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Modelling the ecosystem effects of nitrogen deposition: Simulation of nitrogen saturation in a Sitka spruce forest, Aber, Wales, UK

BRIDGET A. EMMETT[1], BERNARD J. COSBY[2], ROBERT C. FERRIER[3], ALAN JENKINS[4], ALBERT TIETEMA[5] & RICHARD F. WRIGHT[6]

[1]*Institute of Terrestrial Ecology, Bangor Research Unit, Deiniol Road, Bangor, Gwynedd LL57 2UP, UK;* [2]*Department of Environmental Sciences, University of Virginia, Charlottesville, VA, USA 22901;* [3]*Macaulay Land Use Research Institute, Craigiebuckler, Aberdeen AB9 2QJ, UK;* [4]*Institute of Hydrology, Wallingford OXON OX10 8BB, UK;* [5]*Landscape and Environmental Research Group, University of Amsterdam, Nieuwe Prinsengracht 130, 1018 VZ Amsterdam, Netherlands;* [6]*Norwegian Institute for Water Research, Box 173 Kjelsås, 0411 Oslo, Norway*

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Abstract. A new model for simulating nitrogen leaching from forested ecosystems has been applied to data from an experimentally manipulated 30-year-old Sitka spruce stand. The manipulation experiment (at Aber, in north-western Wales, UK) was part of the European NITREX project and involved five years of additions of inorganic nitrogen to the spruce stand. The model (MERLIN) is a catchment-scale, mass-balance model that simulates both biotic and abiotic processes affecting nitrogen in ecosystems.

The structure of MERLIN includes representations of the inorganic soil, one plant compartment and two soil organic compartments. Fluxes in and out of the simulated ecosystem and transfers between compartments are regulated by atmospheric deposition, hydrological discharge and biological processes such as plant uptake, litter production, immobilization, mineralization, nitrification and denitrification. Rates of nitrogen uptake, cycling and release among pools are regulated by carbon productivity, inorganic nitrogen availability and the C:N ratios of the organic pools. Inputs to the model are temporal sequences of carbon fluxes and pools, hydrological discharge and external sources of nitrogen.

The NITREX experiment at Aber began in 1990 with weekly additions of ammonium nitrate (NH_4NO_3) at a rate of 35 kg N ha^{-1} yr^{-1}. Data were collected from both control and treatment plots within the stand. The site-intensive data from the control plots at Aber were augmented by data taken from a chronosequence of 20 Sitka spruce stands and data from a survey of 5 moorland catchments in the same region to provide calibration data for the model. The data were used to establish current conditions at the Aber site and to reconstruct historical sequences of carbon fluxes and pools from 1900 to the present day with which to drive the model. The reconstructed sequences included an increase in nitrogen deposition and a vegetation change from moorland to plantation forest in 1960. The calibrated model was then used to predict the effects of the experimental nitrogen additions begun in 1990.

MERLIN successfully reproduced the observed increase in NO_3 leaching from aging spruce stands that results from forest maturation and increased nitrogen deposition (as inferred from the chronosequence and forest survey data in the region). MERLIN also correctly predicted the increases in soilwater NO_3 concentrations, the changes in nitrogen content of tree and soil organic matter pools, and the changes in nitrogen fluxes that occur in spruce stands in response to increased nitrogen inputs (as observed in the nitrogen addition experiment).

1. Introduction

Nitrogen saturation is characterized by increased and persistent losses of inorganic nitrogen usually as NO_3 in soil leachate, runoff or groundwater (Aber et al. 1989). Saturation occurs when the combined inputs of inorganic nitrogen from internal sources (mineralization and fixation) and external sources (such as atmospheric deposition and fertilizers) exceed the nitrogen uptake capacity of plants and soil microorganisms. In recent years increased inorganic nitrogen concentrations have been reported in lakes and streams in both North America and Europe (Hauhs et al. 1989; Driscoll et al. 1989; Emmett et al. 1993; Stoddard 1994; Dise & Wright 1995). High concentrations of NO_3 and NH_4 in soil solution have been implicated in widespread forest dieback in central Europe (van Breemen & van Dijk 1988).

The NITREX project was designed to investigate the response and recovery of coniferous forests to atmospheric nitrogen deposition at the ecosystem level (Wright & van Breemen 1995). Nitrogen deposition removal and addition experiments have been carried out at the catchment or plot scale at sites across a European gradient of nitrogen deposition and the timing of responses in vegetation, soil and water chemistry recorded (Wright et al. 1995). In the UK, the NITREX site is a Sitka spruce stand on the north Wales coast. The stand was planted in 1960 and experimental plots within the stand have received weekly additions of nitrogen as NH_4NO_3 at a rate of 35 kg N ha^{-1} yr^{-1} since 1990. Stand development from planting to present day can be reconstructed using a chronosequence of Sitka spruce stands in north and mid Wales all planted on similar geology and dominated by one of the major soil types in the uplands of Wales.

This combination of manipulation and survey data provides a robust resource for the testing of a new aggregated, process-oriented model for simulating and predicting nitrogen leaching: MERLIN (**M**odel of **E**cosystem **R**etention and **L**oss of **I**norganic **N**itrogen, Cosby et al. 1997). The model was calibrated to reconstruct the nitrogen pools and fluxes and the C:N ratios in organic matter in the steady-state conditions for the moorland ecosystem prior to 1960 and in the aggrading spruce stand following planting in 1960. The model was driven by increasing atmospheric deposition of nitrogen during the land-use change and subsequent forest growth. Once this calibration simulation was completed, the model was used to predict the response of the forest ecosystem to the experimental inorganic nitrogen additions in a model verification exercise.

