Ecological Controls on N₂O Emission in Surface Litter and Near-surface Soil of a Managed Grassland: Modelling and Measurements

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ABSTRACT

Large variability in N₂O emissions from managed grasslands may occur because most emissions originate in surface litter or near-surface soil where variability in soil water content (θ) and temperature (Tₛ) is greatest. To determine whether temporal variability in θ and Tₛ of surface litter and near-surface soil could explain that in N₂O emissions, a simulation experiment was conducted with ecosys, a comprehensive mathematical model of terrestrial ecosystems in which processes governing N₂O emissions were represented at high temporal and spatial resolution. Model performance was verified by comparing N₂O emissions, CO₂ and energy exchange, and θ and Tₛ modelled by ecosys with those measured by automated chambers, eddy covariance (EC) and soil sensors at an hourly time-scale during several emission events from 2004 to 2009 in an intensively managed pasture at Oensingen, Switzerland. Both modelled and measured events were induced by precipitation following harvesting and subsequent fertilizing or manuring. These events were brief (2 – 5 days) with maximum N₂O effluxes that varied from < 1 mg N m⁻² h⁻¹ in early spring and autumn to > 3 mg N m⁻² h⁻¹ in summer. Only very small emissions were modelled or measured outside these events. In the model, emissions were generated almost entirely in surface litter or near-surface (0 – 2 cm) soil, at rates driven by N availability with fertilization vs. N uptake with grassland regrowth, and by O₂ supply controlled by litter and soil wetting relative to O₂ demand from microbial respiration. In the model, NOₓ availability relative to O₂ limitation governed both the reduction of more oxidized electron acceptors to N₂O and the reduction of N₂O to N₂, so that the magnitude of N₂O emissions was not simply related to surface and
Modelled N$_2$O emissions were found to be sensitive to defoliation intensity and timing which controlled plant N uptake and soil $\theta$ and $T_s$ prior to and during emission events. Reducing LAI remaining after defoliation to one-half that under current practice and delaying harvesting by 5 days raised modelled N$_2$O emissions by as much as 80% during subsequent events and by an average of 43% annually. Modelled N$_2$O emissions were also found to be sensitive to surface soil properties. Increasing near-surface bulk density by 10% raised N$_2$O emissions by as much as 100% during emission events and by an average of 23% annually. Relatively small spatial variation in management practices and soil surface properties could therefore cause the large spatial variation in N$_2$O emissions commonly found in field studies. The global warming potential from annual N$_2$O emissions in this intensively managed grassland largely offset those from net C uptake in both modelled and field experiments. However model results indicated that this offset could be adversely affected by suboptimal land management and soil properties.

### INTRODUCTION

The contribution of managed grasslands to reducing atmospheric greenhouse gas (GHG) concentrations through net uptake of CO$_2$ (Ammann et al., 2005) may be at least partially offset by net emissions of N$_2$O (Conant et al., 2005, Fléchard et al., 2005). These emissions may be substantial, with N$_2$O emission factors of as large as 3% measured in intensively managed grasslands with fertilizer rates of 25 - 30 g N m$^{-2}$ y$^{-1}$ (Imer et al., 2013; Rafique et al., 2011). These emissions are highly variable temporally and spatially because they are determined by complex interactions among short-term weather events (warming, precipitation), land management practices (N amendments, defoliation), and soil properties (e.g. bulk density, water retention). The N$_2$O driving these emissions in managed grasslands is thought to be generated within the upper 2 cm of the soil profile (van der Weerden et al., 2013) and in surface litter left by grazing or harvesting (Pal et al., 2013) so that diurnal heating and precipitation events that cause rapid warming and wetting of the litter and soil surface may cause large but brief emission events. These events are thought to be driven by increased demand for electron acceptors by nitrification and denitrification, and reduced supply of O$_2$ by which these demands are preferentially met, and therefore increased demand for alternative acceptors NO$_3^-$, NO$_2^-$ and N$_2$O by autotrophic nitrifiers and heterotrophic denitrifiers.
The magnitude of N$_2$O emission events in managed grasslands generally increases with the amount of N added as urine, manure or fertilizer, and with the intensity of defoliation by grazing or cutting (Ruzjerez et al. 1994). Thus Imer et al. (2013) found a negative correlation between LAI and N$_2$O emissions at intensively managed grasslands in Switzerland. The increase in emissions with defoliation has been attributed to increased urine and manure deposition and soil compaction with defoliation by grazing, and to slower uptake of N and water by slower-growing plants with defoliation by harvesting (Jackson et al., 2015). Both N additions and defoliation are thought to raise these emissions by increasing the supply of NH$_4^+$ and NO$_3^-$ to autotrophic nitrifiers and heterotrophic denitrifiers. This increase raises the demand for alternative e$^{-}$ acceptors by these microbial populations if the supply of O$_2$, the preferred e- acceptor, fails to meet demand, as may occur when soil water content ($\theta$) after defoliation rises with precipitation or reduced transpiration. This supply is governed by physical and hydrological properties (porosity, water retention) of the near-surface soil. Consequently land use practices and soil properties must be considered when estimating N$_2$O emissions from managed grasslands.

Recognition of the effects of precipitation events, N amendments and soil properties on N$_2$O emissions has led to empirical models in which annual emission inventories are calculated directly from annual precipitation and N inputs (Lu et al., 2006), or monthly emission events are calculated from monthly precipitation, air temperature $T_a$, and $\theta$ (Fléchard et al., 2007). However the soil depth at which most emitted N$_2$O is generated (0 – 2 cm) is much shallower than that at which $\theta$ used in these models is measured (5 – 10 cm) (Fléchard et al., 2007), and the soil temperature $T_s$ at this depth may differ from $T_a$. This is particularly so for grasslands in which N additions are necessarily left on the soil surface without incorporation. Thus large N$_2$O emissions may be caused by surface wetting from precipitation on dry soils following fertilizer application, so that deeper $\theta$ is sometimes found to be of little explanatory value in empirical models (Fléchard et al., 2007). Furthermore the response of denitrification to $\theta$ has been found in experimental studies to rise sharply with $T_s$, likely through the combined effects of $T_s$ on increasing demand and reducing supply of O$_2$ at microbial microsites (Craswell, 1978). The interaction between $T_s$ and $\theta$ on N$_2$O emissions is clearly apparent in the meta-analysis of N$_2$O emissions from European grasslands by Fléchard et al. (2007). This interaction has been represented in empirical models by fitting interdependent threshold values of $T_s$ and $\theta$ above which emissions have been measured in field experiments (Smith and Massheder, 2014). However a more robust simulation of this interaction on
N₂O emissions should be built from basic biological and physical processes that are independent of site-specific measurements.

Process models used to simulate N₂O emissions from managed grasslands must therefore explicitly represent the effects of short-term weather events on near-surface \( T_s \) and \( \theta \) as well as the effects of N additions and defoliation on near-surface \( \text{NH}_4^+ \) and \( \text{NO}_3^- \). These models must also explicitly represent the effects of mineral N, \( T_s \) and \( \theta \), and of soil physical and hydrological properties, on the demand for vs. supply of O₂ and alternative e⁻ acceptors \( \text{NO}_3^- \), \( \text{NO}_2^- \) and N₂O, and on the oxidation-reduction reactions by which these e⁻ acceptors are reduced. However earlier process models have usually simulated N₂O emissions as \( T_s \) -dependent functions of nitrification and denitrification rates, modified by texture-dependent functions of water-filled pore space (WFPS) (e.g. Li et al., 2005). In some models additional empirical functions of \( T_s \) (Chatskikh et al., 2005), or of \( T_s \) and WFPS (Schmid et al., 2001), are used to calculate the fraction of nitrification that generates N₂O, and the fraction of heterotrophic respiration \( R_h \) that drives denitrification (Schmid et al., 2001), thereby avoiding the explicit simulation of O₂ and its control on N₂O emissions. A more detailed summary of functions of mineral N, \( T_s \) and WFPS currently used to model N₂O emissions is given in Fang et al. (2015).

These functions have many model-dependent parameters and function independently of each other, so that key interactions among reduced C and N substrates, \( T_s \) and \( \theta \) on N₂O production may not be simulated. In none of these approaches are the oxidation-reduction reactions by which N₂O is generated or consumed explicitly represented. Furthermore the effects of defoliation and surface litter on N₂O emissions have not been considered in earlier process models.

Process models used to simulate N₂O emissions must also accurately represent the key processes of C cycling that drive those of N cycling from which N₂O is generated and consumed. These include gross and net primary productivity (GPP and NPP) which drive mineral N uptake and assimilation with plant growth. GPP and consequent plant growth also drive autotrophic respiration \( (R_a) \), the below-ground component of which contributes to soil O₂ demand. NPP drives litterfall and root exudation, which in turn drive heterotrophic respiration \( (R_h) \) that also contributes to litter and soil O₂ demand, and thereby to demand for alternative e⁻ acceptors which drive N₂O generation. Heterotrophic respiration also drives key N transformations such as mineralization/immobilization, thereby controlling availability of these alternative e⁻ acceptors. Land use practices such as defoliation from grazing or harvesting, and
soil properties such as porosity and water retention, alter these key C cycling processes, and thereby
N$_2$O emissions. Therefore these emissions are best simulated by comprehensive ecosystem models.

In the mathematical model *ecosys*, the effects of weather and N amendments on $T_s$, $\theta$, and
mineral N, and hence on the demand for vs. supply of O$_2$, NO$_3^-$, NO$_2^-$ and N$_2$O, and thereby on N$_2$O
emissions, are simulated by explicitly coupling the transport processes with the oxidation – reduction
reactions by which these e$^-$ acceptors are known to be generated, transported and consumed in soils
(Grant and Pattey, 1999, 2003, 2008; Grant et al., 2006; Metivier et al., 2009). The development of
model algorithms for these processes was guided by two key principles:

(1) all algorithms in the model must represent physical, biochemical and biological processes
studied in basic research programs (e.g. convective-diffusive transport, oxidation-reduction
reactions) so that these algorithms can be parameterized independently of the model

(2) this parameterization must be conducted at spatial and temporal scales smaller than those of
prediction (in this case seasonal N$_2$O fluxes) so that site-specific effects on predicted values are
not incorporated into the algorithms, limiting their robustness.

