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General model for N_2O and N_2 gas emissions from soils due to dentrification

S. J. Del Grosso,[1] W. J. Parton,[1] A. R. Mosier,[2] D. S. Ojima,[1] A. E. Kulmala,[3] and S. Phongpan[4]

Abstract. Observations of N gas loss from incubations of intact and disturbed soil cores were used to model N_2O and N_2 emissions from soil as a result of denitrification. The model assumes that denitrification rates are controlled by the availability in soil of NO_3 (e^- acceptor), labile C compounds (e^- donor), and O_2 (competing e^- acceptor). Heterotrophic soil respiration is used as a proxy for labile C availability while O_2 availability is a function of soil physical properties that influence gas diffusivity, soil WFPS, and O_2 demand. The potential for O_2 demand, as indicated by respiration rates, to contribute to soil anoxia varies inversely with a soil gas diffusivity coefficient which is regulated by soil porosity and pore size distribution. Model inputs include soil heterotrophic respiration rate, texture, NO_3 concentration, and WFPS. The model selects the minimum of the NO_3 and CO_2 functions to establish a maximum potential denitrification rate for particular levels of e^- acceptor and C substrate and accounts for limitation of O_2 availability to estimate daily N_2+N_2O flux rates. The ratio of soil NO_3 concentration to CO_2 emission was found to reliably (r^2=0.5) model the ratio of N_2 to N_2O gases emitted from the intact cores after accounting for differences in gas diffusivity among the soils. The output of the ratio function is combined with the estimate of total N gas flux rate to infer N_2O emission. The model performed well when comparing observed and simulated values of N_2O flux rates with the data used for model building (r^2=0.50) and when comparing observed and simulated N_2O+N_2 gas emission rates from irrigated field soils used for model testing (r^2=0.47).

1. Introduction

Nitrous oxide (N_2O) concentration in the atmosphere has increased from a preindustrial level of 275 ppb to a modern level of 314 ppb (National Oceanic and Atmospheric Administration (NOAA), www.cmdl.noaa.gov/ftpdata.html). N_2O is long lived (~ 120 years), and its primary sink is the stratosphere, where it contributes to ozone depletion [*Prather et al.*, 1995]. Although the atmospheric concentration of N_2O is ~1000-fold smaller than that of CO_2, an N_2O molecule has ~310 times the warming potential of a CO_2 molecule [*Albritton et al.*, 1995]. The atmospheric concentrations of well-mixed trace gases (CO_2, CH_4, N_2O) can be accurately measured, but estimates of the fluxes associated with various sources and sinks of these gases are highly uncertain [*Matson and Harris*, 1995]. Valid trace gas models can be linked with ecosystem models to calculate global carbon and nitrogen budgets and reduce these uncertainties. Models also test hypothesis regarding the controls of biogeochemical processes such as denitrification and can be used to compare results of laboratory and field experiments.

The major sources of N_2O are terrestrial soils, aquatic systems, combustion of fossil fuels and biomass, and industrial processes other than combustion [*Bouwman*, 1994]. Estimates of annual N_2O emissions from soils range from 5 to 15 TgN and soils are thought to account for over half the total N_2O inputs to the atmosphere [*Prather et al.*, 1995]. N_2O is emitted from soils via two biogeochemical pathways, nitrification and denitrification. Nitrifying microbes oxidize ammonium (NH_4) to nitrate (NO_3), but some N is lost as N_2O and nitric oxide (NO) during the intermediary steps [*Firestone and Davidson*, 1989]. Peak nitrification rates occur in aerobic soils of moderate water content [*Linn and Doran*, 1984]. In contrast, denitrification involves N oxides serving as electron acceptors during oxidation of labile carbon when O_2 is not available. Various genera of heterotrophic bacteria contribute to the NO_3 reduction sequence under anaerobic conditions [*Paul and Clark*, 1989]:

$$NO_3^- \rightarrow NO_2^- \rightarrow NO \rightarrow N_2O \rightarrow N_2. \quad (1)$$

[1]Natural Resource Ecology Laboratory, Colorado State University, Fort Collins.
[2]Agriculture Research Service, U.S. Department of Agriculture, Fort Collins, Colorado.
[3]Agriculture Research Center of Finland, Finland.
[4]Thailand Department of Agriculture, Bangkok.

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Nitrification and denitrification are related in that the oxidized N species that are the by products of nitrification (NO, N_2O, and NO_3) may serve as e^- acceptors for denitrification. Although some NO from denitrification may be released from soil, the amounts tend to be very small because NO is highly reactive under conditions that facilitate denitrification [*Conrad*, 1996]. Consequently, our model simulates N_2O and N_2 but not NO emissions from denitrification in soils.

The major controls on denitrification rates are soil NO_3, O_2, and labile C levels [*Firestone and Davidson*, 1989]. As soils become more anoxic, a higher proportion of N_2O produced from denitrification is further reduced to N_2 before leaving the soil [*Davidson and Schimel*, 1995]. In addition to water content, soil parameters related to texture (porosity, field capacity) affect O_2 availability and N gas flux [*Groffman*, 1991].

Denitrification models simulate processes and use statistical methods to varying degrees. Highly mechanistic models may simulate microbial growth rates [*Myrold and Tiedje*, 1985] and solute and gas diffusion through the soil profile and through aggregates [*Smith*, 1980] or may include dynamics of microbial biomass and gas and solute transport [*Grant and Pattey*, 1999]. Such models usually require detailed data from laboratory experiments. Stochastic models have been developed to simulate the high variability of denitrification rates observed during incubation studies [*Parkin and Robinson*, 1989]. More general models correlate nitrogen gas flux with estimates of soil N cycling and water content [*Potter et al.*, 1996a]. The presented model is a hybrid. It was developed with data from laboratory incubations, but it is intended to predict denitrification rates in field soils, and commonly measured and modeled field parameters are used as inputs. Also, best-fitting equations were empirically determined, but the equations are based on physical and biological principles. The model was designed to be linked with larger-scale nutrient cycling models (e.g., CENTURY [*Parton et al.*, 1994, 1998]) so that estimates of soil N gas flux through natural and managed systems can be improved.

The denitrification submodel of NGAS, a nitrogen gas flux model developed by *Parton et al.* [1996], was modified to account for nitrogen gas flux data from incubations of intact soil cores. NGAS was designed to simulate N_2 and N_2O emissions from soils owing to nitrification and denitrification. The model assumes that denitrification occurs in anoxic microsites when NO_3 and C are available. Heterotrophic respiration is used to indicate labile C availability, while soil water-filled pore space (WFPS) and physical properties related to gas diffusivity are used to estimate the proportion of soil volume that is sufficiently anoxic for NO_3 reduction to occur. Model inputs are soil NO_3 concentration (μgN gsoil^{-1}), heterotrophic CO_2 respiration (μgC gsoil^{-1} d^{-1}), water-filled pore space (WFPS = % relative saturation), bulk density (g cm^{-3}), and field capacity (cm^{3}H$_2$O cm^{3}soil^{-1}). NGAS uses equations relating these inputs to denitrification and assumes that the law of the minimum applies. At daily intervals, total nitrogen gas flux is estimated, then an N_2/N_2O ratio function is used to infer N_2O emission.

The overall structure of our model was based on an application of the law of the minimum; that is, we assumed that denitrification is controlled by the molecular species (NO_3 or labile C) or environmental condition (O_2 availability) that is most limiting. The law of the minimum also dictated how the data were analyzed. To derive appropriate equations to represent how denitrification responds to changes in one of the major input variables (soil NO_3 concentration, respiration, or WFPS), data points that were subjected to strong limitation due to levels of the other inputs were eliminated. For example, soil may have sufficient labile C and NO_3 available to facilitate high rates of denitrification but little denitrification will occur if soil water is below a threshold ranging from ~60 to 70% WFPS [*Clayton et al.*, 1997]. Other researchers have also observed thresholds of soil nutrient levels and environmental conditions that strongly limit denitrification [*Luo et al.*, 1999; *de Klein and van Lotjestijn*, 1996].