2. Model description

MERLIN is a catchment-scale mass-balance model of linked carbon and nitrogen cycling in ecosystems developed for simulating leaching losses of inorganic nitrogen. The model considers linked biotic and abiotic processes affecting the cycling and storage of nitrogen. The model is aggregated in space and time and contains compartments intended to be observable and/or interpretable at the plot or catchment scale. The structure of the model includes the inorganic soil, a plant compartment and two soil organic compartments. Fluxes in and out of the ecosystem and between compartments are regulated by atmospheric deposition, hydrologic discharge, plant uptake, litter production, wood production, microbial immobilization, mineralization, nitrification, and denitrification. Nitrogen fluxes are controlled by carbon productivity, by the C:N ratios of organic compartments and by inorganic nitrogen availability in soil solution.

Inputs required by the model are: 1) temporal sequences of carbon fluxes and pools; 2) time series of hydrologic discharge through the soils, 3) historical and current external sources of inorganic nitrogen; 4) current amounts of nitrogen in the plant and soil organic compartments; 5) constants specifying the nitrogen uptake and immobilization characteristics of the plant and soil organic compartments; and 6) soil characteristics such as depth, porosity, bulk density, and anion/cation exchange constants. Outputs of the model include: 1) concentrations and fluxes of NO_3 and NH_4 in soil solution and runoff; 2) total nitrogen contents of the organic and inorganic compartments; 3) C:N ratios of the aggregated plant and soil organic compartments; and 4) rates of nitrogen uptake and immobilization and nitrogen mineralization. The details of the model, its conceptual basis, the processes included, the mathematical structure, implementation procedures and examples of applications in speculative simulation exercises are given in Cosby et al. (1997).

For the application of MERLIN to the site at Aber, the compartments in the model had to be associated with components of the moorland or forest ecosystems being simulated. The compartments are conceptually defined here and the data sources for each compartment are described below. The plant compartment in the model is an aggregated pool of carbon and nitrogen representing the “living” portion of the ecosystem. It includes both the above- and below-ground components of the living organic material. Litter production likewise includes a below-ground component of root death. Plant growth affects inorganic nitrogen only through uptake of NH_4 and NO_3. Soil organic material is divided into two compartments: labile organic matter (LOM); and refractory organic matter (ROM). Each is an aggregated pool of carbon and nitrogen representing accumulated organic compounds in the ecosystem. These materials provide the energy substrate for growth of

Table 1. Selected soil characteristics at Aber.

	Horizon			
	LFH	E_{ag}	B_1	B_2
Depth	+6–0	0–17	17–53	53+
L.O.I. (%)	81	14	6	4
pH (salt)	3.0	3.5	4.1	4.3
CEC (meq 100 g^{-1} dry soil)	25.8	8.9	5.3	2.6
Base saturation (%)	63	12	10	12
%N	1.6	0.5	0.3	0.2

soil microorganisms, and this activity results in the carbon and nitrogen fluxes of interest in ecosystem soils. The LOM and ROM compartments affect inorganic nitrogen through immobilization and mineralization. These compartments and fluxes are highly aggregated. The LOM pool may be most readily identified with the forest floor in forested systems. Alternately, it may represent an accumulation of a number of years (cohorts) of litter. The A and O horizons of the soil may also comprise part of the LOM compartment. The LOM compartment provides a soil organic matter pool that can respond rather quickly to changing external conditions and inputs. Litter inputs are to the LOM compartment. The ROM pool, on the other hand, represents the bulk of carbon and nitrogen present in soil profiles. Organic matter enters the ROM compartment from the LOM pool. The ROM compartment has a longer turnover time due partly to the recalcitrant nature of the organic matter and partly to its larger pool size.

3. Site description

The Aber site is a Sitka spruce (*Picea sitchensis (Bong.(Carr.)*) stand planted in 1960 on grazed moorland following ploughing. The stand has not been thinned and has a dense canopy and high basal area (59.5 m^{-2} ha^{-1}). The soils are poorly-developed stagnopodzols (Avery 1980) underlain with Ordovician mudstones and siltstone. Altitude of the site is 300 m. Annual rainfall is 1850 mm. Selected soil characteristics are presented in Table 1. Further details of the site are given by Emmett et al. (1995a).

Mean annual nitrogen inputs in bulk precipitation for the period 1990–95 were 39 and 35 mmol N m^{-2} yr^{-1} as ammonium and nitrate, respectively (Emmett et al. in press). Combined throughfall and stemflow were 45, 59 and 16 mmol N m^{-2} yr^{-1} as ammonium, nitrate and dissolved organic nitrogen, respectively. Total nitrogen inputs, including dry deposition, are estimated to be 180 mmol N m^{-2} yr^{-1} (D. Bojanic & D. Fowler, pers. comm.).

As part of the NITREX experiments, weekly additions of NH_4 NO_3 solution have been applied as a spray to the forest floor at the rate of 250 mmol N m^{-2} yr^{-1} on 15 m by 15 m replicated plots. Concentrated nitrogen solutions are mixed with deionized water prior to application. A water-only treatment is included in the experimental design to enable water and nitrogen effects to be identified. Treatment began in October 1990 and continued for five years. Measurements included soil chemistry, biological processes, and tree growth and nutrient status (Emmett et al. 1995a,b). Soil solution samples were collected fortnightly using porous ceramic cup or zero-tension lysimeters at three soil depths. Collections were composited and to provide a single sample every four weeks. Monthly water fluxes (computed using the SOIL model; Jansson 1991) were combined with the chemistry of the soil solution collected below the main rooting zone (50 cm depth) to compute solute fluxes. Outputs from the system are defined as the fluxes through the soil at 50 cm depth. Fluxes of N_2O were recorded weekly in 1994 using sequential gas samples taken from static chambers in the control and nitrogen addition plots (Emmett et al. 1995c).