These principles are designed to avoid as much as possible the use of site- and model-specific
algorithms that may lack application in sites and models other than those for which they were
developed. Although models based on these principles appear complex, they can be better constrained
than simpler models because they are parameterized from independent experiments. The resulting detail
that application of these principles brings to the model enables better constrained tests of model output
against more comprehensive and diverse site data than are possible with simpler models.

In an extension of earlier work with *ecosys*, we propose that temporal and spatial variation in
N$_2$O emissions from an intensively managed grassland can be largely explained from the modelled
effects of N amendments (fertilizer, manure), plant management (e.g. harvest intensity and timing), soil
properties (e.g. bulk density) and weather ($T_s$, precipitation events) on the demand for vs. supply of O$_2$,
NO$_3^-$, NO$_2^-$ and N$_2$O in surface litter and near-surface soil (0 – 2 cm). Testing this explanation requires
frequent measurements to characterize the large temporal variation in N$_2$O emissions found in managed
ecosystems. Such measurements were recorded from 2004 to 2009 using automated chambers in
intensively managed grass-clover grassland at Oensingen, Switzerland, and used here to test our modelled explanation of these fluxes.

MODEL DEVELOPMENT

General Overview

The hypotheses for N$_2$O oxidation-reduction reactions and their coupling with gas transport in ecosys are represented in Fig. 1 and described further below with reference to equations and definitions listed in Appendices A, C, D, E, H of the Supplement (indicated by square brackets in the text below, e.g. [H1] refers to Eq. 1 in Appendix H), as well as in earlier papers (Grant and Pattey, 1999, 2003, 2008; Grant et al., 2006; Metivier et al., 2009). These hypotheses are part of a larger model of soil C, N and P transformations (Grant et al., 1993a,b), coupled to one of soil water, heat and solute transport in surface litter and soil layers, which are in turn components of the comprehensive ecosystem model ecosys (Grant, 2001).

Mineralization and Immobilization of Ammonium by All Microbial Populations

Heterotrophic microbial populations $m$ (obligately aerobic bacteria, obligately aerobic fungi, facultatively anaerobic denitrifiers, anaerobic fermenters, acetotrophic methanogens, and obligately aerobic and anaerobic non-symbiotic diazotrophs) are associated with each organic substrate $i$ ($i =$ animal manure, coarse woody plant residue, fine non-woody plant residue, particulate organic matter, or humus). Autotrophic microbial populations $n$ (aerobic NH$_4^+$ and NO$_2^-$ oxidizers, hydrogenotrophic methanogens and methanotrophs) are associated with inorganic substrates. These populations grow with energy generated from coupled oxidation of reduced dissolved C (DOC) by heterotrophs, or of mineral N (NH$_4^+$ and NO$_2^-$) by nitrifiers, and reduction of e- acceptors O$_2$ and NO$_x$. These populations decay according to first-order rate constants with provision for internal recycling of limiting nutrients (N, P). During growth, each functional component $j$ ($j =$ nonstructural, labile, resistant) of these populations seeks to maintain a set C:N ratio by mineralizing NH$_4^+$ ([H1a]) from, or by immobilizing NH$_4^+$ ([H1b]) or NO$_3^-$ ([H1c]) to, microbial nonstructural N. Nitrogen limitations during growth may cause C:N ratios to rise above set values, and greater recovery of microbial N from structural to nonstructural forms to
reduce N loss during decay, but at a cost to microbial function. These transformations control the exchange of N between organic and inorganic states, and hence affect the availability of alternative $e^-$ acceptors for nitrification and denitrification.

**Oxidation of DOC and Reduction of Oxygen by Heterotrophs**

Constraints on heterotrophic oxidation of DOC imposed by O$_2$ uptake are solved in four steps:

1) DOC oxidation under non-limiting O$_2$ is calculated from active biomass, DOC concentration, and an Arrhenius function of $T_s$ [H2],

2) O$_2$ reduction to H$_2$O under non-limiting O$_2$ (O$_2$ demand) is calculated from 1) using a set respiratory quotient [H3],

3) O$_2$ reduction to H$_2$O under ambient O$_2$ is calculated from radial O$_2$ diffusion through water films of thickness determined by soil water potential [H4a] coupled with active uptake at heterotroph surfaces driven by 2) [H4b]. O$_2$ diffusion and active uptake is calculated for each heterotrophic population associated with each organic substrate, allowing [H4] to calculate lower O$_2$ concentrations at microbial surfaces associated with more biologically active substrates (e.g. manure, litter). Localized zones of low O$_2$ concentration (hotspots) are thereby simulated when O$_2$ uptake by any aerobic population is constrained by O$_2$ diffusion to that population. O$_2$ uptake by each heterotrophic population also accounts for competition for O$_2$ uptake with other heterotrophs, nitrifiers, roots and mycorrhizae, calculated from its O$_2$ demand relative to those of other aerobic populations.

4) DOC oxidation to CO$_2$ under ambient O$_2$ is calculated from 2) and 3) [H5]. The energy yield of DOC oxidation drives the uptake of additional DOC for construction of microbial biomass $M_{i,h}$ according to construction energy costs of each heterotrophic population [A21]. Energy costs of denitrifiers are larger than those of obligately aerobic heterotrophs, placing denitrifiers at a competitive disadvantage for growth and hence DOC oxidation that declines with greater use of $e^-$ acceptors other than O$_2$.

**Oxidation of DOC and Reduction of Nitrate, Nitrite and Nitrous Oxide by Denitrifiers**

Constraints imposed by NO$_3^-$ availability on DOC oxidation by denitrifiers are solved in five steps:

1) NO$_3^-$ reduction to NO$_2^-$ under non-limiting NO$_3^-$ is calculated from electrons demanded by DOC oxidation to CO$_2$ but met by O$_2$ reduction to H$_2$O because of diffusion limitations to O$_2$ supply, and hence transferred to NO$_3^-$ [H6],
2) NO$_3^-$ reduction to NO$_2^-$ under ambient NO$_3^-$ is calculated from 1), accounting for relative concentrations and affinities of NO$_3^-$ and NO$_2^-$ [H7],

3) NO$_2^-$ reduction to N$_2$O under ambient NO$_2^-$ is calculated from demand for electrons not met by NO$_3^-$ reduction in 2), accounting for relative concentrations and affinities of NO$_2^-$ and N$_2$O [H8],

4) N$_2$O reduction to N$_2$ under ambient N$_2$O is calculated from demand for electrons not met by NO$_2^-$ reduction in 3) [H9],

5) additional DOC oxidation to CO$_2$ enabled by NO$_x$ reduction in 2), 3) and 4) is added to that enabled by O$_2$ reduction from [H5], the energy yield of which drives additional DOC uptake for construction of $M_i,n$. This additional uptake offsets the disadvantage incurred by the larger construction energy costs of denitrifiers.

**Oxidation of Ammonia and Reduction of Oxygen by Nitrifiers**

Constraints on nitrifier oxidation of NH$_3$ imposed by O$_2$ uptake are solved in four steps:

1) substrate (NH$_3$) oxidation under non-limiting O$_2$ is calculated from active biomass, NH$_3$ and CO$_2$ concentrations, and an Arrhenius function of $T_s$ [H11],

2) O$_2$ reduction to H$_2$O under non-limiting O$_2$ is calculated from 1) using set respiratory quotients [H12],

3) O$_2$ reduction to H$_2$O under ambient O$_2$ is calculated from radial O$_2$ diffusion through water films of thickness determined by soil water potential [H13a] coupled with active uptake at nitrifier surfaces driven by 2) [H13b]. O$_2$ uptake by nitrifiers also accounts for competition for O$_2$ uptake with heterotrophic DOC oxidizers, roots and mycorrhizae,

4) NH$_3$ oxidation to NO$_2^-$ under ambient O$_2$ is calculated from 2) and 3) [H14]. The energy yield of NH$_3$ oxidation drives the fixation of CO$_2$ for construction of microbial biomass $M_{i,n}$ according to construction energy costs of nitrifier populations.

**Oxidation of Nitrite and Reduction of Oxygen by Nitrifiers**

Constraints on nitrifier oxidation of NO$_2^-$ to NO$_3^-$ imposed by O$_2$ uptake [H15 - H18] are solved in the same way as are those of NH$_3$ [H11 - H14]. The energy yield of NO$_2^-$ oxidation drives the fixation of CO$_2$ for construction of microbial biomass $M_{i,o}$ according to construction energy costs of each nitrifier population.
Oxidation of Ammonia and Reduction of Nitrite by Nitrifiers

Constraints on nitrifier oxidation of NH$_3$ imposed by NO$_2^-$ availability are solved in three steps:
1) NO$_2^-$ reduction to N$_2$O under non-limiting NO$_2^-$ is calculated from electrons demanded by NH$_3$ oxidation but not accepted for O$_2$ reduction to H$_2$O because of diffusion limitations to O$_2$ supply, and hence transferred to NO$_2^-$ [H19],
2) NO$_2^-$ reduction to N$_2$O under ambient NO$_2^-$ and CO$_2$ is calculated from 1) [H20], competing for NO$_2^-$ with denitrifiers [H8] and nitrifiers [H18],
3) additional NH$_3$ oxidation to NO$_2^-$ enabled by NO$_2^-$ reduction in 2) [H21] is added to that enabled by O$_2$ reduction from [H14]. The energy yield from this oxidation drives the fixation of additional CO$_2$ for construction of $M_{i,n}$.