The soils used to develop the original denitrification model [*Weier et al.*, 1993] were sieved and repacked to specific bulk densities and treated with various levels of NO_3, glucose, and water. Gas flux measurements showed peak N gas emission rates from denitrification occurring at lower WFPS in the sandy soil than in the clay soil [*Weier et al.*, 1993]. However, as an anaerobic process, denitrification is thought to occur at higher rates in poorly aerated fine-textured soils than in coarse-textured soils at an equivalent WFPS. To test the hypothesis that the anomalous interaction between soil water content and texture is related to the disturbance effects of sifting and packing and to generate data for model refinement, we performed incubations similar to *Weier et al.* [1993] of intact soil cores. The effect of WFPS on N gas flux from denitrification was found to significantly interact with CO_2 emission in the intact fine-textured soils but not in the repacked fine-textured soils. The ratio of e^- acceptor (NO_3) to CO_2 emission (a proxy for e^- donor availability) was a reliable (r^2=0.50%) predictor of the N_2/N_2O ratio in the intact soils but not for the disturbed soils (r^2=0.18). These results suggest that disturbance alters the response of denitrification rates to soil WFPS and the relative proportions of N_2O and N_2 released from soil as a result of denitrification.

This paper is a product of the U.S. Trace Gas Network (TRAGNET) and a Trace Gas Fluxes Working Group sponsored by the U.S. Center for Ecological Analysis and Synthesis (NCEAS). TRAGNET was established in 1992 with the goals of documenting contemporary fluxes of CO_2, CH_4, and N_2O, determining the major controls of trace gas flows, and improving our ability to predict future fluxes in response to ecosystem and climate change. The objectives of the NCEAS Working Group were to analyze the TRAGNET database and enhance our understanding of the controls and magnitudes of CH_4 and N_2O fluxes in various natural and managed ecosystems by using models and by comparing fluxes at various scales. This paper contributes to this goal by quantifying the primary controls of denitrification, a major contributor to N_2O gas emissions.

2. Experiments

To quantify how soil NO_3, labile C, and water levels affect N gas emissions from denitrification, *Weier et al.* [1993] performed 5 day core incubations of four benchmark soils

Table 1. Properties of Soils Used for Model Development

Soil	Classification	PH	BD	% sand	% clay	FC (% PS)
	Repacked Soils					
Valentine sand	typic mixed, mesic ustipsamment	7.4	1.35	90	3	-
Hord silt loam	cumulic fine-silty, mesic haplustoll	7.3	1.15	34	20	-
Yolo silt loam	typic fine silty, mixed xerorthent	7.0	1.20	22	24	-
Sharpsburg	typic fine, montmoril-lonitic, mesic arguidoll	6.5	1.10	3	34	-
	Intact Soils					
HC	nunn clay loam (fine ontmoril-lontic) mesic Aridic Arguistoll	7.6	0.9 - 1.6	26	47	86
PC	renohill clay loam (fine mont-morillonitic) Ustollic Haplargids	7.0	1.1 - 1.4	34	36	76
SCL	nunn loam (fine montmoril-lonitic) mesic aridic Arguistoll	5.7	1.1 - 1.5	47	27	68
SL	ascolon sandy loam (fine loamy mixed) mesic Arguistoll	6.5	1.0 - 1.5	74	13	40

HC, horticultural clay; PC, pasture clay; SCL, sandy clay loam; and SL, sandy loam, repacked soil data from *Weier et al.* [1993].

(Table 1). Nitrate, glucose, and water levels were varied in a full factorial design (Table 2). Soil cores were sieved and repacked to specific bulk densities to obtain precise nutrient concentrations and water contents. To determine if the ratio of N_2/N_2O gases emitted from soil due to denitrification could be related to the independent variables, *Weier et al.* [1993] treated half of the cores in each treatment with acetylene to prevent N_2O reduction. This allowed both N_2 and N_2O emissions to be inferred for each treatment even though N_2O was the only N gas species measured.

In 1996 we collected 120 soil core samples (inside diameter=5.7 cm, depth=10 cm) from each of four soils from northern Colorado (Table 1) for gas flux incubations. The horticultural clay (HC) soil was collected from the Colorado State University horticultural farm near Fort Collins and has a history of barley and wheat cultivation. The pasture clay (PC) soil was collected near Fort Collins and has a history of moderate grazing. The sandy clay loam (SCL) and sandy loam (SL) soils were collected from the Central Plains Experimental Range (CPER) and have a history of moderate grazing. The samples were collected field moist, stored intact in PVC cylinders, and frozen until use for the incubations.

Prior to treatment for incubations, the cores were allowed to equilibrate to ambient temperature. Three cores from each of the four soils were analyzed by KCl extraction for initial NO_3 concentrations and water contents to establish initial WFPS levels. Sets of soil cores were treated by injecting multiple injections into both ends of each soil core, appropriate amounts of solution containing appropriate concentrations of dextrose, and ^{15}N labeled NO_3 to achieve the nominal nutrient levels and water contents for the treatments listed in Table 3. Dextrose was added to stimulate microbial activity because most denitrifying bacteria are heterotrophs. NO_3 was labeled with ^{15}N (99% enrichment) so that N_2 from denitrification could be distinguished from ambient N_2. Labeling of the added NO_3 also allowed N_2O gas from denitrification to be distinguished from any N_2O from nitrification that may have occurred during the incubations. The soil cores, each with a volume of 255 mL, were then placed in 473 mL jars, leaving a headspace volume of 218

Table 2. Experimental Treatments

Soil	Number of Cores	WFPS, %	Added NO_3, ugN gsoil^1	Added Glucose, UgC gsoil^1
		5-Day Incubations of Repacked Cores		
Valentine sand	27	60, 75, 90	0, 139, 277	0, 500, 1000
Hord silt loam	27	60, 75, 90	0, 139, 277	0, 500, 1000
Yolo silt loam	27	60, 75, 90	0, 139, 277	0, 500, 1000
Sharpsburg clay	27	60, 75, 90	0, 139, 277	0, 500, 1000
		3-Day Incubations of Intact Cores		
HC	92	30 – 100	8 – 456	0 - 570
PC	124	49 – 100	9 – 46	0 - 123
SCL	88	43 – 100	8 – 42	0 - 107
SL	88	41 – 100	9 – 48	0 - 120

Five-day incubations of repacked cores from *Weier et al.* [1993].

Table 3. Nominal Treatment Values of the Independent Variables for Intact Soil Core Incubations

Soil	WFPS,%	NO_3, ugN gsoil[1]	Dextrose, ugC gsoil[1]	Reps
HC	40	10	0	3
HC	40	10	50	3
HC	40	40	0	3
HC	40	40	50	4
HC	50	10	0	4
HC	50	10	50	4
HC	50	40	0	4
HC	50	40	50	4
HC	50	100	0	4
HC	50	100	500	4
HC	50	400	0	4
HC	50	400	500	4
HC	70	10	0	4
HC	70	10	50	4
HC	70	40	0	4
HC	70	40	50	4
HC	70	100	0	4
HC	70	100	500	4
HC	70	400	0	4
HC	70	400	500	4
HC	90	10	0	4
HC	90	10	50	4
HC	90	40	0	4
HC	90	40	50	4
PC	50	10	0	5
PC	70	10	0	5
PC	90	10	0	5
PC	100	10	0	5
PC	70	10	25	4
PC	60	10	100	4
PC	70	10	100	4
PC	80	10	100	4
PC	100	10	100	4
PC	60	20	0	4
PC	80	20	0	4
PC	100	20	0	4
PC	80	20	25	4
PC	80	20	50	4
PC	60	20	100	4
PC	70	20	100	4
PC	100	20	100	4
PC	50	40	0	4
PC	60	40	0	4
PC	80	40	0	4
PC	90	40	0	4
PC	100	40	0	4
PC	70	40	25	4
PC	80	40	50	4
PC	60	40	100	4
PC	70	40	100	5
PC	80	40	100	5
PC	90	40	100	5
PC	100	40	100	3
SL	60	10	0	4
SL	80	10	0	4
SL	100	10	0	4
SL	70	10	25	4
SL	70	10	50	4
SL	90	10	50	4
SL	70	25	0	4
SL	100	25	0	4
SL	70	20	25	4
SL	70	20	50	4
SL	70	20	100	4
SL	100	20	100	4
SL	70	40	0	4
SL	80	40	0	4
SL	90	40	0	4
SL	70	40	25	4
SL	70	40	50	4
SL	40	40	100	4
SL	70	40	100	4
SL	80	40	100	4
SL	90	40	100	4
SCL	70	10	0	3
SCL	90	10	0	5
SCL	100	10	0	4
SCL	70	10	25	4
SCL	80	10	50	4
SCL	80	10	100	4
SCL	100	10	100	4
SCL	70	20	0	4
SCL	100	20	0	4
SCL	70	20	25	4
SCL	70	20	50	4
SCL	70	20	100	4
SCL	100	20	100	4
SCL	90	40	0	4
SCL	80	40	0	4
SCL	100	40	0	4
SCL	70	40	25	4
SCL	70	40	50	4
SCL	40	40	100	4
SCL	60	40	100	4
SCL	80	40	100	4
SCL	100	40	100	4