4. Data sources for the model application

4.1 *The moorland in 1960*

Carbon and nitrogen pools and fluxes in the moorland ecosystem prior to afforestation in 1960 were estimated using measurements made at an adjacent unforested site at Aber together with values reported for similar moorland ecosystems in the UK (Figure 1). It was assumed that present day moorland observations would suffice for estimates of moorland attributes in 1960. There are, however, several sources of uncertainty in this assumption: (i) the management history of grazing is poorly known; (ii) the increased nitrogen deposition over the period 1960–1990 may have resulted in increased primary productivity and increased nitrogen export; and (iii) the sampling location for moorland biomass determinations has a different slope and aspect relative to the spruce stand. Nonetheless, current moorland observations were used as 1960 calibration data for the application of the model.

Total above- and below-ground vegetation in the moorland was sampled in 1993/94 on three separate occasions to determine above- and below-ground biomass. Small intact turves were removed from the moorland adjacent to the forest. All above-ground vegetation was clipped and dry weight was determined. Roots were removed from a subsample using a wet sieving technique and their dry weight determined. Vegetation biomass was highly variable both within and between sampling occasions due to the influence

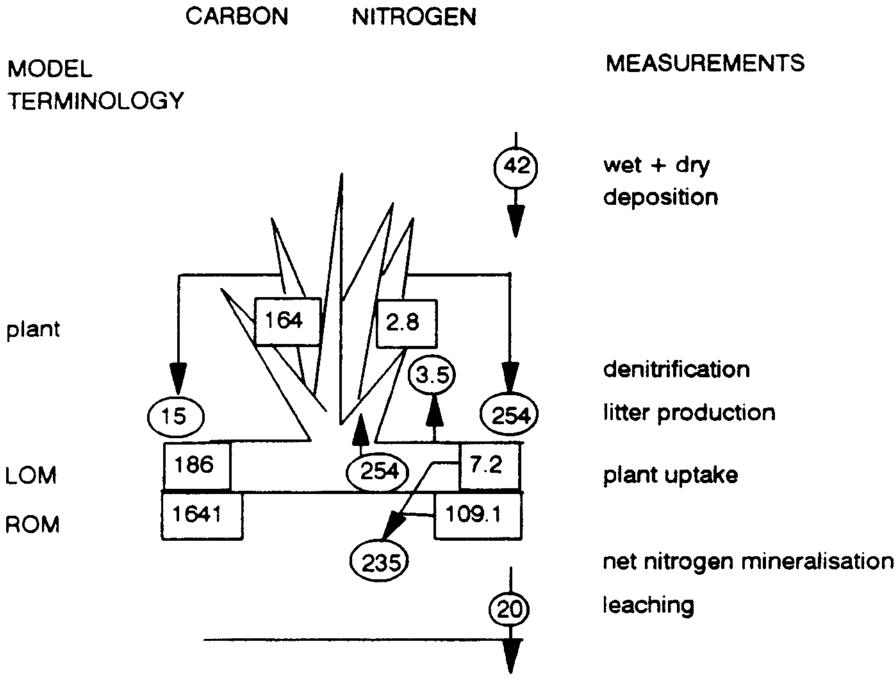

Figure 1. Estimated pools and fluxes of carbon and nitrogen in moorland at Aber. Pools are shown in boxes with carbon on the left and nitrogen on the right (units: mol m^{-2}); fluxes are shown in ovals with carbon on the left (units: mol m^{-2} yr^{-1}) and nitrogen on the right (units: mmol m^{-2} yr^{-1}).

of local topography, altitude and season. Nitrogen content was determined on vegetation samples collected in spring 1994 and was used to represent maximum nitrogen pools. Mean nitrogen content was 1.1% and 0.9% in above- and below-ground vegetation, respectively. Assuming 50% carbon in biomass, carbon and nitrogen pools (including standing dead) ranged from 35 to 400 mol C m^{-2} and from 0.7 to 6.8 mol N m^{-2}. Mean values of 164 mol C m^{-2} and 2.8 mol N m^{-2}were used to represent moorland vegetation biomass in 1960 for the modelling effort. These values are somewhat higher than reported for upland pastures of the UK (Batey 1982).

Total annual production was estimated to be 360 g m^{-2} yr^{-1} (15 mol C m^{-2} yr^{-1}) using a ratio of production to above-ground biomass of 0.7. Reported ratios are in the range 0.7 to 4.0. (Heal & Perkins 1978) with low ratios observed under light or no grazing pressure such as is the case at Aber. This level of annual production is within the 120–363 g m^{-2} yr^{-1} range for upland pasture and montane moorland reported by Batey (1982) and by Harrison et al. (1994). The moorland was assumed to be in steady state prior to 1960 for the model application so the total annual production estimate corresponds to litter production in Figure 1.

The organic horizon in the moorland was sampled and found to be approximately twice the size of the old organic horizon currently observed below the forest floor in the plantation stand. This organic horizon in the moorland will correspond to the LOM compartment in the model for the moorland (Figure 1). The bulk soil organic pool under the moorland (corresponding to the ROM compartment in the model for the moorland, Figure 1) was assumed to be the same as that currently observed under the forest. A major unknown in most applications of the model will be the long-term build-up or decline of carbon and nitrogen in the ROM compartment.

Nitrogen losses in runoff from moorland catchments are about 20 mmol N m^{-2} yr^{-1} (Emmett et al. 1993). Denitrification was assumed to be 3.5 mmol N m^{-2} yr^{-1} (Batey 1982).