Uptake of Ammonium and Reduction of Oxygen by Roots and Mycorrhizae

1) NH$_4^+$ uptake by roots and mycorrhizae under non-limiting O$_2$ is calculated from mass flow and radial diffusion between adjacent roots and mycorrhizae [C23a] coupled with active uptake at root and mycorrhizal surfaces [C23b]. Active uptake is subject to inhibition by root nonstructural N:C ratios [C23g] where nonstructural N is the active uptake product, and nonstructural C is the CO$_2$ fixation product transferred to roots and mycorrhizae from the canopy.
2) O$_2$ reduction to H$_2$O is calculated from 1) plus oxidation of root and mycorrhizal nonstructural C under non-limiting O$_2$ using a set respiratory quotient [C14e],
3) O$_2$ reduction to H$_2$O under ambient O$_2$ is calculated from mass flow and radial diffusion between adjacent roots and mycorrhizae [C14d] coupled with active uptake at root and mycorrhizal surfaces driven by 2) [C14c]. O$_2$ uptake by roots and mycorrhizae also accounts for competition with O$_2$ uptake by heterotrophic DOC oxidizers, and autotrophic nitrifiers, calculated from their O$_2$ demands relative to those of other populations.
4) oxidation of root and mycorrhizal nonstructural C to CO$_2$ under ambient O$_2$ is calculated from 2) and 3) [C14b],
5) NH$_4^+$ uptake by roots and mycorrhizae under ambient O$_2$ is calculated from 1), 2), 3) and 4) [C23b].

Cation Exchange and Ion Pairing of Ammonium

Soil Transport and Surface - Atmosphere Exchange of Gaseous Substrates and Products

Exchange of all modelled gases $\gamma$ ($\gamma = O_2, CO_2, CH_4, N_2, N_2O, NH_3$ and $H_2$) between aqueous and gaseous states is driven by disequilibrium between aqueous and gaseous concentrations according to a $T_s$-dependent solubility coefficient, constrained by a transfer coefficient based on air-water interfacial area that depends on air-filled porosity [D14 – D15] (Fig. 1). These gases undergo convective-dispersive transport through soil in gaseous [D16] and aqueous [D19] states driven by soil water flux and by gas concentration gradients. Dispersive transport is controlled by gaseous diffusion [D17] and aqueous dispersion [D20] coefficients calculated from gas- and water-filled porosity. Exchange of all gases between the atmosphere and both gaseous and aqueous states at the soil surface are driven by atmosphere - surface gas concentration differences and by boundary layer conductance above the soil surface, calculated from wind speed and from structure of vegetation and surface litter [D15].

FIELD EXPERIMENT

Site description

The Oensingen field site is located in the central Swiss lowlands (7° 44’E, 47° 17’N) at an altitude of 450 m. The climate is temperate with an average annual rainfall of about 1100 mm and a mean air temperature of 9.5 °C. The soil is classified as a Eutri-Stagnic Cambisol developed on clayey alluvial deposits, key properties of which are given in Table 1. Prior to the experiment, the field site was managed as a ley-arable rotation. In December 2000, the field was ploughed and left in fallow until 11 May 2001. The field was then sown with a grass-clover mixture typical for permanent grassland under intensive management. The field was ploughed again on 19 December 2007, left in fallow until 5 May 2008, when it was tilled and re-sown with the same grass-clover mix as in 2001. The period of study extended from sowing in 2001 to the end of 2009, during which the field was cut between three and five times per year and harvested as hay, silage or fresh grass, fertilized two to three times per year with manure as liquid cattle slurry and two to three times per year with mineral fertilizer as
ammonium nitrate (NH$_4$NO$_3$) pellets, for an average annual N application of 23 g N m$^{-2}$. All key management operations during this period are summarized in Table 2.

**Soil, plant and meteorological measurements**

Soil $\theta$ and $T_s$ were recorded continuously using TDR (Time Domain Reflectometry, ThetaProbe ML2x, Delta-T Devices, Cambridge, UK) and thermocouples at 5, 10, 30 and 50 cm for $\theta$ and at 2, 5, 10, 30 and 50 cm for $T_s$. Leaf area index (LAI) was measured weekly with an optical leaf area meter (LI-2000, Li-Cor, Lincoln, NB, USA). Plants were collected every 2 to 4 weeks and the samples were dried for 48 h at 80°C, weighed and analyzed for C, N, P and K by using an elemental analyzer. Hourly climatic data were recorded continuously with an automated meteorological station, including air temperature ($^\circ$C), rainfall (mm), relative humidity (%), global radiation (W m$^{-2}$) and windspeed (m s$^{-1}$).

**Nitrous oxide flux measurements**

$\text{N}_2\text{O}$ fluxes were measured with a fully automated system consisting of up to eight stainless steel chambers (30 cm $\times$ 30 cm $\times$ 25 cm) (Flechard et al., 2005, Felber et al., 2014) fixed on PVC frames permanently inserted 10-cm deep into the soil. The positions of the chambers were changed about every two months. During measurements, the lids of the chambers were sequentially closed for 15 min. every 2 hours to allow $\text{N}_2\text{O}$ accumulation in the chamber headspace. During closure the chamber atmosphere was recirculated at a rate of 1000 ml min.$^{-1}$ through polyamide tube lines (4-mm ID) to analytical instruments installed in a temperature-controlled field cabin adjacent to the field plots (10 m) and then back to the chamber headspace. Until autumn 2006 concentrations of $\text{N}_2\text{O}$, CO$_2$ and H$_2$O in the head space were measured once per minute with an INNOVA 1312 photoacoustic multi-gas analyzer (INNOVA Air Tech Instruments, Ballerup, Denmark; www.innova.dk). Interferences in the measurements caused by overlaps in the absorption spectra of the different gases and by temperature effects were corrected with a calibration algorithm described in detail by Flechard et al (2005). In autumn 2006 the system was changed to the gas filter correlation technique for $\text{N}_2\text{O}$ (Model 46C, Thermo 279 Environmental Instruments Inc., Sunnyvale, CA, USA). This system was calibrated every 8 hours using certified standard gas mixtures (Messer Schweiz AG, Lenzburg, Switzerland) (Felber et al. 2014).
These measurements were used to calculate N$_2$O fluxes from the rate of change in concentration by using a linear or non-linear approach determined by the HMR R-package (Pedersen et al., 2010). The first three of the fifteen 1-min. measurements were omitted from the flux calculation to exclude gas exchange during closing that did not result from changes in emission/production in the soil. This procedure caused a mean increase of about 30% in the fluxes compared to values published in Fléchard et al. (2005) and Ammann et al. (2009), which were evaluated using linear regression. Fluxes from all chambers were averaged over 4-hourly intervals and resulting values attributed to the mid-points of the intervals. Standard errors of these averages were calculated from all fluxes measured during each interval, and thus included both spatial and temporal variation. The fluxes measured from 2002 to 2003 were summarized in Fléchard et al. (2005). Those from 2004 to 2007 were re-evaluated from values described in Ammann et al. (2009). Those from 2008 and 2009 were reprocessed from the EU-Project NitroEurope-IP database using the HMR algorithm.

**CO$_2$ and Energy Flux Measurements**

CO$_2$ and energy fluxes were measured by an eddy covariance (EC) system consisting of three-axis sonic anemometers (models R2 and HS, Gill instruments, Lymington, UK) and an open-path infrared CO$_2$/H$_2$O gas analyzer (model LI-7500, Li-Cor, Lincoln, USA). The EC system used in this study is described in Ammann et al. (2007). The EC tower was located in the centre of the field (52m x 146m), whereas the chambers were located in the south east corner. For most meteorological conditions, the chambers were not within the footprint of the EC towers, although for the main wind directions 80% or more of the footprint was within the field (Neftel et al. 2008). The management of the entire field was uniform throughout the experiment.

**MODEL EXPERIMENT**

_Ecosys_ was initialized with the biological properties of plant functional types (PFTs) representing the ryegrass and clover planted at Oensingen. These properties were identical to those in an earlier study (Grant et al., 2012) except for a perennial rather than annual growth habit. These PFTs competed for common resources of radiation, water and nutrients, based on their vertical distributions of leaf area and root length driven by uptake and allocation of C, N and P in each PFT. _Ecosys_ was also initialized with the physical and chemical properties of the Eutri-Stagnic Cambisol at Oensingen (Table
The model was then run from model dates 1 Jan. 1931 to 31 Dec. 2000 under repeating sequences of land management practices and continuous hourly weather data (radiation, $T_a$, RH, wind speed and precipitation) recorded at Oensingen from 1 Jan. 2001 to 31 Dec. 2007 (i.e. 10 cycles of 7 years). This run was long enough for C, N and energy cycles in the model to attain equilibrium under the Oensingen site conditions well before the end of the spinup run. The modelled site was plowed on 19 Dec. 2000, terminating all PFTs.

The model run was then continued from model dates 1 Jan. 2001 to 31 Dec. 2009 under continuous hourly weather data recorded at Oensingen from 1 Jan. 2001 to 31 Dec. 2009 with the same PFTs and land management practices as those at the field site listed in Table 2. For each manure application in the model, an irrigation of 4 mm was added to account for the water in the slurry. For each harvest in the model, the fraction of canopy LAI to be cut (usually 0.85 – 0.95) was calculated from measurements of LAI before and after the corresponding harvest in the field. In ecosys, leaves of each PFT are aggregated into a common canopy which is dynamically resolved into a selected number of layers (10 in this case) of equal LAI for calculating irradiance interception. The leaf fraction to be cut was removed from successive leaf layers from the top of the combined canopy downwards until the cumulative removal attained the set fraction, so that the LAI cut from each PFT depended on the leaf area of the PFT in these layers. Of the phytomass cut with the LAI, 0.76 was removed as harvest and the remainder was added to surface litter, as determined in the intensively managed grassland at Oensingen by Amman et al. (2009). $N_2O$ emissions modelled from 2004 through 2009 were compared with those measured by the automated chambers by regressing log-transformed 4-hour averages of modelled on measured values during each year of the study, and also by regressing total emissions modelled vs. measured during emission events following each fertilizer or manure application. These comparisons were supported by ones with thermistor and TDR measurements of $T_s$, $\theta$, and with EC measurements of $CO_2$ and energy exchange.

**Model Sensitivity Studies**

Modelled $N_2O$ emissions may be affected by three general sources of uncertainty in model inputs: land management practices, soil properties and model parameters. To examine the possible effects of some different land management practices on $N_2O$ emissions, the model run from 2001 to 2009 (field) was repeated with (1) increased harvest intensity in which canopy LAI remaining after each harvest was reduced to one-half of those in the first run (1/2), and (2) increased harvest intensity...
with each harvest delayed by 5 days \((1/2 + 5d)\). These alternative practices caused canopy regrowth and hence N uptake to be slower during emission events following subsequent manure and fertilizer applications.