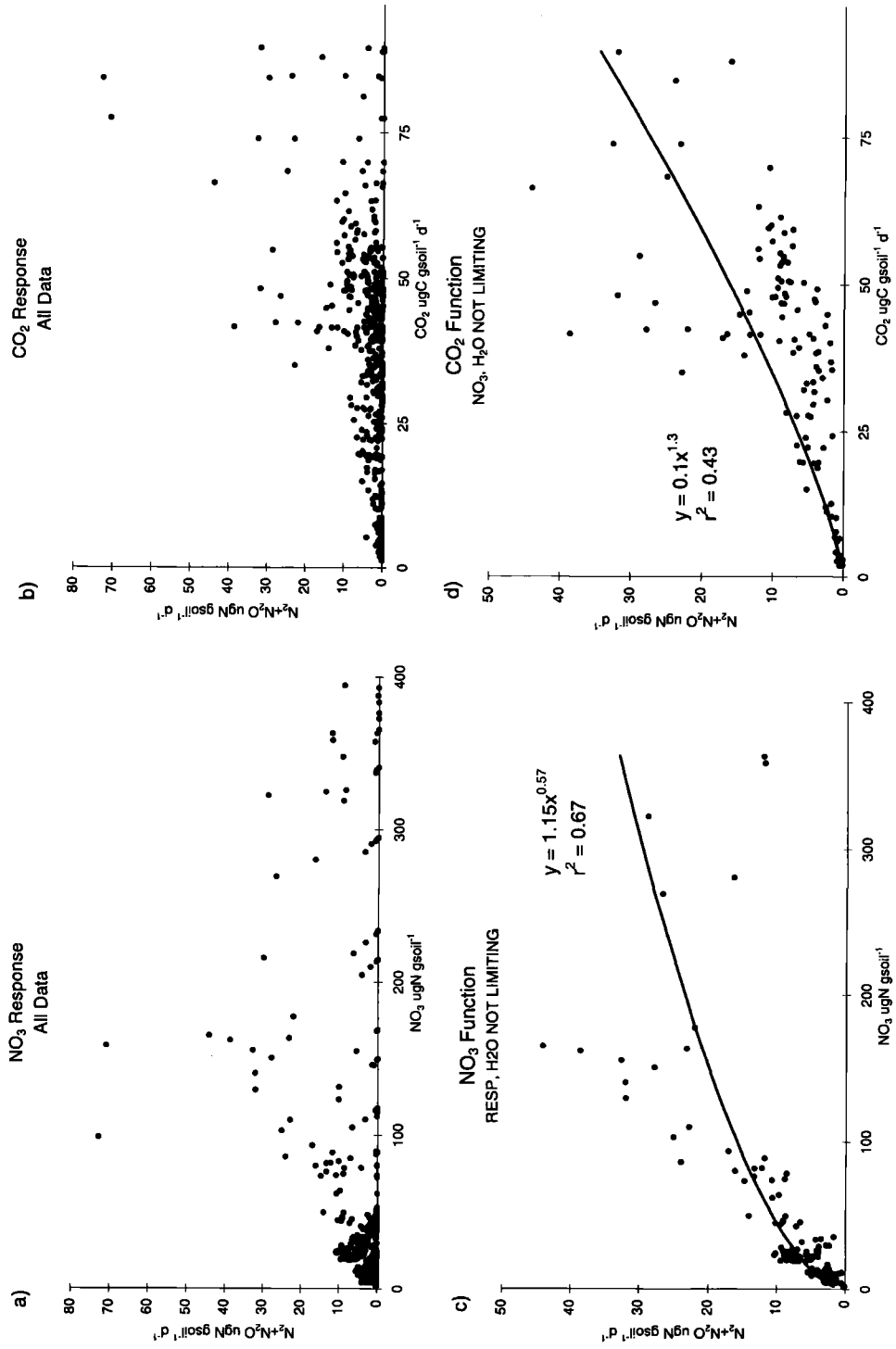

Figure 1. Response of $N_2 + N_2O$ flux from denitrification to soil NO_3 concentration and CO_2 flux using combined data from repacked and intact soil cores. (a,b) NO_3 and CO_2 response using the entire data set. (c) NO_3 function. Data were stratified for $CO_2 > 20$ µgC gsoil^{-1}, and WFPS was not limiting. (d) CO_2 function. Data were stratified for $NO_3 > 20$ µgN gsoil^{-1}, and WFPS was not limiting.

mL. The jars were sealed with a lid that was fitted with a gas sampling septum and incubated at 25°C for 3 days. Forty milliliters of headspace gas were removed by syringe, and the gas samples were analyzed for N_2O and CO_2 by gas chromatography and for N_2 by isotope ratio mass spectrometry within 6 hours of sampling. After sampling, jar lids were removed, and the jar atmosphere was flushed with air. The jars were then resealed and incubated for another 24 hours. Gas flux rates were calculated from changes in headspace concentration of the gases as described by *Mosier and Klemedtsson* [1994]. Both N_2O and N_2 were measured so that the effects of the independent variables on the N_2/N_2O ratio could be investigated. At the end of the incubation period, soil NO_3 concentration in each core was measured by KCl extraction, and soil water content was measured gravimetrically. Soil bulk density was estimated by measuring the soil level in each core before the soil was removed and relating soil volume to the weight of soil. Although discrete amounts of NO_3, dextrose, and water were added to each soil core in a factorial design (see Table 3), sample bulk densities varied among treatment repetitions because cores were not always completely full. As there was a different amount of soil in each core, nutrient concentrations and water contents varied continuously as indicated in Table 2.

3. Data Analysis

We first briefly describe how the model inputs were derived from measurements and then describe in detail how the equations for the model were parameterized by using subsets of the overall data set. For each soil core the initial and final NO_3 concentrations were combined to derive average NO_3 levels for the incubation periods. Total CO_2, N_2, and N_2O emissions for the incubation periods were used to derive average daily gas flux rates for each core.

Heterotrophic CO_2 respiration is used as a model input because it is correlated with labile C availability [*Pascual et al.*, 1998; *Rochette and Gregorich*, 1998; *Parkin*, 1987]. However, respiration can also be limited by soil water content [*Skop et al.*, 1990; *Linn and Doran*,1984]. For the purposes of our model, we need to adjust the measured respiration rates that reflect limitation due to O_2 stress when WFPS is high. Heterotrophic CO_2 emission rates were corrected to account for inhibition of respiration at water contents greater than 60 to 80% WFPS that does not reflect substrate limitation. CO_2 emission was plotted versus WFPS for each intact soil so that a threshold could be established above which WFPS levels inhibit heterotrophic respiration. Then CO_2 emission rates for data points above the established threshold for each soil were appropriately adjusted upward by accounting for how much the WFPS exceeded the threshold and for how sensitive the particular soil was to respiration limitation related to high WFPS levels. We found that the finer-textured soils showed proportionally lower WFPS thresholds and required larger corrections than the coarser textured soils we studied. This is not surprising because the finer-textured soils have lower gas diffusivity at a given WFPS than the coarser textured soils, and thus O_2 diffusion is reduced, and respiration is limited to a greater degree.

Soil volumetric water content at field capacity (FC) for the intact soils was inferred from estimates based on texture analysis [*Saxton et al.*, 1986]. Although FC commonly refers to the water-holding capacity of field soils, we use it to estimate the relative proportions of micropores and macropores and as a driver to calculate soil gas diffusivity in the nondisturbed cores.

The effects of the major input variables (NO_3, CO_2, and WFPS) on N_2+N_2O flux from denitrification were weak when the entire data set was used (Figures 1a-1b). Presumably, the effects of the other inputs confounded the relationships we wanted to establish between denitrification and particular inputs. To minimize this problem, we defined thresholds below which each of the major inputs is assumed to strongly limit denitrification. The thresholds selected to represent limitation due to a particular input reflect the trade off between selectivity of criteria and statistical power as a function of sample size. In cases where the response of denitrification to an input did not suggest an obvious threshold of strong limitation, we erred on the side of keeping marginal data points to avoid establishing relations that are based on fitting a small number of data points rather well but that run the risk of not being applicable to other data sets.