4.2 *The Sitka spruce stand in 1990*

Tree biomass at Aber was determined using a combination of destructive sampling of trees, regressions of biomass on basal area and production forestry yield class tables. Five trees representing the range of tree sizes (141–769 cm^2) were removed from the experimental area. Carbon and nitrogen in above-ground biomass on an areal basis were estimated by linear regressions of total amount in ‘crown’ and ‘bole’ components on basal area recorded in the experimental plots. Carbon pools in the structural and active above-ground biomass were estimated to be 898 and 244 mol C m^{-2}, respectively. Corresponding nitrogen pools were 1.53 and 3.52 mol N m^{-2}. Structural root biomass and nitrogen and carbon content was not measured at the Aber site. Roots have been observed to represent 15–30% of total biomass in Sitka spruce stands and approximately 10% of the total-nitrogen pool (Carey & O’Brien 1979; Heal & Perkins 1978). Assuming roots represented 15% of total biomass at Aber, total root biomass was estimated as 48 tonnes ha^{-1} (202 mol C m^{-2}). Sampling of roots less than 5 mm, defined here as the non-structural or active roots, was carried out and 46.3 tonnes ha^{-1} (193 mol C m^{-2}, 345 mmol N m^{-2}) were defined as ‘structural roots’ and 2.2 tonnes (9 mol C m^{-2}, 157 mmol N m^{-2}) as ‘fine’ roots. Together these data are used to estimate carbon pools in active and structural plant biomass in 1990 (Figure 2).

Temporal changes in tree biomass during stand maturation during the period from 1960 to 1990 was calculated assuming that the proportion of crown to total above-ground tree weight declined from 50% to 15% as the stand matured (Miller & Miller 1993). The crown represented 21% of total above-ground biomass in the Aber stand in 1990 which is similar to the

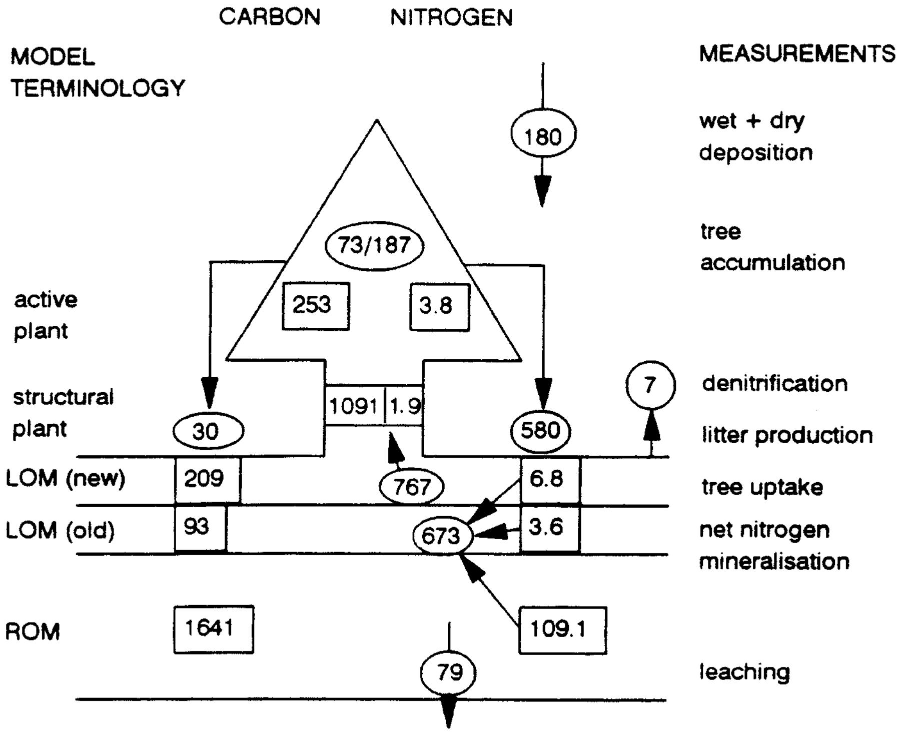

Figure 2. Measured pools and fluxes of carbon and nitrogen in the 30-year old Sitka spruce stand at Aber. Pools are shown in boxes with carbon on the left and nitrogen on the right (units: mol m^{-2}); fluxes are shown in ovals with carbon on the left (units: mol m^{-2} yr^{-1}) and nitrogen on the right (units: mmol m^{-2} yr^{-1}).

proportion reported by both Miller & Miller (1993) and Anderson (1984) for stands of approximately 30 years of age. The contribution of roots to total biomass probably changes as a stand develops, but no information is available about this effect. A constant proportion of total biomass for all ages is thus assumed, both for total root biomass and for the proportion of total root biomass present as structural or active roots.

Mean annual above-ground litter production in the Aber stand during the 3-year period from 1990 to 1995 was 21 mol C m^{-2} yr^{-1} (Emmett et al. 1995b; Gundersen et al. in press). Changes in litter production since planting in 1960 to the present-day (Figure 3) were assumed to be similar to those recorded across an age sequence of Sitka spruce stands in 1990/91 (P. Stevens unpublished data). Maximum litter production was observed in 15 to 25-year-old stands presumably as a result of canopy closure. Below-ground litter production was assumed to be 100% turnover of all ‘active’ roots for