To examine the possible effects of spatial variability in soil properties on N\(_2\)O emissions, the model run from 2001 to 2009 (field) was repeated with bulk density (BD) of the upper 3 cm in the soil profile (Table 1) increased by 5% or 10%. These larger BDs reduced soil porosity in the upper 3 cm of the soil, thereby slowing gas exchange with the atmosphere, particularly when the soil was wet (Fig. 1). All other soil properties used in the model remained unchanged (Table 1).

To examine an effect of uncertainty in model parameterization, the model run from 2001 to 2009 (field) was repeated with the values of two key parameters governing N\(_2\)O emissions, the Michaelis-Menten constants for reduction of O\(_2\) \((K_{O_2}\) in [H4]) or of NO\(_3^-\) and NO\(_2^-\) \((K_{NOx}\) in [H7], [H8] and [H20]), halved or doubled from those used in the model. Halving or doubling \(K_{O_2}\) hastened or slowed the reduction of O\(_2\) by nitrifiers and denitrifiers and hence slowed or hastened the transfer of electrons to reduce NO\(_2^-\) and NO\(_3^-\) during nitrification and denitrification. Halving or doubling \(K_{NOx}\) hastened or slowed the reduction of NO\(_2^-\) by nitrifiers and of NO\(_3^-\) and NO\(_2^-\) by denitrifiers. All other parameters in the model remained unchanged.

**RESULTS**

**LAI Modelled vs. Measured from 2002 to 2009**

Accurate modelling of ecosystem C cycling and hence N\(_2\)O emissions requires accurate modelling of plant growth as determined by land management practices. LAI modelled and measured from 2002 to 2009 rose rapidly from low values remaining in spring and after each harvest (Table 1) to 4 – 6 m\(^2\) m\(^{-2}\) before the next harvest, except during 2003 (Fig. 2). Regrowth of LAI in *ecosys* was driven by plant nonstructural C, N and P pools replenished from storage reserves remobilized after harvests, and from products of current C, N and P uptake, those of C being governed by irradiance interception calculated from regrowing LAI. Regrowth in the model was less rapid than that measured in 2009 (Fig. 2) because more frequent cutting forced more frequent replenishment of plant
nonstructural C, N and P pools which gradually depleted storage reserves and hence slowed
subsequent regrowth. Hence rates of regrowth modelled after harvests were affected by harvest timing
and intensity, as represented by the fractions of LAI removed at harvest.

**N2O Fluxes Modelled vs. Measured from 2004 to 2009**

During peak emissions, standard deviations of N$_2$O fluxes measured within each 4-hourly
interval were found to be as much as 85% relative to mean values. These deviations were largely
attributed to small-scale spatial variation in land management (manure and fertilizer application,
surface litter from harvesting) and in soil properties (bulk density, water retention), which was not
represented in the model run, rather than to temporal variation in environmental conditions (θ, $T_s$)
which was represented in the model run. Therefore only a limited fraction of variation in the
measured values was amenable to correlation with modelled values. Consequently slopes and
coefficients of determination ($R^2$) from regressions of modelled on measured log-transformed fluxes
varied from 0.5 to 1.0 and from 0.1 to 0.5 respectively, while intercepts remained close to zero (Table
3a). However ratios of mean squares for regression vs. error (F) were highly significant (P < 0.001) in
all years of the study, indicating some agreement in the timing and magnitude of modelled and
measured emission events. Improved agreement would require that more detailed information about
land management and soil properties at each chamber site be provided to the model.

**Daily-Aggregated N$_2$O Fluxes Modelled vs. Measured from 2004 to 2009**

Daily aggregations of both measured and modelled N$_2$O emissions indicated that emission
events during the study period were confined to intervals of no longer than 5 days when precipitation
followed manure or fertilizer applications (Fig. 3). Outside of these intervals emissions remained very
small except for a period of emissions modelled, but not measured, after manure application in
autumn 2006 (Fig. 3c) and measured, but not modelled, before fertilizer application in spring 2008
(Fig. 3e).

The largest emissions followed manure applications in July and August, but their magnitudes
did not vary with the amount of manure N applied. For example, emissions during an event in August
2009 (244 vs. 185 mg N m$^{-2}$ measured vs. modelled in Fig. 3f) were greater than those during an
event in July 2007 (86 vs. 112 mg N m$^{-2}$ measured vs. modelled in Fig. 3d) which in turn were greater
than those during an event in July 2005 (54 vs. 96 mg N m\(^{-2}\) measured vs. modelled in Fig.2b).

However manure N application preceding the event in August 2009 (4.5 g N m\(^{-2}\)) was less than that in July 2007 (6.7 g N m\(^{-2}\)) which in turn was less than that in July 2005 (8.5 g N m\(^{-2}\)) (Table 2), so that smaller applications were followed by greater emissions, precluding a simple emission factor for manure N application.

The magnitude of emission events following fertilizer application also varied. For example, emissions during an event in late August 2007 (105 vs. 82 mg N m\(^{-2}\) measured vs. modelled in Fig. 3d) were greater than those during events in September 2004 (24 vs. 2 mg N m\(^{-2}\) measured vs. modelled in Fig. 2a) and 2005 (6 vs. 11 mg N m\(^{-2}\) measured vs. modelled in Fig. 3b), although the fertilizer N applications of 3.0 g N m\(^{-2}\) preceding each event were the same (Table 2). These differences in emissions indicated important differences in ecological controls imposed by environmental conditions (\(\theta\) and \(T_s\)) and plant management during each event.

The standard deviations of \(\sim\)85% relative to the mean values of fluxes measured within each 4-hourly interval during emission events was used to estimate an uncertainty in daily-aggregated fluxes of \(\sim\)30%. Uncertainty in daily fluxes measured during emission events was smaller than the several-fold differences among the events indicating that the magnitude of these events likely differed significantly. Regressions of modelled on measured magnitudes of emission events following each fertilizer or manure application from 2004 to 2009 gave better agreement than did those of the 4-hourly averaged fluxes (Table 3b), indicating that modelling the precise timing of fluxes during these events remains a challenge.

**Relationships between N\(_2\)O Fluxes and Environmental Conditions during Selected Emission Events**

Environmental conditions measured and modelled from harvest to the end of the two largest emission events following manure applications in July 2007 (Fig. 3d) and August 2009 (Fig. 3f) were examined in greater detail to investigate relationships among near-surface \(T_s\), \(\theta\), aqueous gas concentrations, and surface fluxes of energy, CO\(_2\) and N\(_2\)O (Figs. 4 and 5). In July 2007, several small precipitation events wetted and cooled the soil between harvesting on DOY 187 and manure application on DOY 194 (Fig. 4a,b). The soil then dried during several days without precipitation and
warmed with reduced shading from defoliation (Fig. 2) until DOY 200, after which the soil wetted
with further precipitation and cooled with increased shading from plant regrowth (Fig. 4a,b). The
higher \( \theta \) measured during this period (Fig. 4b) may have been caused by difficulties in maintaining
calibration of the TDR probes over long periods in the high-clay soil at Oensingen (Table 1). This
higher \( \theta \) was not likely caused by overestimated evapotranspiration because modelled LE fluxes,
reduced by low LAI after harvesting but increasing with subsequent regrowth, were close to those
measured (Fig. 4c), suggesting that total water uptake was accurately modelled. Comparison of
modelled and measured \( \theta \) was further complicated by soil cracking which altered infiltration at low \( \theta \).
The effects of \( \theta \)–dependent macroporosity on preferential flow are explicitly modelled in ecosys, but
have not yet been tested in detail.

CO2 influxes were also reduced by low LAI after cutting, but recovered to pre-cut levels by the
end of the emission event (Fig. 4d), driving rapid regrowth of LAI (Fig. 2). Large CO2 effluxes
measured and modelled after manure application indicated rapid \( R_h \) and hence O2 demand that
persisted for several days.. Influxes measured in the field were reduced from those in the model for
several days after manure application, suggesting temporary interference of CO2 fixation by the
manure application which was not accounted for in the model.

Litterfall from plant growth [C18, C19] and cutting, as well as from manure application caused
a litter layer of 1 – 2 cm to develop on the soil surface in the model. During the N2O emission event
from DOY 200 to DOY 205 in 2007 (Fig. 3d), several precipitation events (Fig. 4a) wetted the
modelled surface litter and near-surface soil (layers 1 and 2 in Table 1) (Fig. 4e) without increasing \( \theta \)
at 5 cm (Fig. 4b). This surface wetting slowed gas exchange with the atmosphere, sharply reducing
aqueous O2 concentrations \([O_2(s)]\) (Fig. 4f) and thereby raising aqueous N2O concentrations \([N_2O(s)]\)
(Fig. 4g). Between precipitation events, drying of the surface litter and near-surface soil in the model
allowed recovery of \([O_2(s)]\) and forced declines in \([N_2O(s)]\). These rises and declines in \([N_2O(s)]\) drove
rises and declines in N2O emissions that tracked those measured in the chambers (Fig. 4h). These
emissions rose immediately with the onset of precipitation on DOY 200 (Fig. 4a) before wetting
occurred at 5 cm (Fig. 4b), indicating that emissions were driven by surface wetting (Fig. 4e)
combined with rapid O2 demand (Fig. 4d). The net generation of N2O modelled in each soil zone,
calculated from \([H8] + [H20] – [H9]\), indicated that 0.21 of surface emissions originated in the surface
litter and the remainder in the 0 – 1 cm soil layer as indicated by higher \([\text{N}_2\text{O}(s)]\) (Fig. 4g), while the deeper soil layers were a very small net sink of \(\text{N}_2\text{O}\). Rises and declines in \([\text{N}_2\text{O}(s)]\) also drove rises and declines in \(\text{N}_2\) emissions that persisted until DOY 205, after which more rapid mineral \(\text{N}\) uptake with recovering plant growth, driven by rising LAI (Fig. 2) and hence \(\text{CO}_2\) influxes (Fig. 4d), caused both emissions to return to background levels (Fig. 4h).