Graphs of N gas emission versus soil NO_3 concentration and CO_2 emission were used to estimate the thresholds below which NO_3 and CO_2 strongly limit denitrification. Figure 1a suggests that soil NO_3 concentrations below 20 μgN gsoil^{-1} strongly inhibit denitrification rates. Figure 1b is somewhat more ambiguous, but CO_2 emissions below 20 μgC gsoil^{-1} d^{-1} appear to strongly limit denitrification rates. Filtering out data points strongly influenced by water limitation was more complicated because WFPS interacts with soil physical properties and O_2 demand to determine the O_2 status of the soil. Data points constrained by strong e^- acceptor (NO_3) or e^- donor (labile C as indicated by CO_2 flux) were eliminated using the above criteria. N_2 + N_2O gas flux was then plotted versus WFPS for each of the repacked soils (Figure 2). Figure 2a suggests that data points below 70% WFPS are strongly influenced by water limitation in the repacked sand, while Figures 2b and 2c suggest that data points below 80% WFPS were strongly limited by water in the repacked loam and clay soils, respectively.

Heterotrophic respiration interacted with WFPS in the intact soils, so plots of N gas flux versus WFPS under low (< 37 μgC gsoil^{-1} d^{-1}) and high (> 37 μgC gsoil^{-1} d^{-1}) respiration were made for each soil (Figure 3). The threshold for high versus low respiration was derived empirically because our goal here is merely to show that respiration may significantly interact with WFPS to influence the O_2 status of some soils. Figures 3a and 3b suggest that the HC soil under low respiration shows strong water limitation below 80% WFPS when respiration is low but that water may not strongly limit denitrification in this soil when respiration is high until WFPS falls below 50%. Figures 3c and 3d suggests that data points below 80% WFPS strongly limit denitrification in the PC soil when respiration is low but that WFPS must fall below 65% to strongly limit denitrification when respiration is high. The SCL and SL soils showed similar responses to WFPS so data points from these soils were combined to establish WFPS thresholds. Figures 3e and 3f suggest that WFPS values below 80% strongly limit denitrification in these soils, regardless of respiration rates. Comparisons of the overall data and stratified data show that the response of denitrification to each input variable was significantly stronger when the other variables were not limiting (Table 4, Figure 1).

To derive a function for the effect of soil NO_3 concentration on denitrification, data points that showed

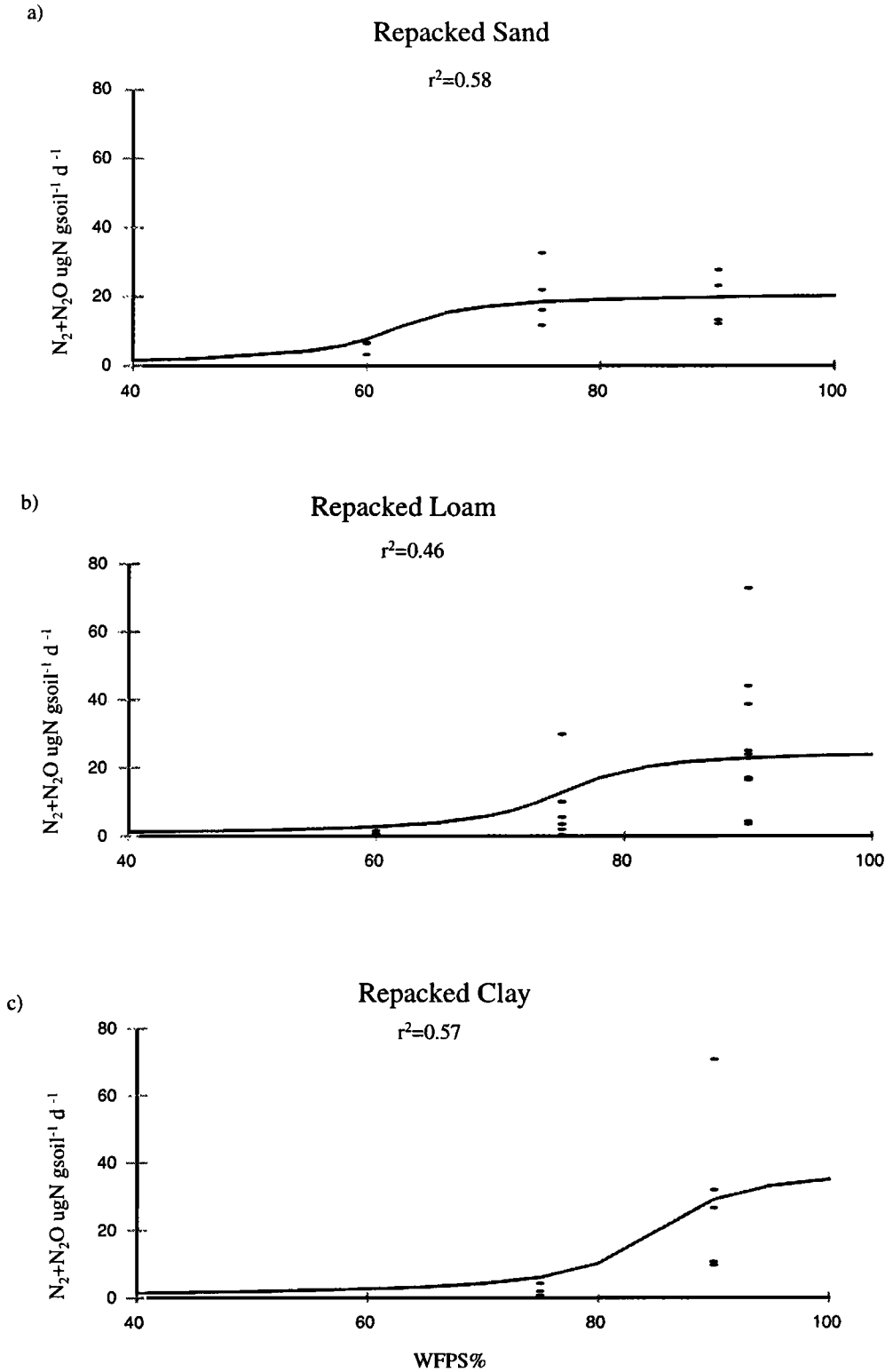

Figure 2. Response of denitrification to soil water-filled pore space with NO_3 and CO_2 not limiting and best fitting arctangent functions for (a) coarse (b) medium, and (c) fine-textured soils from incubations of repacked soil cores [*Weier et al.*, 1993].