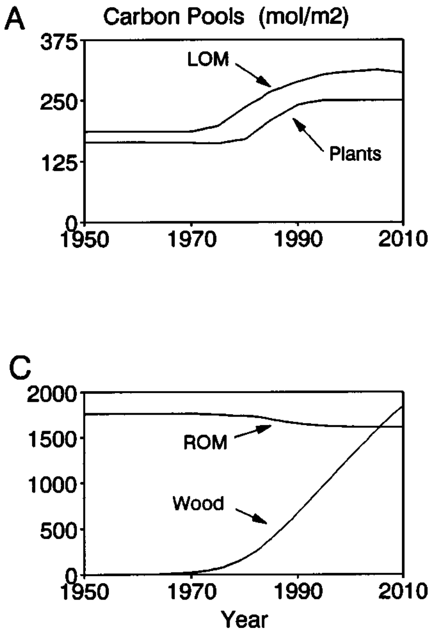

Figure 3. Carbon pools and fluxes at Aber, inferred for the period 1950–2010 from measurements at moorland and forested sites at Aber and the chronosequence of Sitka spruce stands in Wales (Emmett et al. 1993; P. Stevens unpublished data). A) Carbon pools in active plant biomass and labile organic matter (LOM). B) Carbon fluxes in net primary production (NPP) and litterfall. C) Carbon pools in refractory organic matter (ROM) and inactive biomass (wood). D) Carbon fluxes as decomposition of labile organic matter (Dcmp LOM), decay of labile organic matter (Dcy LOM), and decomposition of refractory organic matter (Dcmp ROM).

all stand ages (Emmett et al. 1995b). In 1990, fine root biomass was 9 mol C m^{-2}, resulting in total litter production of 30 mol C m^{-2} yr^{-1}.

Present-day soil carbon and nitrogen pools within the main rooting zone have been determined from extensive soil sampling within the experimental plots. Some mixing of old organic and upper mineral soil occurred during ploughing but has been ignored here. Labile organic matter (the LOM compartment in the model) was defined as the forest floor horizon plus old organic material in unploughed areas. Refractory organic matter (the ROM compartment) was defined as the organic content of the mineral soil to a total soil depth of 60 cm. The accumulation of the forest floor horizon following afforestation (Figure 3) is assumed to be similar to that observed in the chronosequence of present-day stands (Emmett et al. 1993). The large increase in forest floor biomass observed between the ages of 10–25 years is possibly due to large inputs of litter during canopy closure.

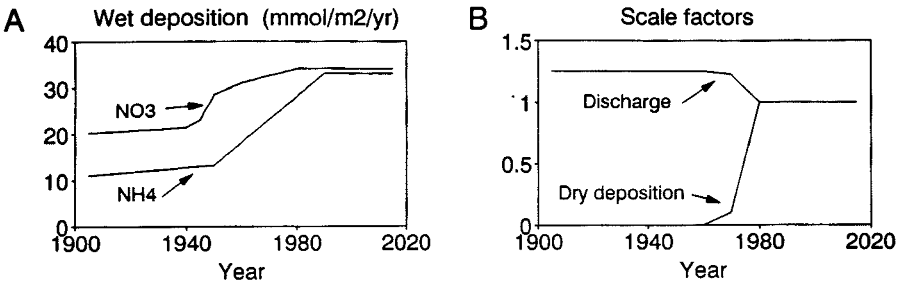

Figure 4. Nitrogen deposition and hydrologic discharge at Aber. A) Wet deposition of NH_4 and NO_3 measured in 1990 (Emmett et al. 1995a) and estimated from emissions trends for the UK (UKRGAR 1990). Future deposition is assumed to remain constant. B) Dry deposition and discharge factors relative to 1990 values. Growth of the forest increases dry deposition and evapotranspiration.

Annual net nitrogen mineralization and nitrification rates in forest floor material (LOM) were estimated from monthly field incubations of undisturbed forest floor material in 1992/93 (Emmett et al. 1995b). In addition, laboratory incubations of samples of all soil horizons were carried out over a 4–8 week period in all years to determine the relative potential contribution of organic and lower soil horizons to mineralization on an area basis. On average, the forest floor contributed approximately 60% of net mineralization and 18% of net nitrification (Emmett et al. 1995b)

4.3 *Nitrogen inputs and export*

Current wet and dry deposition of nitrogen from the atmosphere and inorganic nitrogen in soil water drainage were estimated from measurements in moorland and forest (Emmett et al. 1993; Emmett et al. in press; D. Bojanic unpublished data). Historical trends in atmospheric deposition of nitrogen used to drive the model (Figure 4) were calculated using estimates of historical emissions of NO_x and NH_4 (UKRGAR 1990; Pitcairn et al. 1995). The growth of the forest was assumed to increase dry deposition due to increased canopy filtering processes and to increase evapotranspiration (decrease runoff) through increased water use (Figure 4).

5. Response to nitrogen treatments

Effects of nitrogen treatments have been assessed from nutrient contents of current year foliage, wood accumulation rates, litterfall carbon and nitrogen fluxes and leaf area index measurements. No significant effects of the nitrogen treatments have been detected for any of these parameters with the exception of an increase in %N in current year foliage in year 4 of the treatments (Emmett et al. 1995b; Gundersen et al. in press). No significant effects of the nitrogen treatments on net nitrogen mineralization or nitrification rates has been recorded at any soil depth (Emmett et al. 1995b; Gundersen et al. in press). During the 5-years (1990–95) of experimental nitrogen addition at Aber, mean export of NO_3 in the control (ambient) treatment plot was approximately 98 mmol N m^{-2} yr^{-1} (Emmett et al. in press). Mean losses from the treatment plots during the same period were 172 mmol N m^{-2} yr^{-1}. Annual leaching losses were highly variable between years depending on climatic conditions. Leaching losses and ^{15}N studies indicated that ambient and applied nitrate was leached through the soil profile resulting in a 1:1 relationship between nitrate inputs and leaching losses. In contrast, ammonium inputs were retained in the soil and did not contribute to leaching losses from below the rooting zone (Emmett et al. in press; Tietema et al. in press). Denitrification losses have been calculated from weekly measurements as about 7 mmol N m^{-2} yr^{-1} and 14 mmol N m^{-2} yr^{-1} in the control and nitrogen treated plots, respectively (Emmett et al. 1995c; Gundersen et al. in press).