In 2009, a period of low precipitation with soil drying and warming occurred between harvesting in late July and manure application on DOY 218 in early August, followed by heavy precipitation with soil wetting and cooling on DOY 220 (Fig. 5a,b). LE effluxes and \(\text{CO}_2\) influxes declined sharply with LAI after cutting, and did not recover to pre-cut levels by the end of the subsequent emission event on DOY 224 (Fig. 5c,d), indicating a slow recovery of plant growth. Slurry application caused brief surface wetting on DOY 218 (Fig. 5e) and heavy precipitation on DOY 220 caused prolonged soil wetting at the surface (Fig. 5e) and at 5 cm (Fig. 5b). Wetting caused declines in \([\text{O}_2(s)]\) (Fig. 5f) and thereby rises in \([\text{N}_2\text{O}(s)]\) (Fig. 5g) that were sustained over 3 days. These rises drove particularly rapid \(\text{N}_2\text{O}\) emissions in the model which were consistent in magnitude with those measured in the chambers (Fig. 5h). Diurnal variation modelled with soil warming and cooling (Fig. 5a) was not apparent in the measurements, although modelled values remained within the large uncertainty of the measured values during the emission event. These large emissions were enabled in the model by slow plant uptake of manure \(\text{N}\) (Table 2) caused by the slow recovery of plant \(\text{CO}_2\) uptake and hence growth after cutting (Fig. 5d). The rises in \([\text{N}_2\text{O}(s)]\) also drove rises in modelled \(\text{N}_2\) emissions (Fig. 5h). Emissions declined with surface litter drying on DOY 223 (Fig. 5e) which allowed surface \([\text{O}_2(s)]\) to rise (Fig. 5f) and \([\text{N}_2\text{O}(s)]\) to fall (Fig. 5g) while \(\theta\) at 5 cm remained high (Fig. 5b), again indicating that \(\text{N}_2\text{O}\) emissions were largely determined by ecological controls in the surface litter and soil. The net generation of \(\text{N}_2\text{O}\) modelled in each soil zone indicated that 0.48 of surface emissions originated in the surface litter, 0.48 in the 0 – 1 cm soil layer and 0.05 in the 1 – 3 cm soil layer, while the deeper soil layers were a very small net sink of \(\text{N}_2\text{O}\), as indicated by near-surface gradients of \([\text{N}_2\text{O}(s)]\) (Fig. 5g).

Greater \(\text{N}_2\text{O}\) emissions were modelled and measured during the event in August 2009 than in July 2007 (Fig. 5h vs. Fig. 4h), in spite of smaller \(\text{N}\) addition (Fig. 3f vs. Fig. 3d; Table 2) and similar \(\theta\) and \(T_s\) modelled and measured at 5 cm (Fig. 5a,b vs. Fig. 4a,b). These greater emissions were
attributed in the model to (1) earlier and heavier precipitation after manure application (2 days after
application in Fig. 5a vs. 6 days in Fig. 4a), and (2) slower recovery of CO₂ fixation after defoliation,
indicated by slower rises in diurnal amplitude of CO₂ fluxes (Fig. 5d vs. Fig. 4d). Heavier
precipitation in 2009 vs. 2007 drove sustained vs. intermittent surface and near-surface wetting (Fig.
5e vs. Fig. 4e) and hence sustained vs. intermittent declines in [O₂(s)] and rises in [N₂O(s)] (Fig. 5f,g
vs. Fig. 4f,g). Slower recovery of CO₂ fixation after cutting in 2009 vs. 2007 slowed removal of added
NH₄⁺ and NO₃⁻ from soil. This slower removal, combined with the shorter period between manure
application and precipitation, left larger NO₃⁻ concentrations ([NO₃⁻]) in litter and surface soil to drive
N₂O production following precipitation [H7]. These model findings indicated the importance to N₂O
emissions of surface and near-surface θ after precipitation, and of plant management (intensity and
timing of defoliation in relation to N application) and its effect on subsequent plant CO₂ fixation and
N uptake.

**Effects of Intensity and Timing of Defoliation on N₂O Emission Events**

Increasing harvest intensity and delaying harvest dates slowed LAI regrowth modelled after
harvests (Fig. 6). The effects of this slowing on N₂O emissions during selected events modelled after
subsequent fertilizer and manure applications were examined under diverse θ and Tₛ (Figs. 7, 8).
Following manure application on DOY 194 in 2006 (Table 2), slower LAI regrowth from increasing
and delaying defoliation slowed the recovery of CO₂ fixation (Fig. 7a) and of NH₄⁺ uptake (Fig. 7b),
allowing more nitrification of manure N and hence greater surface [NO₃⁻] (Fig. 7c). Slower LAI
regrowth (Fig. 6) also reduced shading and ET, raising Tₛ (Fig. 7d) and θ (Fig. 7e). N₂O emissions
modelled under field management remained small because of soil drying, in spite of high Tₛ,
consistent with measurements (Fig. 3c, Fig. 7f). Increases in emissions modelled with slower LAI
regrowth, particularly from delayed harvesting (Fig. 7f), were attributed to slower N uptake (Fig. 7b)
and hence larger [NO₃⁻] in litter and surface soil (Fig. 7c), and to warmer and wetter soil (Fig. 7d,e)
which increased O₂ demand while reducing O₂ supply.

Following a similar manure application on DOY 194 in 2007 (Table 2; Fig. 6), slower LAI
regrowth from increasing and delaying defoliation also caused reductions in CO₂ fixation (Fig. 7g),
which slowed NH₄⁺ and NO₃⁻ uptake (Fig. 7h), allowing more nitrification of manure N and hence
greater [NO₃⁻] (Fig. 7i). Lower LAI also caused increases in Tₛ (Fig. 7j) and θ (Fig. 7k). Emissions
modelled and measured under field management in 2007 (Fig. 7l) were greater than those in 2006 (Fig. 7f), in spite of lower $T_s$ (Fig. 7j vs. Fig. 7d), because near-surface wetting from several precipitation events (Fig. 4a,e) reduced $[O_2(s)]$ and increased $[N_2O(s)]$ (Fig. 4f,g). Emissions modelled with increased and delayed harvesting rose from those with field harvesting as the emission event progressed (Fig. 7l) because elevated $[NO_3^-]$ from the manure application persisted longer during the event (Fig. 7i).

Following fertilizer application on DOY 259 in 2005 (Table 2), modelled and measured emissions remained small after soil wetting (Fig. 8f) because lower $T_s$ (Fig. 8d) slowed soil respiration after wetting, manifested as smaller measured and modelled CO$_2$ effluxes (Fig. 8a), and so slowed demand for e$^-$ acceptors. Under these conditions, increasing and delaying defoliation had little effect on modelled N$_2$O emissions (Fig. 8f), while CO$_2$ fixation (Fig. 8a) and N uptake (Fig. 8b) were only slightly reduced and surface NO$_3^-$ only slightly increased (Fig. 8c). Following the same fertilizer application on DOY 240 in 2007, modelled and measured emissions were greater than those in 2005 (Fig. 8l) because soils were warmer (Fig. 8j) with more rapid respiration (Fig. 8g), and because fertilizer application and subsequent wetting occurred sooner after cutting (Table 2). Consequently recovery of CO$_2$ fixation was less advanced (Fig. 8g), reducing cumulative N uptake (Fig. 8h) and leaving larger $[NO_3^-]$ to drive N$_2$O generation during the event (Fig. 8h). However reducing LAI remaining after each harvest did not raise N$_2$O emissions after this application (Fig. 8l), because slower LAI regrowth from earlier harvests had reduced primary productivity and consequently litterfall and hence the mass of the surface litter from which much of the emitted N$_2$O was generated. Consequently more intense harvests could cause surface litter later in the year to decline to levels at which N$_2$O generation modelled in the litter was reduced.

**Annual Productivity, N$_2$O Emissions and the Effects of Defoliation Intensity and Timing**

In the model, plant management practices affected LAI regrowth (Fig. 6), CO$_2$ fixation, N uptake, and hence soil $[NO_3^-]$ and N$_2$O emissions (Figs. 7,8). These effects were summarized at an annual time scale in Table 4. Modelled and EC-derived gross primary productivity (GPP) remained close to 2000 g C m$^{-2}$ y$^{-1}$ during most years except with low precipitation in 2003 and replanting in 2008, indicating a highly productive ecosystem with rapid C cycling and hence rapid demand for e$^-$ acceptors (Table 4). Larger modelled vs. measured GPP caused larger modelled vs. measured NEP in
2003, 2005 and 2007. Harvest removals in the model varied with NEP except during replanting in
2008, but tended to exceed those recorded in the field, particularly with low EC-derived NEP in 2005
and 2006. Modelled values were determined in part by the assumed constant harvest efficiency of
0.76. Including C inputs from manure applications, modelled and estimated net biome productivity
(NBP) were positive except during replanting in 2008, indicating that this intensively managed
grassland was a C sink unless replanted. Average annual NBP modelled vs. measured from 2002 to
2009 was 30 vs. 58 g C m⁻², with the lower modelled value attributed to greater modelled harvest
removals, particularly in 2006.

Slower LAI regrowth from increasing and delaying defoliation (Fig. 6) reduced modelled GPP, $R_e$ and hence NEP by 5 - 10% during years with greater productivity. However increasing and
delaying defoliation did not much affect harvest removals because reduced NEP was offset by greater
harvest intensity, so that NBP was reduced except with replanting in 2008.