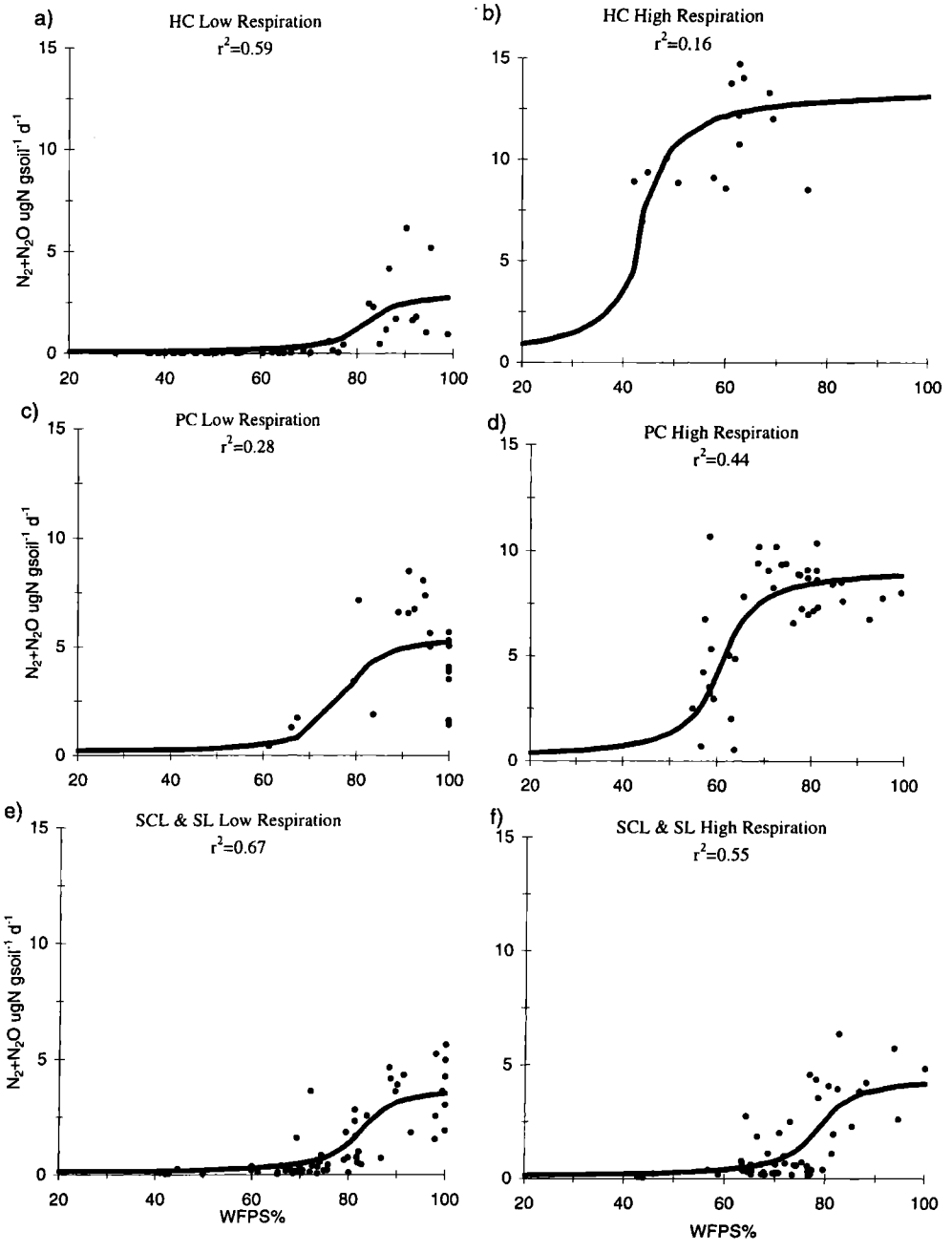

Figure 3. Response of denitrification to soil water-filled pore space with NO_3 not limiting and best fitting arctangent functions for the intact soils under high (>37 μgC gsoil^{-1} d^{-1}) and low (<37 μgC gsoil^{-1} d^{-1}) CO_2 emission.

compared to clay soils (Figure 2). In contrast, peak N gas emission rates occurred at lower water levels in the intact clays, particularly when respiration was high (Figure 3). The significance of the interaction between WFPS and CO_2 in the intact soils was tested by eliminating data points subject to strong NO_3 limitation. The WFPS/CO_2 interaction was found to be highly significant (p<0.0001), whereas the primary effect of water was insignificant (p=0.48) in the clay soils (HC and PC). However, the WFPS/CO_2 interaction was insignificant (p>0.1), and the primary effect of water was highly significant (p<0.0001) in the coarser textured soils (SCL and SL).

To include the interaction of water and respiration in the intact soils, the parameter controlling the inflection point of the arctangent function was allowed to deviate from a fixed value (90% WFPS) as a continuous linear function of respiration. The curve for each soil was optimized by varying a CO_2 multiplier (M) that represents the magnitude of the WFPS/CO_2 interaction.

To infer N_2O flux given total N gas emission from denitrification, it is necessary to estimate the N_2/N_2O ratio. To develop the N_2/N_2O ratio function, data were stratified to filter out records with very low N_2O emission rates (< 0.1 μgN gsoil^{-1}d^{-1}). This was done because N_2O emission rates

Table 4. Comparisons of the Correlation Coefficients (r^2) for the Linear Model Relating N Gas Flux From Denitrification to the Primary Model Input Variables for the Entire Data Set and Stratified Data

	NO_3	CO_2	WFPS%
r^2 entire data set	0.03	0.16	0.16
r^2 stratified data	0.54	0.41	0.38

For each input variable the data were stratified such that the other variables were not strongly limiting.

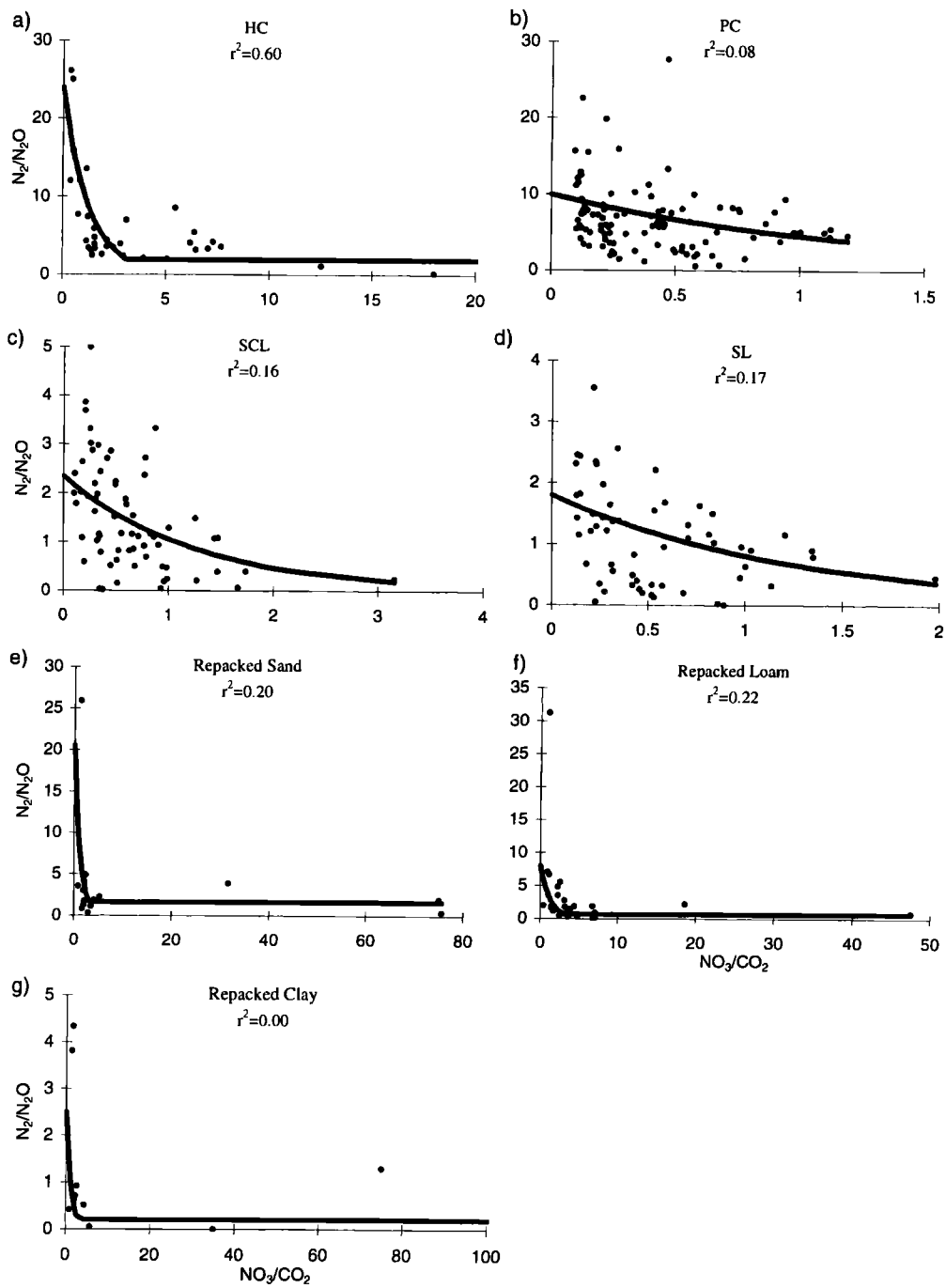

Figure 4. Response of the N_2/N_2O ratio to the ratio of NO_3 (μgN gsoil^{-1}) to heterotrophic CO_2 respiration (μgC gsoil^{-1} d^{-1}) and best fitting exponential functions for (a-d) intact soil cores and (e-g) repacked soil cores [*Weier et al.*, 1993].