6. Calibration procedure

MERLIN was calibrated to Aber to reproduce estimated and observed characteristics for both the moorland in 1960 and the thirty year old forest in 1990. Calibration was a trial-and-error procedure in which the model was run using the assumed carbon dynamics (Figure 3) and atmospheric deposition history (Figure 4) to produce simulated values of carbon and nitrogen pools and fluxes. These simulated values were compared to the observed or estimated values for the steady state moorland (Figure 1) and the 30 year old spruce stand (Figure 2). The nitrogen uptake parameters in the model were adjusted after each simulation until the simulated ecosystems maintained the observed or inferred C:N ratios in all compartments and the simulated soil losses of inorganic nitrogen also matched those observed for both the steady state moorland (until 1960) and the forest subsequent to planting. The definitions of the adjustable uptake parameters used for calibration and explanations of their actions within the model are given by Cosby et al. (1997).

The calibrated model was then used: 1) to simulate a further 21 years (1995–2015) into the future to simulate growth and maturation of the stand to an age of 55 years; and 2) to predict the response of the 30 year old forest to the four years of experimental NH_4 NO_3 addition (1990–1995). The predictions of responses as the unmanipulated forest ages from 30 to 55 years were compared to data from the chronosequence of Sitka spruce stands in the region. The predictions of responses to five years of nitrogen addition were compared to the results of the NITREX experimental manipulations at the site. Both comparisons provide tests of the model predictions using independent data (model "verifications").

7. Results and discussion

7.1 *Grassland simulation*

During the grazed moorland period 1905–1960 the ecosystem was assumed to be in steady-state, with no change in carbon pools and little or no loss of nitrogen to drainage water. Calibration of the model within these constraints, results in accumulation of increasing nitrogen deposition in the soil ROM, with a minor fraction being lost in leaching and to the atmosphere by denitrification (Figure 5). Soil ROM accumulates nitrogen at a rate of about 23 mmol m^{-2} yr^{-1}, which is somewhat higher than the average rate of nitrogen immobilization of 15 mmol m^{-2} yr^{-1} since glaciation (11500 yr.) as calculated from total nitrogen in the soil profile in 1990 (Emmett & Reynolds 1996a).

7.2 *Simulation of forest maturation (1960–1990)*

A change in uptake functions for the grassland and forest was found to be necessary to match observed changes in nitrogen pools and fluxes. This illustrates a major change in the biological functioning in the two systems. The relative sensitivity of plant uptake to changes in internal and external C:N ratios have changed presumably in response to the different life strategies. Below ground changes in the relationship between C:N ratios and uptake and release of nitrogen in the LOM and ROM probably reflect changes in the microbial and invertebrate community and in particular an increase in the importance of lignin-decomposers.

During the period 1961–1990 of forest planting and growth, the chronosequence data indicated a net accumulation of carbon in the ecosystem, both as wood and new LOM (Figure 3). However, the mass-balance constraints provided by MERLIN indicated a decrease in the carbon and thus nitrogen pool in the ROM was necessary to grow the forest (4700 mmol N m^{-2}) and the LOM (2950 mmol N m^{-2}). Atmospheric deposition of nitrogen (3250 mmol N m^{-2}) was insufficient to account for these two nitrogen pools (Table 2). Nitrogen must have been "mined" from ROM and transferred into tree biomass and then to the forest floor (Figure 5). Calibration of the model thus involved a reducing ROM carbon pools and adjusting uptake parameters to

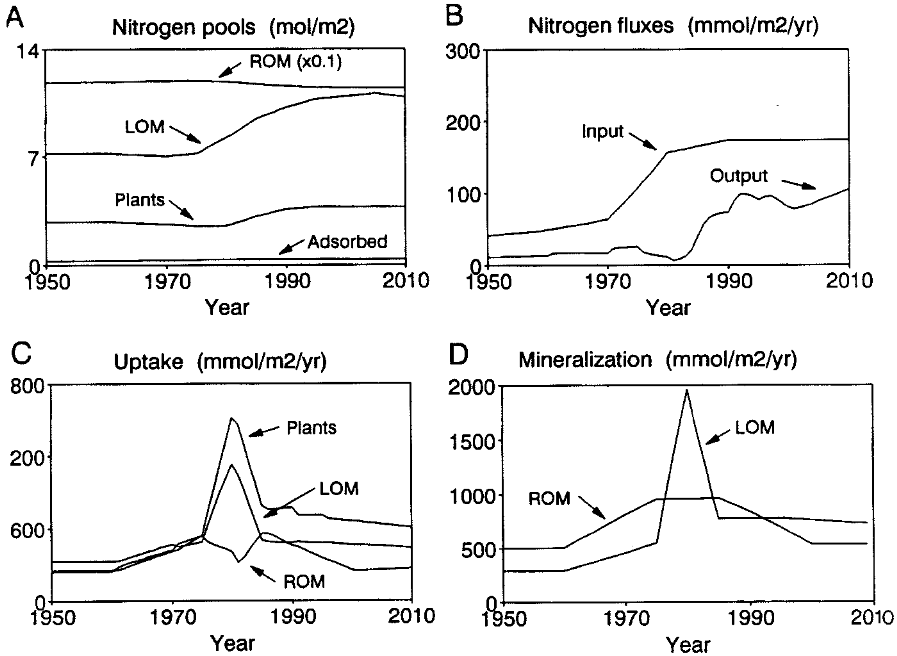

Figure 5. Simulated nitrogen pools and fluxes at Aber. A) Nitrogen pools in active plant biomass, labile organic matter (LOM), refractory organic matter (ROM) and adsorbed on the soil matrix. B) Nitrogen fluxes in atmospheric deposition and soil leachate. C) Uptake and immobilization by plants and soil microorganisms in LOM and ROM. D) Gross mineralization in LOM and ROM.

provide sufficient nitrogen to grow the forest. The redistribution of nitrogen within the ecosystem thus included a large build-up of forest floor and transfer of nitrogen through the trees to upper soil horizons from the lower ROM. The calibration procedure resulted in reproduction of this historical mining of the ROM by setting changes in ROM carbon pools in combination with the forest uptake functions for nitrogen.