Annual N₂O emissions were estimated from chamber measurements for each year of the study
by scaling the mean measured fluxes to annual values. These values are presented in Table 4 as upper
boundaries for annual emissions because flux measurements from which means were calculated were
more frequent during emission events. A lower boundary for annual emissions was also estimated in
Table 4 by replacing missing flux measurements with zero. Average lower and upper boundaries for
annual emissions estimated from 2002 to 2009 were 0.220 and 0.355 g N m⁻² respectively vs. an
average annual emission in the model of 0.260 g N m⁻² (Table 4). Modelled emissions were nearer to
upper boundaries during years with lower measured emissions (2003, 2004, 2006), and to lower
boundaries during years with higher measured emissions (2007, 2008, 2009). There was no significant
correlation between annual N inputs and measured or modelled emissions. Although annual emissions
in the model were close to 1% of annual N inputs during most years, they were greater in 2008 and
2009 in spite of smaller N inputs because of the large emission events modelled after summer
applications of fertilizer and manure (Fig. 3e,f; Fig. 5h). Annual N inputs (Table 4), supplemented by
3 – 6 g N m⁻² y⁻¹ modelled from symbiotic fixation by clover [F1 – F26]), were only slightly larger
than annual N removals with harvesting, supplemented by losses of 2 – 3 g N m⁻² y⁻¹ from all other
gaseous and aqueous emissions (N₂ from denitrification, NH₃ from volatilization, NO₃⁻ from
leaching). Consequently residual soil NO₃⁻, while present in the model, did not accumulate during the
study period, and so did not drive increasing N$_2$O emissions with sustained N applications. Modelled
and measured annual N$_2$O emissions, if expressed in C equivalents (~130 g C g N$^{-1}$), largely offset net
C uptake expressed as NBP (Table 4).

Increasing harvest intensity and delaying harvest dates had little effect on annual N$_2$O
emissions modelled during the first two years after planting in 2001 and 2008, but raised them
substantially thereafter (2003 – 2007) (Table 4). During this period, annual emissions rose by an
average of 24% with increased harvest intensity, and by an average of 43% with increased harvest
intensity combined with delayed harvest dates. These increases were attributed to reduced N uptake,
and to increased $T_s$ and $\theta$ (Figs. 7, 8).

**Effects of increased bulk density on N$_2$O emissions**

Increasing near-surface (0 – 3 cm) soil BD by 5% or 10% at the beginning of 2001 in the model
reduced [O$_2(s)$] after rainfall events and slowed recovery of [O$_2(s)$] during subsequent drying as shown
following the manure application in July 2007 (Fig. 9a) and the fertilizer application in late August
2007 (Fig. 9c). These reductions caused increases in modelled N$_2$O effluxes that varied during
emission events (Fig. 9b,d). Effluxes modelled with increases of 10% in near-surface BD were at times
double those modelled without (e.g. DOY 201 and 240 in Fig. 9), indicating that relatively small
changes in soil surface properties could at times cause large changes in emissions. The effects of
increased BD on modelled $T_s$, $\theta$, CO$_2$ exchange, crop production and N uptake during these events
were small (results not shown). Increasing near-surface BD by 10% raised annual N$_2$O emissions by
amounts that increased with annual precipitation from *ca.* 10% in drier years (e.g. 2003) to *ca.* 50% in
wetter (e.g. 2006) (Table 5).

**Effects of Changes in $K_{O2}$ and $K_{NOx}$ on N$_2$O emissions**

Lowering $K_{O2}$ to one-half that used in *ecosys* reduced annual N$_2$O emissions modelled from
2004 to 2009 by 16% to an average of 0.218 g N m$^{-2}$ y$^{-1}$, near the average lower boundary of the
measured values (Table 5). Raising $K_{O2h}$ to double that used *ecosys* increased these emissions by 28%
to an average of 0.334 g N m$^{-2}$ y$^{-1}$, near the average upper boundary of the measured values. Lowering
$K_{NOx}$ to one-half that used in *ecosys* increased annual N$_2$O emissions modelled from 2004 to 2009 by
30% to an average of 0.338 g N m$^{-2}$ y$^{-1}$, near the average upper boundary of the measured values
(Table 5). Raising $K_{NOx}$ to double that used ecosys reduced these emissions by 27% to an average of 0.189 g N m$^{-2}$ y$^{-1}$, near the average lower boundary of the measured values. In years with lower annual emissions (2003, 2004, 2006 in Table 4), the lower $K_O2$ or higher $K_{NOx}$ gave modelled values that were closer to measured values. However in years with higher annual emissions (2008 and 2009 in Table 4), the higher $K_O2$ or lower $K_{NOx}$ gave modelled values that were closer.

**DISCUSSION**

**Modelled vs. Measured N$_2$O Emissions**

Most N$_2$O emission events measured from 2004 to 2009 were simulated within the range of measurement uncertainty, estimated to be about 30% of mean daily values (Fig. 3). However some deviations between modelled and measured N$_2$O emissions were apparent, such as the larger emissions modelled in autumn 2006 (Fig. 3c) and the smaller emissions modelled in spring 2008 (Fig. 3e). These deviations may be attributed to uncertainties in both the measurements and the model. In the automated measurement system, the static chambers were rotated about every two months among fixed positions in a corner of the field. During these periods, surface conditions in the chamber could deviate from the mean field conditions represented in the model. However we do not have an explanation for the very small emissions measured after the three manure slurry applications 2006. The chambers had been removed before the applications and were reinstalled within two hours, during which the cut grass was removed so that the surface litter in the chambers may have been reduced from that outside. In the model, emissions following manure or fertilizer applications were sensitive to the amount of surface litter as noted earlier. The absence of emission events measured after slurry applications in 2006 was unusual (Fig. 3) given the large precipitation that year (Table 4), demonstrating that large variability at small spatial scales inevitably affects these measurements. Such variability adversely affects agreement between modelled and measured emissions (Table 3).

During spring 2008 sustained emissions of about 5 mg N m$^{-2}$ d$^{-1}$ were measured by the chambers in the absence of any manure or fertilizer applications (Fig. 3e). These emissions were related to the ploughing of the field to a depth of 25cm in December 2007 (Table 2) which hastened soil organic matter decomposition, and hence N mineralization that increased mineral N substrate for
nitrification and denitrification, and possibly microbial nitrifier and denitrifier populations. These increases must remain conjectural as the Oensingen study did not include stratified analysis of N₂O production factors (e.g. microbial biomass, potential denitrification) within the chamber soils. Although *ecosys* simulates hastened SOM decomposition with tillage (Grant et al., 1998), large amounts of above- and below-ground plant litter with relatively high C:N ratios were incorporated in the model with tillage in December 2007 which slowed net N mineralization and hence accumulation of mineral N products in the model during spring 2008. Consequently modelled N₂O emissions remained small until mineral N was raised by fertilizer applications in July (Fig. 3c).

Modelling Controls on N₂O Emissions by Litter and Near-Surface θ and Tₕ

In the model, almost all the N₂O emissions originated in the surface litter and in the near-surface (0 – 1 cm) soil layer, so that emissions were strongly controlled by litter and near-surface θ and Tₕ (Figs. 3 – 4). This model finding is consistent with the experimental finding of Pal et al. (2013) from¹⁵N enrichment studies that approximately 70% of N₂O measured during emission events in a managed grassland originated in the surface litter. Similarly van der Weerden et al. (2013) inferred from diurnal variation in Tₕ and N₂O emissions measured after urine amendments on a managed grassland that N₂O production was at or near the soil surface (0 - 2 cm). Also Fléchard et al. (2007) inferred in a meta-analysis of N₂O emissions from grasslands in Europe that θ measured at 5 cm was not in some cases an adequate scaling factor for N₂O source strength because N₂O production and emission took place at or near the soil surface. *Ecosys* simulated little net production, and even a small net consumption, of N₂O in soil below 2 cm during emission events, as may be inferred from peak [N₂Oₗ] modelled in the 0 – 1 cm soil layer and much lower [N₂Oₗ] modelled in the 1 – 3 cm soil layer below (Figs. 3g and 4g). This model finding was consistent with the experimental finding of Neftel et al. (2000) that N₂O concentrations below near-surface soil layers in a managed grassland remained below atmospheric values during emission events, from which they inferred that any N₂O generated at depths greater than ~3 cm would not likely reach the soil surface. Thus attempts to relate N₂O emissions to Tₕ and θ measured at greater depths than 3 cm in grasslands are unlikely to be informative if these differ from near-surface values. These emissions should rather be related to conditions in the litter and near-surface soil, which need to be better characterized in future studies.
Consequently modelled N\textsubscript{2}O emissions were highly sensitive to surface wetting and drying (e.g. Fig. 4e,h) modelled from precipitation vs. ET (e.g. Fig. 4a,c), or to surface warming and cooling (e.g. Fig. 8j,l) modelled from surface energy balance (e.g. Fig. 4c). The sensitivity to surface wetting and drying was modelled from the effects of $\theta$ on air- vs. water-filled porosity and hence on diffusivity of gases in gaseous [D17] and aqueous [D20] phases, and on gaseous volatilization - dissolution transfer coefficients and hence gas exchange between gaseous and aqueous phases [D14, D15]. These transfers controlled O\textsubscript{2} supply, and hence demand for alternative e\textsuperscript{−} acceptors as the O\textsubscript{2} supply fell below O\textsubscript{2} demand, which drove N\textsubscript{2}O generation from denitrification [H6 – H8] and nitrification [H19]. The control of O\textsubscript{2} supply on e\textsuperscript{−} acceptors used in nitrification thereby simulated the effect of WFPS on the fraction of N\textsubscript{2}O generated during nitrification identified by Fang et al. (2015) as necessary to modelling N\textsubscript{2}O emissions, while avoiding the model-specific parameterization needed in simpler models. The sensitivity to surface wetting in ecosys enabled sharp rises in N\textsubscript{2}O emissions to be modelled from surface litter and near-surface soil after small precipitation events during DOY 200 - 201 in 2007 (Fig. 4a,h), and after slurry application during DOY 218 in 2009 (Fig. 5a,h), even when the soil at 5 cm remained dry (Fig. 4b; Fig. 5b). Such rises were consistent with the experimental findings of Fléchard et al. (2007) that precipitation on dry soil can cause substantial N\textsubscript{2}O emissions after fertilizer application in grasslands.

