from cattle slurry. *Grass and Forage Science* 49: 391–400.

Goudriaan, J. & J.L. Monteith, 1990. A mathematical function for crop growth based on light interception and leaf area expansion. *Annals of Botany* 66: 695–701.

Goulding, K.W.T., D.V. Murphy, A. MacDonald, E.A. Stockdale, J.L. Gaunt, L. Blake, G. Ayaga & P. Brookes, 2001. The role of soil organic matter and manures in sustainable nutrient cycling. In: R.M. Rees, B.C. Ball, C.D. Campbell & C.A. Watson (Eds), Sustainable Management of Soil Organic Matter. CAB International, Wallingford, pp. 221–232.

Hansson, A.C. & R. Petterson, 1989. Uptake and above- and below-ground allocation of soil mineral-N and fertilizer ^{15}N in a perennial grass ley (*Festuca pratensis*). *Journal of Applied Ecology* 26: 259–271.

Henkens, P.L.C.M & H. Van Keulen, 2001. Mineral policy in the Netherlands and nitrate policy within the European Community. *Netherlands Journal of Agricultural Science* 49: 117–134.

Hilhorst, G.J., J. Oenema & H. Van Keulen, 2001. Nitrogen management on experimental dairy farm 'De Marke'; farming system, objectives and results. *Netherlands Journal of Agricultural Science* 49: 135–151.

Hutchings, N.J., S.G. Sommer & S.C. Jarvis, 1996. A model of ammonia volatilization from a grazing livestock farm. *Atmospheric Environment* 30: 589–599.

Illius, A.W. & T.G. O'Connor, 1999. On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. *Ecological Applications* 9: 798–813.

Janssen, B.H., 1996. Nitrogen mineralization in relation to C:N ratio and decomposability of organic materials. *Plant and Soil* 181: 39–45.

Jarvis, S.C., R.J. Wilkins & B.F. Pain, 1996. Opportunities for reducing the environmental impact of dairy farming managements: a systems approach. *Grass and Forage Science* 51: 21–31.

Jenkinson, D.S., 2001. The impact of humans on the nitrogen cycle, with focus on temperate arable agriculture. *Plant and Soil* 228: 3–15.

Kemp A., O.J. Hemkes & T. Van Steenbergen, 1979. The crude protein production of grassland and the utilization by milking cows. *Netherlands Journal of Agricultural Science* 27: 36–47.

Kohn, R.A., Z. Dou, J.D. Ferguson & R.C. Boston, 1997. A sensitivity analysis of nitrogen losses from dairy farms. *Journal of Environmental Management* 50: 417–428.

Lantinga, E.A., P.J.A.G. Deenen & H. Van Keulen, 1999. Herbage and animal production responses to fertilizer nitrogen in perennial ryegrass swards. II. Rotational grazing and cutting. *Netherlands Journal of Agricultural Science* 47: 243–261.

Lantinga, E.A. & J.C.J. Groot, 1996. Optimization of grassland production and herbage feed quality in an ecological context. In: A.F. Groen & J. Van Bruchem (Eds), Utilization of Local Feed Resources in Dairy Cattle. Publication No 84, European Association for Animal Production (EAAP), Wageningen Pers, Wageningen, pp. 58–66.

Laven, R.A. & S.B. Drew, 1999. Dietary protein and the reproductive performance of cows. *Veterinary Record* 145: 687–695.

Ledgard, S.F., J.W. Penno & M.S. Sprosen, 1999. Nitrogen inputs and losses from grass/clover pastures grazed by dairy cows, as affected by nitrogen fertilizer application. *Journal of Agricultural Science, Cambridge* 132: 215–225.

Loladze, I., Y. Kuang & J.J. Elser, 2000. Stoichiometry in producer-grazer systems: linking energy flow with element cycling. *Bulletin of Mathematical Biology* 62: 1137–1162.

Misselbrook, T.H., J.A. Laws & B.F. Pain, 1996. Surface application and shallow injection of cattle slurry on grassland: nitrogen losses, herbage yields and nitrogen recoveries. *Grass and Forage Science* 51: 270–277.

Neher, D.A., 1999. Soil community composition and ecosystem processes - comparing agricultural

ecosystems with natural ecosystems. *Agroforestry Systems* 45: 159–185.