Nitrogen in the LOM or forest floor pool continued to accumulate in parallel with carbon due to litter inputs until 2005. This pool became a major source of available nitrogen due to mineralization of the forest floor material. Net mineralization was divided equally between the LOM and ROM pools in 1990 in contrast to 1960 when grassland LOM was a net sink for nitrogen (Table 3). The equal split between the LOM and ROM pools as sources of available nitrogen (Table 3) has been confirmed in field and laboratory studies of nitrogen mineralization rates using forest floor material and soil from lower mineral horizons (Emmett et al. 1995b). The peak in litterfall in about 1980 necessitates concurrent pulses of decomposition (Figure 3)

Table 2. Simulated nitrogen pools and budgets for the periods of pre-afforestation (1905–1960), during stand maturation (1961–1990) and for the mature stand (1991–2015). Units: mmol N m^{-2}.

Pool	Year			
	1905	1960	1990	2015
Plant biomass, active	2800	2800	3600	3700
Plant biomass, structural	0	0	1100	3600
LOM	7200	7200	10160	10120
ROM	117000	118250	115700	114850
Adsorbed	280	280	330	330
Soil solution	5	5	45	55
Change in pools and cumulative fluxes	1905–1959	1960–1989	1990–2015	
Plant biomass, active	0	+800	−100	
Plant biomass, structural	0	+1100	+2500	
LOM	0	+2960	−40	
ROM	+1250	−2550	−850	
Adsorbed	0	+50	0	
Soil solution	0	+40	+10	
Total net gain (+) or loss (−)	+1250	+2400	−1720	
Deposition inputs	2000	3250	4350	
Leaching losses	550	700	2380	
Denitrification	200	150	250	
Net flux	+1250	+2400	−1720	

and nitrogen mineralization indicating a large change in carbon and nitrogen dynamics at canopy closure (Figure 5). A mineralization study across the chronosequence of stands confirms 2–4 fold greater net mineralization in forest floor material on an area basis relative to most older stands (Emmett et al. 1993).

The increase in denitrification rates to 7mmol N m^{-2} yr^{-1} in 1990, as recorded in field measurements, is presumably in response to the increased availability of nitrogen in the system and is an input variable to the model. MERLIN simulated an additional increase in adsorbed NH_4 and higher concentrations of nitrogen in soil solution in response to this increase in nitrogen deposition.

During the next 25-year period 1991–2015 an increase in nitrogen output was simulated (Figure 5). This is in agreement with the observed increased loss of nitrogen to streamwater in older forest stands in Wales (Stevens et al. 1994) and indicates that mature Sitka spruce stands in Wales are generally not nitrogen limited. The results from the experimental nitrogen addition at

Table 3. Comparison of observed and predicted nitrogen concentrations in soil solution (mmol m^{-3}), C:N ratios in the plant, LOM and ROM pools and gross and net mineralization fluxes (mmol N m^{-2} yr^{-1}) in the 2 soil pools. Observed values are measured 1990 and 1995 values for Aber in control (cont.) and NH_4NO_3 treatment (treat.) plots. Inferred values for moorland in 1960 using present day values are also presented.

Fluxes	1960		1990		1995		1995		2015	
					Cont.		Treat.		Cont.	Treat.
	Obs.	Pred.	Obs.	Pred.	Obs.	Pred.	Obs.	Pred.	Pred.	Pred.
NO_3 conc	10–20	18	95	113	68	150	210	511	196	543
C:N plant	59	59	67	67	67	67	66	67	67	67
C:N LOM	26	26	29	28	27	28	27	28	28	28
C:N ROM	15	15	15	14	15	14	15	14	14	14
LOM gross min.	na	290	na	780	na	780	na	780	780	780
LOM immob.	na	330	na	480	na	480	na	490	420	420
LOM net min.	na	−40	490[1]	300	490[3]	300	490[3]	290	290	290
ROM gross min.	na	510	na	840	na	690	na	790	530	530
ROM immob.	na	550	na	460	na	350	na	470	280	300
ROM net min.	na	260	300[2]	380	300[3]	340	300[3]	320	250	230

na – no data available
[1] results from field incubations for forest floor material (LOM) in control plots in 1992/93 (Emmett et al. 1995b)
[2] inferred from a comparison of mineralisation rates in LOM and mineral soil (ROM) material in laboratory incubations (Emmett et al. 1995b)
[3] indicates no treatment effect on mineralization rates in laboratory incubations of LOM or ROM material. No fields data available (Gundersen et al., in press).

Aber also indicate that such stands of Sitka spruce are at least 'NO_3 saturated' (Emmett et al. 1996b). The nitrogen loss in these mature stands is due to (i) continued large inputs of nitrogen, (ii) switch to wood production which has low nitrogen concentration (high C:N ratio) rather than high-nitrogen canopy production (iii) mineralization of the LOM, and (iv) an assumed increase in denitrification to 14 mmol m^{-2} yr^{-1}.

7.3 *Simulation of nitrogen additions*

The nitrogen-addition treatment provided an independent test of the model. Model input is adjusted to account for the nitrogen addition, and run without further modification to uptake parameters or mining rates of the ROM pool.