The sensitivity to surface warming and cooling was modelled from the effects of $T_s$ on diffusivity of gases in gaseous [D17] and aqueous [D20] phases, and on solubility of gases and hence exchange of gases between gaseous and aqueous phases [D14, D15], both parameterized from basic physical relationships independently from the model. These transfers controlled [O\textsubscript{2(s)}] in the surface litter and soil (Figs. 3f and 4f), and hence O\textsubscript{2} uptake by aerobic heterotrophs [H4] and autotrophs [H13] through a Michaelis-Menten constant [H4b, H13b]. The sensitivity to surface warming and cooling was also modelled from the effects of $T_s$ on SOC oxidation [H2] and hence O\textsubscript{2} demand by aerobic heterotrophs [H3], and on NH\textsubscript{4}\textsuperscript{+} and NO\textsubscript{2}\textsuperscript{−} oxidation [H11, H15] and hence O\textsubscript{2} demand by aerobic autotrophs [H12, H16]. These effects were driven by a single Arrhenius function used for all biological transformations [A6] parameterized from basic research conducted independently from the model. Under sustained high surface $\theta$, this combination of physical and biological processes drove large diurnal variation in N\textsubscript{2}O emissions modelled with diurnal surface warming and cooling during emission events (e.g. DOY 221 in Fig. 5h, DOY 243 in Fig. 8l), as observed experimentally by van
der Weerden et al. (2013). By explicitly simulating the diverse processes that determine N₂O emissions, *ecosys* could model the large sensitivity of emissions to $T_s$ without the use of unrealistically large parameters for temperature sensitivity inferred from controlled temperature studies of N₂O emissions (e.g. Dobbie and Smith, 2001). This large sensitivity to $T_s$ has been inadequately represented in simpler models, causing underestimation of large emissions measured from warm soils (e.g. Saggar et al., 2004). At a seasonal time scale, higher $T_s$ could cause large increases in N₂O emissions modelled with comparable $\theta$ after the same fertilizer application (Fig. 8l vs. Fig. 8f). However the effects of $T_s$ on N₂O emissions were dominated by those of $\theta$ during surface wetting and drying (e.g. Figs. 4h, 7l).

Values of both $\theta$ and $T_s$ thus determined O₂ demand not met by O₂ uptake which drove demand for alternative e⁻ acceptors by heterotrophic denitrifiers [H6] and autotrophic nitrifiers [H19]. This demand drove the sequential reduction of NO₃⁻, NO₂⁻ and N₂O to NO₂⁻, N₂O and N₂ respectively by heterotrophic denitrifiers [H7, H8, H9], and the reduction of NO₂⁻ to N₂O by autotrophic nitrifiers [H20]. The consequent production of N₂O (Fig. 4g, Fig. 5g) and N₂ drove emissions of both N₂O and N₂ (Fig. 4h, Fig. 5h) through volatilization [D14, D15] and through gaseous and aqueous diffusion [D16, D19]. Ratios of N₂O and N₂ emissions in *ecosys* (Fig. 4h, Fig. 5h) were not parameterized as done in other models, but rather were determined by relative affinities determined from basic research [H8, H9], and by environmental conditions. When demand from heterotrophic denitrifiers for alternative e⁻ acceptors was small relative to their availability, the preferential reduction of more oxidized e⁻ acceptors generated larger emissions of N₂O [H7, H8] relative to N₂ [H9]. Such conditions occurred during the early part of an emission event when surface [NO₃⁻] rose with nitrification of fertilizer or manure NH₄⁺ after application (e.g. DOY 200 – 201 in Fig. 4h). However when demand for alternative e⁻ acceptors was large relative to their availability, this same reduction sequence forced more rapid reduction of N₂O to N₂ and hence smaller emissions of N₂O relative to N₂. Such conditions occurred during the later part of emission events when surface [NO₃⁻] declined with plant uptake (e.g. DOY 202 – 205 in Fig. 4h and DOY 222 in Fig. 5h), or when greater surface wetting reduced O₂ supply (e.g. DOY 220 in Fig. 5h). This greater demand for alternative e⁻ acceptors with wetting provided a process-based explanation for declines in N₂O emissions frequently found at higher $\theta$ in field studies (e.g. Rafique et al., 2011) without explicit parameterization of N₂O:N₂ ratios.
Nitrification and denitrification were also driven by the concentrations of NH$_4^+$ [H11], NO$_3^-$ [H7], NO$_2^-$ [H8, H15, H20] and N$_2$O [H9] relative to Michaelis-Menten constants evaluated from basic research. The concentrations of NH$_4^+$ and NO$_3^-$ in ecosys were increased by N additions from manure and fertilizer N applications (Table 2), and by net mineralization soil organic N from oxidation of litterfall, manure and SOM [A26] as indicated by soil CO$_2$ effluxes. These concentrations were reduced by root uptake of NH$_4^+$ and NO$_3^-$ [C23] and consequent plant N assimilation with growth, indicated by more rapid CO$_2$ fixation with time after cutting (Figs 3 – 4 and Figs. 6 - 7). In the model, more rapid CO$_2$ fixation drove more rapid production of nonstructural C, and hence more rapid exchange of nonstructural C and N between canopy and roots [C50], and so hastened root active N uptake by increasing $R_a$ driving root growth [C14b], and by hastening removal of N uptake products and hence reducing their inhibition of active uptake [C23g]. The diversity of controls on key substrates for N$_2$O generation suggests that robust simulations of N$_2$O emissions require comprehensive ecosystem models in which these controls are fully represented.

**Modelling Effects of Defoliation Intensity and Timing on N$_2$O Emissions**

The control of NH$_4^+$ and NO$_3^-$ availability by root N uptake indicated that plant management practices determining uptake would thereby affect N$_2$O emissions. In the model, increasing harvest intensity and delaying harvest dates both slowed N uptake (Fig. 7b,h and Fig. 8b,h) by slowing the recovery of LAI (Fig. 6) and CO$_2$ fixation (Fig. 7a,g and Fig. 8a,g). Both thereby increased [NO$_3^-$] (Fig. 7c,i and Fig. 8c,i), $T_s$ (Fig. 7d,j and Fig. 8d,j) and $\theta$ (Fig. 7e,k and Fig. 8e,k), raising N$_2$O effluxes modelled during most emission events (Fig. 7f,l and Fig. 8f,l), and hence annually (Table 4). This model finding was consistent with the field observations of Jackson et al. (2015) that increased N$_2$O emissions after defoliation in grasslands were caused by reduced uptake of N and water by slower-growing plants.

The effects of defoliation on N$_2$O emissions during modelled emission events were similar to, or greater than, those of $T_s$ and $\theta$ (e.g. Fig. 7f,l), consistent with the experimental finding of Imer et al. (2013) that plant management, as represented by its effects on LAI, had a larger effect on N$_2$O fluxes than did the environment, as represented by $T_{as}$ at an intensively managed grassland in Switzerland. Reducing LAI remaining after harvest by one-half and delaying harvest by 5 days had little effect on modelled harvest removals (Table 4), suggesting that N$_2$O emissions from managed grasslands are
more sensitive to plant management practices than are yields. Intensity and timing of harvests should therefore be selected to avoid slow regrowth of LAI following N additions by avoiding excessive defoliation and by allowing as much time as possible between defoliation and subsequent fertilizer or manure application. Neftel et al. (2010) reported enhanced N2O emissions after cuts in managed grassland and hypothesized that a simple mitigation option would be to optimize the timing of the fertilizer applications. To our knowledge this option has not been systematically investigated.

Modelling Effects of Soil Bulk Density on N2O Emissions

The small increases in near-surface BD included in this study were typical of those arising from natural variation in soil properties or from compaction by vehicular traffic during field management operations. In the model, these increases reduced soil porosity and hence gaseous diffusivity [D17] which slowed O2 uptake from the atmosphere [D15] and O2 transfer through the soil profile [D16]. Consequent reductions in near-surface [O2(s)] (Fig. 9a,c) slowed O2 reduction by denitrifiers [H4] and nitrifiers [H13], forcing more rapid e´ transfer to NO3 by denitrifiers [H6] and to NO2 by nitrifiers [H19] and hence more rapid emissions of N2O following applications of manure (Fig. 9b) and fertilizer (Fig. 9d).

In a study of soil compaction effects on N2O emissions from a fertilized agricultural field in a climate similar to that at Oensingen, Bessou et al. (2010) found that increasing the BD of the upper 30 cm of the soil profile by ca. 15% raised annual N2O emissions measured with automated chambers by at least 50% during each of two growing seasons. This rises were similar to that modelled with a smaller increase in BD of the upper 3 cm during the wettest year of this study (Table 5). During emission events, Bessou et al. (2010) measured peak fluxes from compacted soil that were double those from uncompacted, as also modelled here (Fig. 9b,d).

The detailed algorithms from which ecosys was constructed enabled increases in N2O emissions from surface compaction to be simulated from specified changes to surface BD, a measureable site characteristic, without further model parameterization. The marked increases in N2O emissions modelled with these increases in BD (Table 5) indicated that some of the large spatial variation in these emissions commonly found in field measurements could arise from relatively small variation in physical properties of near-surface soil. In future studies of N2O emissions, near-surface
soil properties could be determined at each measurement site to establish the extent to which variation in these properties are associated with those in emissions.

**Modelling Effects of $K_{O_2}$ and $K_{NO_3}$ on N$_2$O Emissions**

The value of $K_{O_2}$ used in *ecosys* (=2 µM) was taken from the upper range of values determined experimentally for intact cells of heterotrophic bacteria by Longmuir (1954). Halving or doubling $K_{O_2}$ changed modelled N$_2$O emissions (Table 5) by amounts similar to uncertainty in measured emissions expressed as lower and upper boundaries of likely values (Table 4), although the doubled value of $K_{O_2}$ was larger than those derived from experiments. The value of $K_{NO_3}$ used in *ecosys* (=100 µM) was within the range of values determined experimentally by Yoshinari et al. (1977). As for $K_{O_2}$, halving or doubling $K_{NO_3}$ changed modelled N$_2$O emissions (Table 5) by amounts similar to uncertainty in measured emissions expressed as lower and upper boundaries of likely values (Table 4). The halved value of $K_{NO_3}$ was closer to those measured by Betlach and Tiedje (1981) and Khalil et al. (2007) while the doubled value was closer to that measured by Klemedtsson et al. (1977). These changes indicate that key parameters used in process models must be capable of being constrained by accurate evaluation in independent experiments.

**CONCLUSIONS**

N$_2$O emissions modelled in this managed grassland originated in the surface litter and upper 2 cm of the soil profile. The shallow origin of these emissions enabled *ecosys* to simulate the response of measured emissions to changes in near-surface $\theta$ and $T_s$ during brief emission events when rainfall followed manure or mineral fertilizer applications. Measurements of $\theta$ and $T_s$ used to estimate N$_2$O emissions from managed grasslands should therefore be taken in surface litter and near-surface soil (0 – 2 cm), rather than deeper in the soil profile (5 – 10 cm) as is currently done.