Nørgaard, N.H., K.M. Lind & J.F. Agger, 1999. Cointegration analysis used in a study of dairy-cow mortality. *Preventive Veterinary Medicine* 42: 99–119.

Noy-Meir, I., 1975. Stability of grazing systems: an application of predator-prey graphs. *Journal of Ecology* 63: 459–481.

Oomen, G.J.M., E.A. Lantinga, E.A. Goewie & K.W. Van Der Hoek, 1998. Mixed farming systems as a way towards a more efficient use of nitrogen in European Union agriculture. *Environmental Pollution* 102(S1): 697–704.

Pain, B.F., R.B. Thompson, L.C.N. De La Lande Cremer & L. Ten Holte, 1987. The use of additives in livestock slurries to improve their flow properties, conserve nitrogen and reduce odours. In: H.G. Van Der Meer, R.J. Unwin, T.A. Van Dijk & G.C. Ennik (Eds), Animal Manure on Grassland and Fodder crops, Fertilizer or Waste? Developments in Plant and Soil Science Vol. 30. Martinus Nijhoff, The Hague, pp. 229–246.

Rees, Y.J., B.F. Pain, V.R. Phillips & T.H. Misselbrook, 1993. The influence of surface and sub-surface application methods for pig slurry on herbage yields and nitrogen recovery. *Grass and Forage Science* 48: 38–44.

Richards, I.R., 1977. Influence of soil and sward characteristics on the response to nitrogen. In: B. Gilsenan (Ed.), Proceedings International Meeting on Animal Production from Temperate Grassland. Irish Grassland and Animal Production Association, Dublin, pp. 45–49.

Rinaldi, S. & M. Scheffer, 2000. Geometric analysis of ecological models with slow and fast processes. *Ecosystems* 3: 507–521.

Rosenzweig, M.L. & R.H. MacArthur, 1963. Graphic representation and stability conditions of predator-prey interactions. *American Naturalist* 97: 209–203.

Scheffer, M., H. Hosper, M.-L. Meijer, B. Moss & E. Jeppesen, 1993. Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution* 8: 260–262.

Scholefield, D., D.R. Lockyer, D.C. Whitehead & K.C. Tyson, 1991. A model to predict transformations and losses of nitrogen in UK pastures grazed by beef cattle. *Plant and Soil* 132: 165–177.

Snijders, P.J.M., J.J. Woldring & J.H. Geurink, 1987. Nitrogen use of injected cattle slurry manure on grassland: report of an investigation into the effects of nitrogen from injected and surface-applied cattle slurry on the yield and quality of grass. Report No 103, Proefstation voor de Rundveehouderij, Schapenhouderij en Paardenhouderij, Lelystad, 156 pp. (In Dutch)

Ten Berge, H.F.M., J.C.M. Withagen, F.J. De Ruijter, M.J.W. Jansen & H.G. Van Der Meer, 2000. Nitrogen responses in grass and selected field crops - QUAD-MOD parameterisation and extensions for STONE-application. Report No 24, Plant Research International, Wageningen, 45 pp.

Thompson, P.B. & A. Nardone, 1999. Sustainable livestock production: methodological and ethical challenges. *Livestock Production Science* 61: 111–119.

Thompson, R.B., J.C. Ruden & D.R. Lockyer, 1987. Fate of nitrogen in cattle slurry following surface application or injection to grassland. *Journal of Soil Science* 38: 689–700.

Valk, H., 2002. Nitrogen and phosphorus supply of dairy cows. PhD thesis Wageningen University, Wageningen, 204 pp.

Van Alphen, B.J. & J.J. Stoorvogel, 2000. A methodology for precision nitrogen fertilization in high-input farming systems. *Precision Agriculture* 2: 319–332.

Van Bruchem, J., H. Schiere & H. Van Keulen, 1999a. Dairy farming in the Netherlands in transition towards more efficient nutrient use. *Livestock Production Science* 61: 145–153.