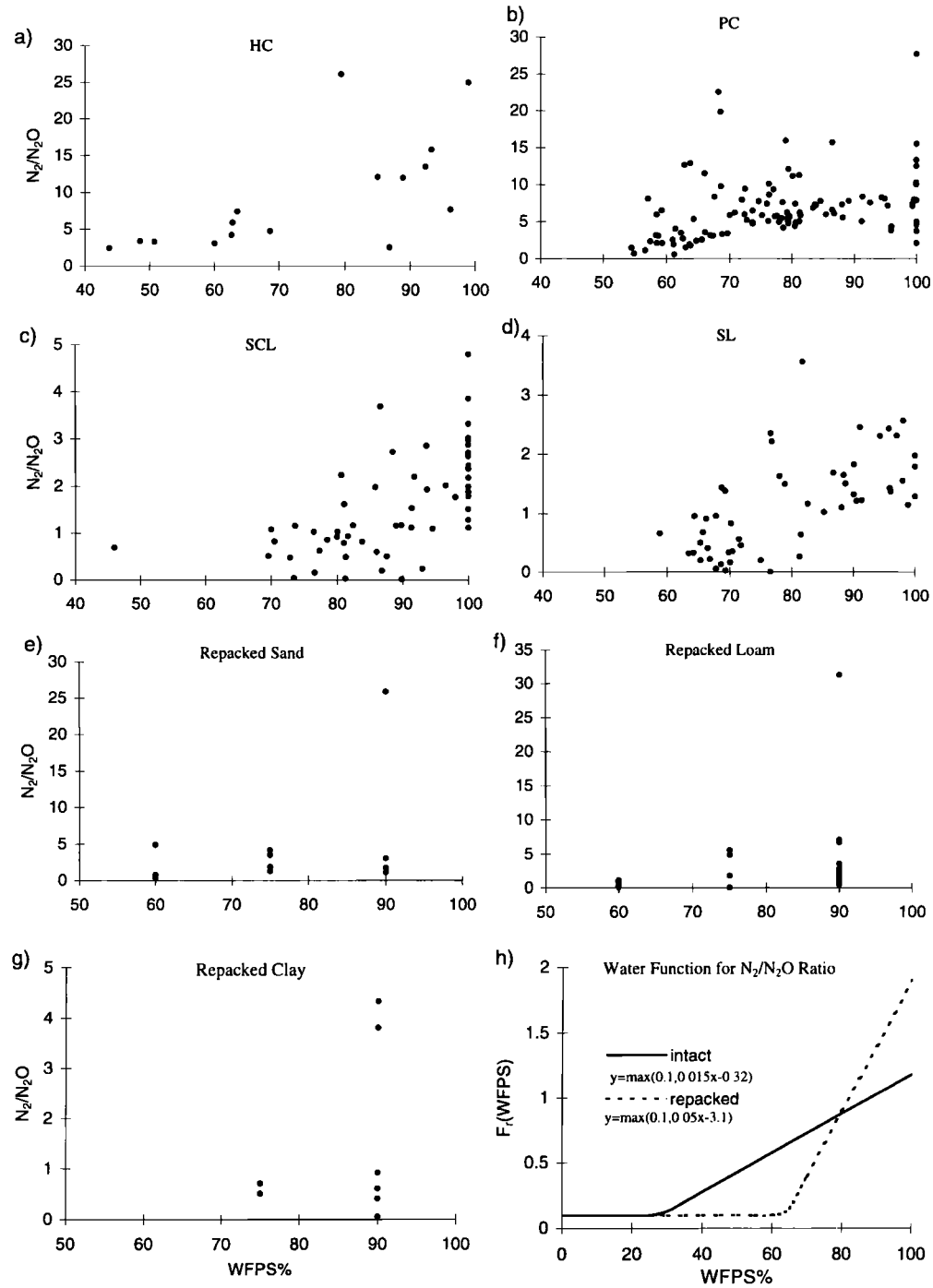

Figure 5. Response of the N_2/N_2O ratio to soil water-filled pore space in (a-d) intact soils and (e-g) repacked soils [*Weier et al.*, 1993] and (h) optimized disturbance specific water multipliers.

close to 0 can lead to extremely high (50-200) N_2/N_2O ratios and it is more important to predict the N_2/N_2O ratio correctly when N_2O fluxes are significant. The ratio of NO_3/CO_2 and soil WFPS had significant effects on the observed N_2/N_2O ratios. The soils were analyzed separately because soil properties also influence the N_2/N_2O ratio. All of the soils showed stable N_2/N_2O ratios when NO_3/CO_2 was high and increasing N_2/N_2O ratios as NO_3/CO_2 approached 0 so an exponential function was fit for each soil (Figure 4). The parameter controlling curve shape was fixed, and equations were optimized by varying the maximum N_2/N_2O ratio (k_1) for each soil. The N_2/N_2O ratio increased with soil water content when the NO_3/CO_2 ratio was not limiting (Figure 5). Because the effect of NO_3/CO_2 on N_2/N_2O ratios was stronger than the effect of WFPS (r^2=0.50 versus 0.37), water was included in the model as a multiplier of the estimate from the

NO_3/CO_2 function. Optimizing the interaction resulted in linear best fitting water functions for the intact and repacked soils (Figure 5h).

To quantify the differences in soil physical properties that influence the extent to which respiration may contribute to soil anoxia and the maximum N_2/N_2O ratio, a gas diffusivity coefficient (D_{FC}) was calculated for each of the nondisturbed soils. D_{FC}, a relative index of gas diffusivity through soil assuming a water content of field capacity, was calculated as a function of porosity and FC using the method described by *Potter et al.*, [1996b] for aggregated soils. The parameter controlling the potential for respiration to shift the x inflection point of the denitrification water curve to lower WFPS values varied inversely with D_{FC} (Figure 6a). The parameter controlling the maximum value of the N_2/N_2O ratio function was also correlated with D_{FC} (Figure 6b).

4. The Model

A simple spreadsheet model was developed to simulate N gas flux from denitrification in soils. The inputs are soil NO_3, heterotrophic respiration, WFPS, field capacity, and bulk density. A daily time step is used so that the model is sensitive to the irrigation, rainfall, and snow melt events that often accompany high rates of denitrification. The equation for total nitrogen gas (N_2+N_2O) flux from denitrification is

$$D_t = \min[F_d(NO_3), F_d(CO_2)]F_d(\text{WFPS}). \quad (2)$$

$F_d(CO_2)$ and $F_d(NO_3)$ are general functions relating N gas flux to soil respiration and nitrate levels (Figures 1c-1d). The total N gas flux equation (D_t) estimates potential N gas flux by selecting the minimum of the CO_2 and NO_3 functions. This is modified by F_d(WFPS), a dimensionless multiplier. For intact soils, the x inflection point is a function of respiration and soil

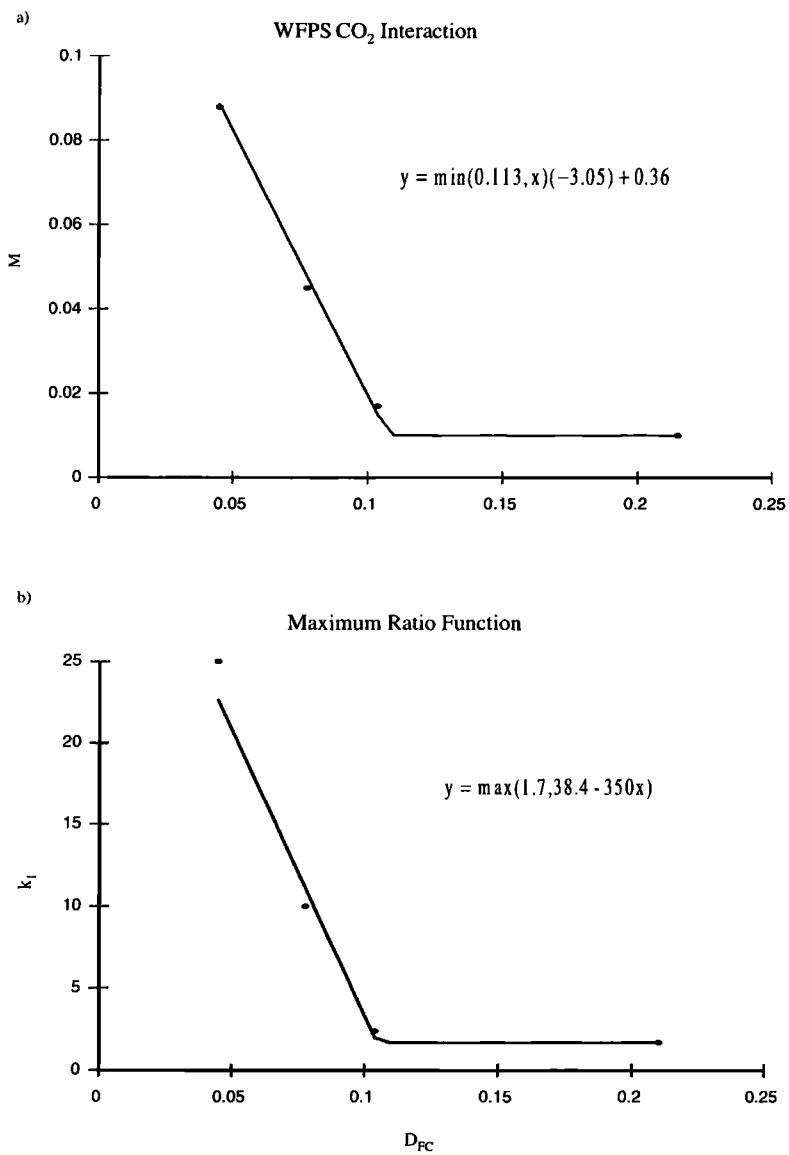

Figure 6. Intact soil specific parameters as functions of soil gas diffusivity at field capacity (D_{FC}). (a) Parameter controlling the magnitude of the effect of CO_2 on the denitrification water curve. (b) Parameter controlling the maximum value of the N_2/N_2O ratio curve.