A comparison between observed and predicted in nitrogen concentrations and C:N ratios of various pools and changes in nitrogen fluxes is presented in Table 3. A summary of the fate of applied nitrogen as simulated by MERLIN is presented in Table 4 as the difference in pool sizes or fluxes relative to the control plots.

Table 4. The fate of applied nitrogen as predicted by MERLIN expressed as the change (mmol N m^{-2}) in various nitrogen pools and fluxes in nitrogen-treated plots relative to controls. Values in parentheses are changes expressed as a percentage of applied fertilizer nitrogen.

	1991–1995	1996–2015
Pools		
Plant	+9 (<1%)	−1
LOM	+57 (5%)	−8
ROM	+247 (20%)	+716 (14%)
Adsorption + soil soln	+96 (8%)	+8 (<1%)
Losses		
Denitrification	+8 (<1%)	+268 (5%)
Leaching	+828 (66%)	+4016 (80%)

Most of the applied nitrogen is leached, as observed experimentally in the period 1990–1995 (Figure 6), with an increasing proportion leached as nitrogen applications continue (Table 4). The remaining nitrogen increases the LOM and ROM nitrogen pools relative to the controls although the relative importance of the LOM pool decreases with time (Table 4). This agrees with data from a ^{15}N study which indicates that the ammonium component of the nitrogen applied is retained in the forest floor and mineral soil (Tietema et al. in press). No immediate increase in net nitrogen mineralization of nitrogen in the LOM pool is predicted which agrees with observed measurements (Table 3). In the ROM pool, a decline of 6% in net nitrogen mineralization is predicted coinciding with immobilization of incoming ammonium-nitrogen identified from leachate fluxes. Incubation studies are not sufficiently sensitive to allow such small changes to be identified. In the long term, MERLIN predicts that the experimentally increased nitrogen deposition will result in increased mobilization of nitrogen from the LOM pool between 1995–2015, although only a very small amount (8 mmol N m^{-2} or 0.4 mmol N m^{-2} yr^{-1}) and less than that originally immobilized between 1990–1995 (Table 4). The increase in the ROM nitrogen pool in the treatment plots relative to the control plots reflects retention of applied and deposited nitrogen as described above (Table 4). The predicted plant sink of applied nitrogen was small, as observed, representing only 1% of inputs between 1990–1995. Experimentally, a transient 0.1% increase in foliar nitrogen in Year 4 and no change in wood accumulation rates or litterfall nitrogen flux was observed (Gundersen et al. in press). MERLIN predicts the relative importance of this sink to decline with time. The adsorption pool represented 8% in 1991–1994 with the remaining <1% in soil solution (Table 4).

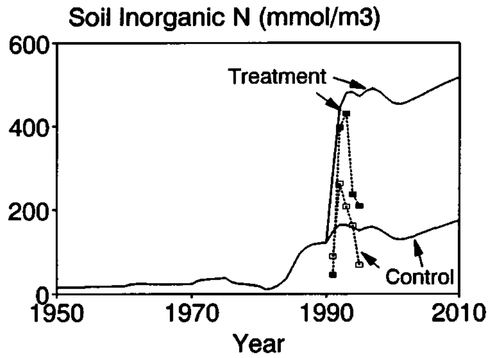

Figure 6. Measured and simulated annual mean nigrogen concentrations in soil solution at 50cm depth at Aber in the untreated control plots and the $NH_4M)_3$ treated plots. The solid lines are model simulations, the symbols are experimental observations; control (□) and NH_4NO_3 (■).

7.4 *Model evaluation*

The success of the MERLIN calibration was judged primarily on the ability of the model to correctly simulate: 1) the C:N ratios in the 3 pools (plants, LOM and ROM); and 2) the flux of nitrogen in runoff. In addition, the rate of mineralization in the soil should also be correctly simulated, although because mineralization is difficult to measure, this criterion is less critical. MERLIN satisfactorily satisfies all these criteria for all 3 times (1960, 1990, 1994) (Table 3). Furthermore the transition between ecosystem types (1960 moorland to 1990 forest) proceeds in a smooth and regular fashion (Figures 3 & 5) and follows the observed pattern of nitrogen leaching across an age sequence of stands (Stevens et al. 1994).

As a successful simulation was achieved without changes in uptake parameters or the rate of mining from the ROM pool, biological changes due to nitrogen additions after four years appeared to be small relative to that observed following afforestation. Thus MERLIN may be used for predictive purposes as long as there is no perturbation or major biological change which would be expected to cause a large change in; (i) the relationship between uptake by the plants and soil and their C:N ratios or (ii) the dynamics of the large ROM pool. MERLIN's predictive capacity may be improved in such conditions if previously described functions can be re-used or generalized functions become available. This is one of the major aims of future applications of MERLIN at the other NITREX sites in Denmark, Norway, Sweden, the Netherlands.

8. Conclusions

This application of the MERLIN model to Aber demonstrates that the model provides a useful tool by which the diverse and disparate data at a site with a complex site history are placed into a consistent framework constrained by mass-balance considerations. Internal consistency of data from a given site can thus be systematically checked and historical changes such as changes in the dynamics of the ROM pool or uptake functions inferred.

MERLIN focuses on simulation and prediction of nitrogen concentrations in soil leachate and runoff. Many other models of nitrogen cycling in terrestrial ecosystems traditionally focus on the internal nitrogen cycling and treat soil leachate simply as a "remainder". Nitrogen in soil leachate is of central interest with respect to determination of nitrogen saturation, estimation of critical loads for nitrogen, and evaluation of effects on aquatic and coastal marine ecosystems. The robustness of MERLIN should be now be evaluated by application to other sites, to whole regions using Monte-Carlo techniques, and by systematic tests of the sensitivity of various key parameters.

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