Van Bruchem, J., F. Verhoeven, L. Brussaard & S. Tamminga, 1999b. Diet and manure characteristics

in relation to nitrogen flows in a dairy farming system. In: D. Van Der Heide, E.A. Huisman, E. Kanis, J.W.M. Osse & M.W.A. Verstegen (Eds), Regulation of Feed Intake, CAB International, Wallingford, pp. 219–225.

Van De Koppel, J., J. Huisman, R. Van Der Wal & H. Olff, 1996. Patterns of herbivory along a productivity gradient: an emperical and theoretical investigation. *Ecology* 77: 736–745.

Vandermeer, J.H., 1973. Generalized models of two species interactions: a graphical analysis. *Ecology* 54: 809–818.

Van Der Meer, H.G. & P.C. Meeuwissen, 1989. Emission of nitrogen from soils in agricultural use in relation to fertilizer application and farm management. *Landschap* 1: 19–32. (In Dutch)

Van Keulen, H., H.F.M Aarts, B. Habekotté, H.G. Van Der Meer & J.H.J. Spiertz, 2000. Soil-plant-animal relations in nutrient cycling: the case of dairy farming system 'De Marke'. *European Journal of Agronomy* 13: 245–261.

Van Keulen, H., H.G. Van Der Meer & I.J.M. De Boer, 1996. Nutrient balances of livestock production systems in the Netherlands. In: A.F. Groen & J. Van Bruchem (Eds), Utilization of Local Feed Resources by Dairy Cattle. Publication No 84, European Association for Animal Production (EAAP), Wageningen Pers, Wageningen, pp. 3–18.

Van Loo, E.N., 1993. On the relation between tillering, leaf area dynamics and growth of perennial ryegrass *(Lolium perenne* L.*)*. PhD thesis Wageningen Agricultural University, Wageningen, 169 pp.

Vitousek, P.M., J.D. Aber, R.W. Howarth, G.E. Likens, P.A. Matson, D.W. Schindler, W.H. Schlesinger & D.G. Tilman, 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* 7: 737–750.

Watson, C.J. & R.H. Foy, 2001. Environmental impacts of nitrogen and phosphorus cycling in grassland systems. *Outlook on Agriculture* 30: 117–127.

Whitehead, D.C., 1995. Grassland Nitrogen. CAB International, Wallingford, 397 pp.

Whitehead, D.C., A.W. Bristow & D.R. Lockyer, 1990. Organic matter and nitrogen in the unharvested fractions of grass swards in relation to the potential for nitrate leaching after ploughing. *Plant and Soil* 123: 39–49.

Williams, P.E.V., 1995. Animal production and European pollution problems. *Animal Feed Science and Technology* 53: 135–144.

Appendix 1

Derivation of nitrogen and biomass production curves

Total dry matter (DM) and N yields

The data from the cutting experiment reported by Lantinga *et al.* (1999, p. 253, Figure 3a) were used, as partly reproduced in Figure 1.1 (quadrant IV). To derive the mass of DM and N in total (harvestable and unharvestable) biomass, the observations for quadrants I and IV of the three-quadrant analysis (De Wit, 1953) were processed as follows:

– The relationship between harvested DM yield and root DM at different fertilizer N application levels was fitted using data of Baan Hofman (1988). This relationship was used to calculate values of root DM in the experiment of Lantinga *et al.* (1999).

– A value of 2 was adopted for the ratio between root DM and stubble DM, based on data of Whitehead *et al.* (1990). This ratio was used to estimate the amount of stubble DM (0–5 cm above ground level) in the experiment of Lantinga *et al.* (1999).

– The changes in N content of roots and stubble with increasing N fertilizer application were fitted using data of Whitehead *et al.* (1990), so that amounts of N in roots and stubble at a given moment within a growing season could be calculated. These quantities were corrected for decay throughout the growing season (factor 1.5; Hansson & Pettersson, 1989) to arrive at total annual N uptake.

Available inorganic N

The amount of available inorganic N may be estimated from the intersection with the x-axis of the relation between N application and total N uptake (Figure 1.1). Because this relationship is based on experimental field data with inorganic fertilizer N, a correction is needed for losses at farm level, e.g. from animal excreta after deposition in the field or the stable, and during slurry manure storage or application. We assumed these losses to amount to 20% of total available N in the standard farm situation.