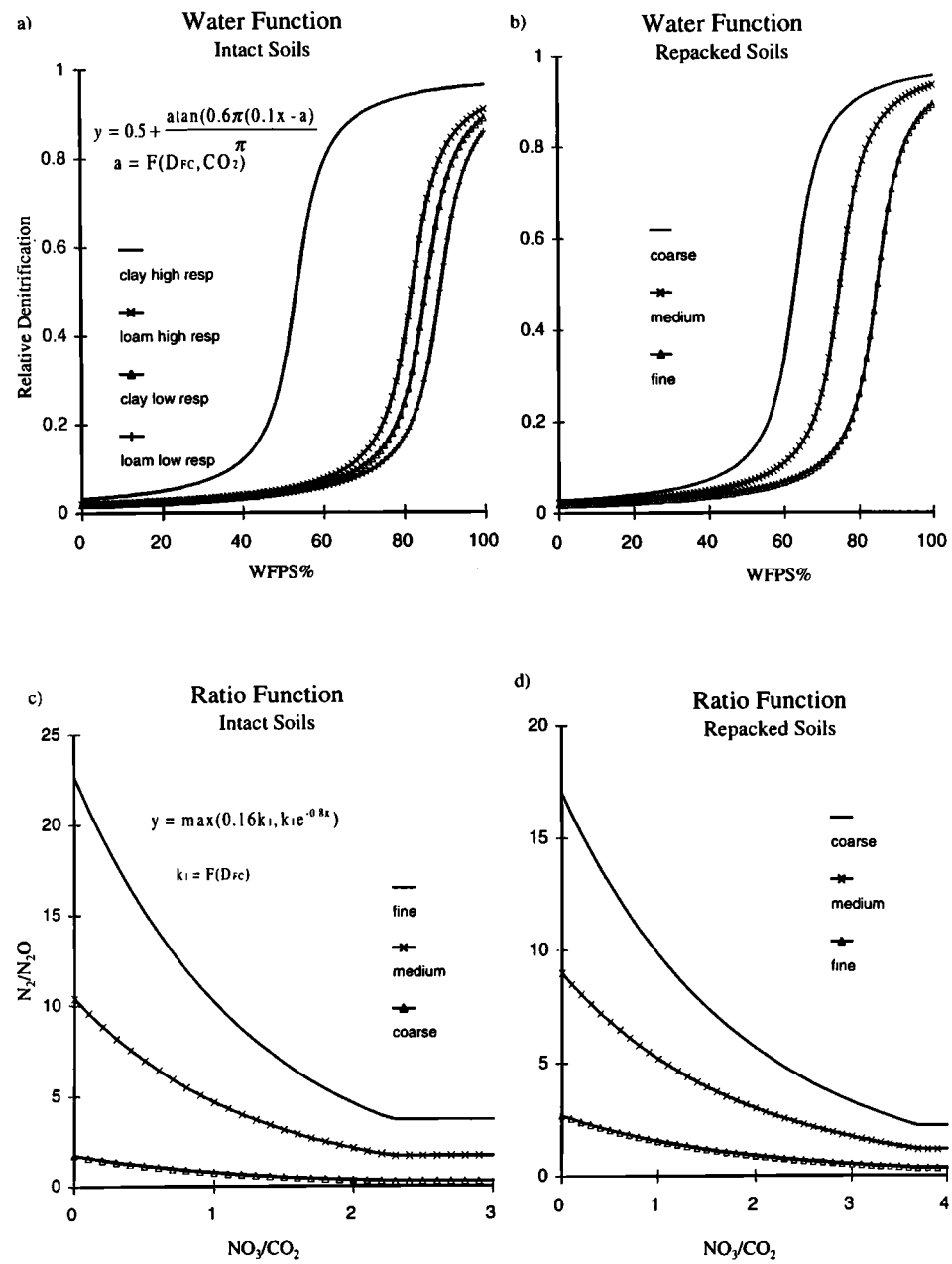

Figure 7. Soil specific total nitrogen gas flux from denitrification water curves for (a) intact and (b) disturbed soils, and N_2/N_2O ratio functions for (c) intact and (d) disturbed soils.

gas diffusivity at field capacity:

$$x \text{ inflection} = 0.90 - M(CO_2), \quad (3)$$

where the multiplier (M) is a function of D_{FC} (Figure 6a). Respiration has a much stronger effect on the water curve in clay soils with low D_{FC} than loam or sandy soils with high D_{FC} (Figure 7a). The x inflection point of the water function is texture specific in disturbed soils (Figure 7b).

After calculating total N gas flux the ratio of N_2/N_2O is estimated:

$$R_{N2/N2O} = F_r(NO_3/CO_2)F_r(\text{WFPS}). \quad (4)$$

$F_r(NO_3/CO_2)$ estimates the ratio as a function of electron donor to substrate (Figures 7c-7d). The intercept of $F_r(NO_3/CO_2)$ is a function of D_{FC} in the intact soils (Figure 6b) and is texture specific in the repacked soils (Figure 7d). The ratio is modified by F_r(WFPS), a disturbance specific multiplier to account for the effect of soil water on N_2/N_2O (Figure 5h). The simulated N_2O flux from denitrification is

$$D_{N2O} = D_t/(1 + R_{N2/N2O}). \quad (5)$$

To convert CO_2 inputs and N gas outputs between laboratory units of μgC or μgN $gsoil^{-1}$ d^{-1} and field units of kgC or kgN ha^{-1} d^{-1}, an active soil depth of 20 cm is assumed because the majority of N cycling occurs in the top 5 cm of mineral soil and N cycling decreases dramatically with depth [*Schimel and Parton*, 1986].

5. Results and Discussion

The model simulated N_2O+N_2 gas fluxes from denitrification rather well in the intact soils (r^2=0.74, mean error < 15%), but N gas flux rates in the repacked soils used for model development were underestimated (Figures 8a-8b). The N_2/N_2O ratio function also performed better in the intact (r^2=0.52) soils compared to the disturbed (r^2=0.24) soils (Figures 8c-8d). Estimates of N_2O emission include the error of the total N gas function and the error of the ratio function, but the model still achieved r^2 values of 0.53 and 0.41 when comparing simulated and observed N_2O flux rates in the intact and disturbed soils, respectively (Figures 8e-8f). These results support the assumptions that denitrification is a function of labile C, NO_3, and water levels, and the process is controlled by the factor that is most limiting.

Field data from irrigated agricultural soils in Pakistan [*Mahmood*, 1997] were used for model validation. The model achieved an r^2 of 0.47 with the independent data set, and the mean error was less than 5% in these soils (Figure 8g). The performance of the model with the field data suggests that labile C, NO_3, and water levels are significant controls of denitrification, but other factors not accounted for by the model, such as microbial biomass and species composition, may be important controls in field soils. Model error could also result from finer-scale variation in the input parameters than the model is designed to resolve or differences in experimental methodologies among the data sets.

Denitrification rates in the repacked soils were underestimated because these soils showed stronger responses to high labile C and NO_3 additions than the intact soils, but the model is biased toward the intact cores by the sample sizes of the data sets. This bias in favor of the intact soils is justified because the intact cores more closely resemble field soils in that they were less disturbed and they received generally lower additions of C and NO_3 than the repacked soils (Table 2).

The structure of our model and the parameterization of the equations assumed that the law of the minimum applies to denitrification. Evidence showing that the response of N gas flux from denitrification to the input variables was significantly stronger when the other inputs were not limiting (Table 4) supports this assumption. *Dobbie et al.* [1999] showed that WFPS had a significant effect on N_2O emissions from agricultural soils when data points strongly limited by soil NO_3 concentration were removed. Similarly, *Luo et al.* [1999] observed that additions of carbon to a soil that was nitrate limited had little effect on denitrification rates but nitrate additions stimulated denitrification rates.

Subsets of data from intact and disturbed soil core incubations were used to derive NO_3 and CO_2 functions. The response of denitrification to NO_3 was stronger at low NO_3 levels, implying some degree of NO_3 saturation exists (Figure 1a). Other researchers have also observed an N saturation effect [*Sholefield and Hawkins*, 1997]. The response of denitrification to respiration was fairly linear but increased slightly at high CO_2 levels (Figure 1b).