N$_2$O fluxes modelled during emission events were greater when grassland regrowth and hence mineral N uptake was slower following harvest and subsequent N application. The control of N$_2$O emissions by grassland N uptake indicated that N$_2$O emissions from managed grassland could be
increased by harvesting practices and fertilizer timing that resulted in slower regrowth during periods when emission events are most likely to occur. N₂O fluxes modelled during emission events rose sharply with small increases in surface BD, indicating the importance of avoiding surface compaction in fields to which large amounts of N are applied.

The basic and comprehensive approach to model development in ecosys allowed diverse responses of N₂O emissions to changes in weather (\(T_s, \theta\)), land management and soil properties to be modelled from specified changes to readily measured inputs with parameters constrained by basic experiments conducted independently of the model rather than derived from site-specific observations. This approach enabled concurrent, well-constrained tests of model performance against a diverse set of field measurements, and so is expected to confer robustness to the modelling of these emissions under different climates, soils and land uses in future studies.

ACKNOWLEDGEMENTS

Computational facilities for ecosys were provided by the University of Alberta and by the Compute Canada high performance computing infrastructure. A PC version of ecosys with GUI can be obtained by contacting the corresponding author at rgrant@ualberta.ca. The authors also acknowledge contributions from valuable discussions with Christoph Amman concerning measurement methodology.


Table 1. Key soil properties of the Eutri-Stagnic Cambisol at Oensingen as used in ecosys.

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>BD (Mg m$^{-3}$)</th>
<th>TOC (g kg$^{-1}$)</th>
<th>TON (g kg$^{-1}$)</th>
<th>FC (m$^3$ m$^{-3}$)</th>
<th>WP (mm h$^{-1}$)</th>
<th>$K_{sat}$ (mm h$^{-1}$)</th>
<th>pH</th>
<th>Sand (g kg$^{-1}$)</th>
<th>Silt (g kg$^{-1}$)</th>
<th>Clay (g kg$^{-1}$)</th>
<th>CF (m$^3$ m$^{-3}$)</th>
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† abbreviations  BD: bulk density, TOC and TON: total organic C and N, FC: field capacity, WP: wilting point, $K_{sat}$: saturated hydraulic conductivity, CF: coarse fragments.
‡ BD, TOC and texture were determined from soil cores taken in 2001 and 2006. Details are given in Leifeld et al. (2011).
† FC, WP and $K_{sat}$ were estimated from BD, TOC and texture according to Saxton et al. (1996) and Saxton and Rawls (2006).
Table 2. Plant and soil management operations at the Oensingen intensively managed grassland from 2001 to 2009.

<table>
<thead>
<tr>
<th>Year</th>
<th>Plant Management</th>
<th>Date</th>
<th>Management</th>
<th>Date</th>
<th>Management</th>
<th>Amount (g m(^{-2}))</th>
<th>NH(_4^+)</th>
<th>NO(_3^-)</th>
<th>ON</th>
<th>OC</th>
</tr>
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<tr>
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<tr>
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<tr>
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<tr>
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Table 3: Intercepts (a), slopes (b) coefficients of determination (R²), ratios of mean squares for regression vs. error (F) and number of data pairs from regressions of (a) log-transformed 4-hour averages of N₂O fluxes (mg N m⁻² h⁻¹) modelled vs. measured during each year from 2004 to 2009, and (b) total N₂O fluxes (mg N m⁻²) modelled vs. measured during emission events following each fertilizer or manure application from 2004 to 2009 (see Fig. 3) at the Oensingen intensively managed grassland.

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<th>Year</th>
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<th>b</th>
<th>R²</th>
<th>F</th>
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<td>1.25 ± 0.88 x 10⁻⁵</td>
<td>0.49 ± 0.06</td>
<td>0.08</td>
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<td>818</td>
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<td>1.63 ± 0.43 x 10⁻⁵</td>
<td>0.59 ± 0.03</td>
<td>0.24</td>
<td>368</td>
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<td>2006</td>
<td>4.28 ± 0.44 x 10⁻⁵</td>
<td>1.04 ± 0.08</td>
<td>0.14</td>
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<td>2007</td>
<td>1.21 ± 0.33 x 10⁻⁵</td>
<td>0.67 ± 0.02</td>
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<td>2008</td>
<td>1.44 ± 0.51 x 10⁻⁵</td>
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<td>2009</td>
<td>-0.03 ± 0.25 x 10⁻⁵</td>
<td>0.71 ± 0.02</td>
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<td>2004 - 2009</td>
<td>28 ± 9 mg N m⁻²</td>
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All values of F were highly significant (P < 0.001).
Table 4. Annual gross primary productivity (GPP), ecosystem respiration ($R_e$), net ecosystem productivity (NEP = GPP - $R_e$), harvest, net biome productivity (NBP) and N$_2$O emissions derived from EC or chambers and modelled (M) with current land management (Table 2), and with defoliation increased so that LAI remaining after harvesting was reduced by one-half (1/2), with defoliation increased and delayed by 5 days (1/2 + 5d). Positive values indicate uptake, negative values emissions.

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Table 5. Annual N$_2$O emissions modelled with current field management (Table 2) and soil properties (Table 1) (current), with soil bulk density (BD) increased by 5% and 10% to a depth of 3 cm, and with the Michaelis-Menten constants for reduction of O$_2$ ($K_{O2}$) and of NO$_3^-$ and NO$_2^-$ ($K_{NOx}$) halved or doubled from those used in the model.

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<th>N$_2$O (g N m$^{-2}$ y$^{-1}$)</th>
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<td>$K_{NOx} \times 0.5$</td>
<td>-0.382</td>
<td>-0.261</td>
</tr>
<tr>
<td></td>
<td>$K_{NOx} \times 2.0$</td>
<td>-0.234</td>
<td>-0.163</td>
</tr>
</tbody>
</table>
Fig. 1: Summary of key processes governing generation and emission of N₂O as represented in *ecosys*. 
Fig. 2. LAI measured (symbols) and modelled (lines) from 2002 through 2009 at the Oensingen intensively managed grassland.
Fig. 3. Daily-aggregated N$_2$O emissions measured (symbols) and N$_2$O and N$_2$ emissions modelled (lines) from 2004 through 2009 at the Oensingen intensively managed grassland. Numbers above and beside each fertilizer or manure addition indicate total measured/modelled N$_2$O-N emitted during emission events (mg N m$^{-2}$), and total N applied (g N m$^{-2}$). Negative values indicate effluxes to the atmosphere.
Fig. 4. (a) Precipitation and soil temperature at 0.05 m, (b) soil water content ($\theta$) at 0.05, 0.10, 0.30 and 0.50 m, (c) energy and (d) CO$_2$ fluxes measured (closed symbols), gap-filled (open symbols) and modelled (lines) during 20 days from harvest (cut) to the end of the emission event following manure application (manure) in July 2007. (e) $\theta$, (f and g) aqueous concentrations of O$_2$ and N$_2$O modelled in the surface litter and at 0.01 and 0.02 m in the soil, and (h) N$_2$O and N$_2$ fluxes measured (symbols) and modelled (lines) during the last 10 days of this period when the emission event occurred. For fluxes, positive values represent influxes to the soil, negative values effluxes to the atmosphere.
Fig. 5. (a) Precipitation and soil temperature at 0.05 m, (b) soil water content ($\theta$) at 0.05, 0.10, 0.30 and 0.50 m, (c) energy and (d) CO$_2$ fluxes measured (closed symbols), gap-filled (open symbols) and modelled (lines) during 20 days from harvest (cut) to the end of the emission event following manure application (manure) in August 2008. (e) $\theta$, (f and g) aqueous concentrations of O$_2$ and N$_2$O modelled in the surface litter and at 0.01 and 0.02 m in the soil, and (h) N$_2$O and N$_2$ fluxes measured (symbols) and modelled (lines) during the last 10 days of this period when the emission event occurred. Positive flux values represent influxes to the soil, negative values effluxes to the atmosphere.
Fig. 6. LAI modelled from 2002 through 2009, with LAI after each cut reduced to one-half of that estimated from the field experiment without or with a delay of 5 days at the Oensingen intensively managed grassland.
Fig. 7. (a,g) CO₂ fluxes, (b,h) cumulative NH₄⁺ (dashed) and NO₃⁻ (solid) uptake since manure application, (c,i) aqueous NO₃⁻ concentrations at 0 – 1 cm, (d,j) Tₛ and (e,k) θ at 5 cm, and (f,l) N₂O fluxes measured (symbols) and modelled (lines) with LAI after each cut reduced to one-half of that estimated from the field experiment without or with a delay of 5 days during emission events following manure applications on DOY 194 in (a-f) 2006 and (g-l) 2007 (see Table 2). For fluxes, positive values represent influxes to the soil, negative values effluxes to the atmosphere.
Fig. 8 (a,g) CO₂ fluxes, (b,h) cumulative NH₄⁺ (dashed) and NO₃⁻ (solid) uptake since fertilizer application, (c,i) aqueous NO₃⁻ concentrations at 0 – 1 cm, (d,j) Tₓ and (e,k) θ at 5 cm, and (f,l) N₂O fluxes measured (symbols) and modelled (lines) with LAI after each cut reduced to one-half of that estimated from the field experiment without or with a delay of 5 days during emission events following fertilizer applications on DOY 259 in 2005 (a-f) and DOY 240 in 2007 (g-l) (see Table 2). For fluxes, positive values represent influxes to the soil, negative values effluxes to the atmosphere.
Fig. 9. (a,c) Aqueous O$_2$ concentrations, and (b,d) N$_2$O fluxes measured (symbols) and modelled (lines) with bulk density (BD) from field measurements, and with BD raised by 5% or 10% following (a,b) manure application on DOY 194 and (c,d) fertilizer application on DOY 240 in 2007 (see Table 2). For fluxes, positive values represent influxes to the soil, negative values effluxes to the atmosphere.