These calculations resulted in Figures 3a and 3b and in the fitted and derived parameter values for biomass DM and N accumulation in Table 2 in the text.
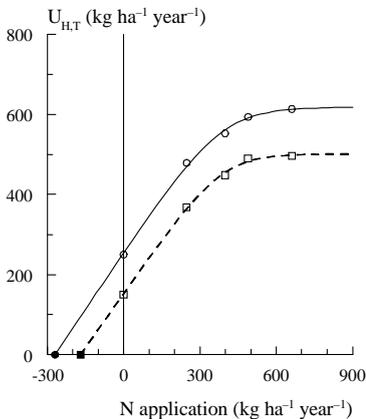
Figure 1.1. Relation between fertilizer N application and N uptake (U_T and U_H) for total (U_T, solid line) and harvestable (U_H, broken line) biomass. Lines are fitted and solid points are calculated by extrapolation of fitted curves to the intersection with the x-axis. Original data from Lantinga *et al.* (1999).

J.C.J. Groot, W.A.H. Rossing, E.A. Lantinga and H. Van Keulen

Appendix 2

Calculation of flow metrics

Two-system compartments representing inorganic and organic N were defined (Figure 2.1). In contrast with the definition of the **s** pool in the text, the organic N compartment defined here comprises all organic N, including the amount that is mineralized to inorganic forms within the same year, e.g. the time step in which it is incorporated into organic compounds. Each compartment has an inflow (z_{io}) from and an outflow (y_{oi}) to the environment, one outflow (f_{ji}) to the other compartment and one inflow (f_{ij}) from the other compartment (Bailey, 2000). In a system where the equilibrium is not yet reached, positive compartment derivatives are treated as outflows and negative compartment derivatives as inflows (Finn, 1976). This yields the following set of equations for calculation of the flows (2.1 to 2.6):

$$z_{10} = i + |\min(d\mathbf{n}/dt,0)| \tag{2.1}$$
$$z_{20} = |\max(F,0)| + |\max(S,0)| + |\min(d\mathbf{s}/dt,0)| \tag{2.2}$$
$$y_{01} = E + |\max(d\mathbf{n}/dt,0)| \tag{2.3}$$
$$y_{02} = \varphi_P U_H^{'} + |\min(F,0)| + |\min(S,0)| + |\max(d\mathbf{s}/dt,0)| \tag{2.4}$$
$$f_{12} = M_S + |\max(R,0)| \tag{2.5}$$
$$f_{21} = U_T + |\min(R,0)| \tag{2.6}$$

In these equations, F and S denote the import or export of feeds and slurry manure, respectively. All other parameters are explained in the text. The cycling indicators total system throughflow (TST), cycling index (CI) and path length (PL) are calculated from the flows, using Equations 2.7 – 2.10, where TST_C is the amount of cycled flows in the system.

$$TST = f_{12} + f_{21} + z_{10} + z_{20} \tag{2.7}$$

$$TST_C = f_{12}f_{21}[1/(f_{12} + y_{02}) + 1/(z_{10} + f_{12})] \tag{2.8}$$

$$CI = TST_C/TST \tag{2.9}$$

$$PL = 1 + (f_{12} + f_{21})/(z_{10} + z_{20}) \tag{2.10}$$
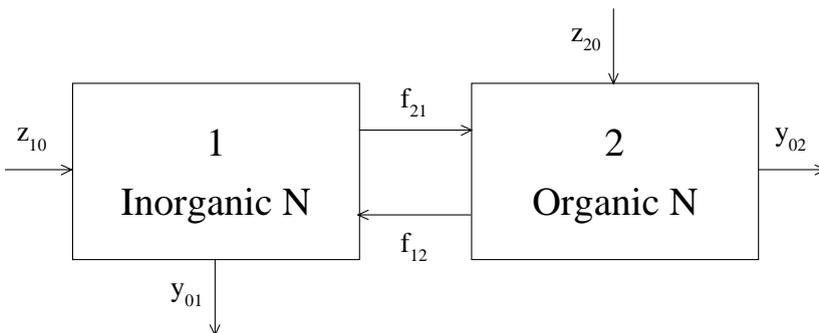
Figure 2.1. Schematic representation of the 2-compartment system of inorganic and organic N and the flows between these compartments.