The shape of our water curve is consistent with curves developed from different data sets, but our water function is different in two ways. Whereas previous models have used an exponential function to represent the effect of soil WFPS on denitrification (*Linn and Doran*, 1984; *Mosier and Parton*, 1985), we use an arctangent function because denitrification rates tend to level off once WFPS exceeds 70-90%. This is consistent with data presented by *Dobbie et al.* [1999] and *Clayton et al.* [1997]. Also, previous curves show denitrification reaching 1/2 its maximum potential rate at 75-80% WFPS, but our curve predicts that denitrification can reach 1/2 its maximum rate at WFPS as low as 50-60% in diffusion limited soils when O_2 demand is high. The potential for O_2 demand, as indicated by respiration rates, to contribute to microsite anoxia is soil specific because particle size distribution and aggregation influence the diffusivity of gases in soil. At low respiration rates the intact soils did not become sufficiently anoxic for peak denitrification rates to occur until WFPS exceeded 85%, regardless of texture. However, when CO_2 flux exceeded ~40 μgC gsoil^{-1} d^{-1}, peak denitrification rates occurred at lower water contents in the intact clays (Figure 3). Intact clay soils contain a large proportion of microsites in aggregates that can remain or become anoxic after the large interaggregate pores have drained [*Smith and Dowdell*, 1974]. This phenomenon may explain the high rates of denitrification observed in the intact clay soils at relatively low water contents.

Nitrate reduction may occur in the presence of O_2 when microbial activity is high [*Cady and Bartholomew*, 1961]. The potential for respiration to contribute to soil anoxia is inversely proportional to soil gas diffusivity calculated at field capacity (Figure 6a). D_{FC} is a function of total soil pore space and pore size distribution. The HC and PC soils have high field capacities and hence a large proportion of micropores so gas diffusivity is inhibited. When respiration is high, O_2 may not diffuse fast enough to entirely supply microbial demand and some gas-filled pores may become anoxic. The SCL and SL soils have high D_{FC} and respiration rate had little effect on the water curve for these soils (Figures 3e-3f). The model predicts that high gas diffusivity and a small proportion of micropores maintain aerobic conditions in sandy soils unless a majority of the macropores are saturated, regardless of labile C availability.

Contrary to expectations, peak denitrification rates occurred at lower (< 80%) WFPS in the repacked sandy soil compared to the repacked clay, but disturbance effects may account for this. The sand was packed at a higher bulk density than the other soils (Table 1a). The decrease in soil gas diffusivity associated with lower porosity may allow the sand to reach anaerobic status at lower water levels. The water curve for the repacked clay is similar to that of the intact clay under low respiration (Figures 7a-7b). In other words, the disturbed clay exhibited no effect of CO_2 on the x inflection point of the WFPS function. Field soils may contain blocked or tortuous pores that do not contribute to gas diffusion even though they are filled with air and disturbance has been shown to alter the proportion of these pores, particularly in fine textured soils [*Gradwell*, 1961]. This may explain why the repacked clay soil showed little evidence of anoxia at WFPS less than 80%. Also, *Weier et al.* [1993] passed soils through a 2 mm sieve. *Sexstone et al.* [1985] measured O_2 levels in aggregates and found that aggregates of radius larger than 2 mm often harbored anaerobic micropores even though the bulk soil was aerobic. The repacked clays showed high denitrification rates only at high water contents because the

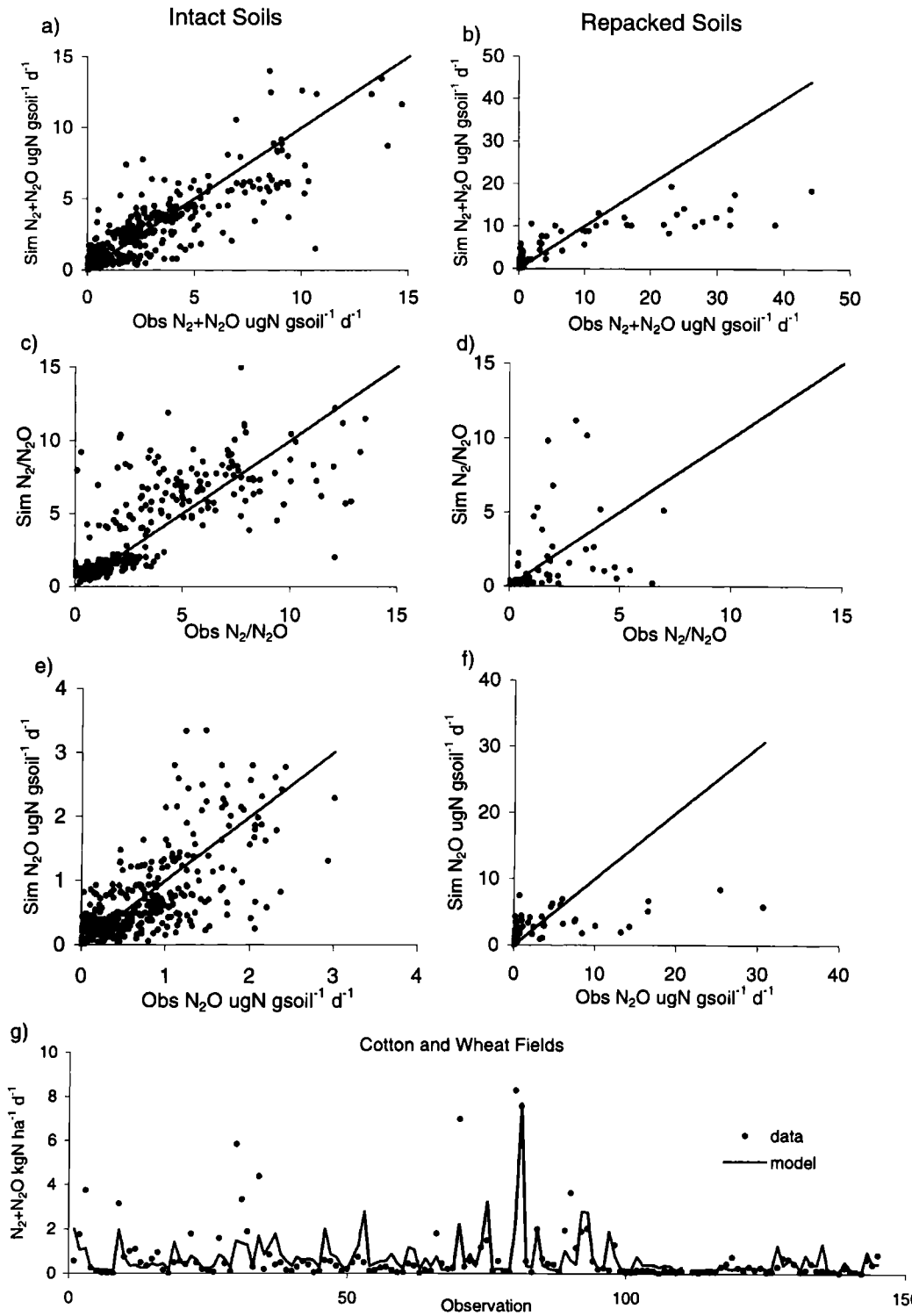

Figure 8. Simulated versus observed N gas flux rates and N_2/N_2O ratios with 1-1 lines: (a,b) Total N gas flux rates in the soils used for model building, r^2=0.74 and 0.75, respectively. (c,d) The N_2/N_2O ratios in the soils used for model building, r^2=0.52 and 0.24, respectively. (e,f) N_2O flux rates in the soils used for model building r^2=0.53 and 0.41, respectively. (g) Total N gas flux rates from irrigated fields [*Mahmood*, 1997] and model simulations, r^2=0.47.

change in soil aggregate structure and pore size distribution induced by disturbance and sieving decreased the proportion of micropores that can become anoxic at moderate water contents.

The ratio of N_2/N_2O reflects the completeness of nitrogen reduction. It is a function of soil gas diffusivity and the relative proportion of electron acceptor to electron donor. N_2/N_2O increased with water content, supporting the assertion that as soils become more anoxic more N_2O will be further reduced to N_2 before being emitted from the soil (*Davidson and Schimel*, 1995). The data also support the suggestion of *Firestone and Davidson* [1989] that N_2O is more likely to be further reduced when substrate (labile C) is in excess compared to the initial electron acceptor, NO_3, (Figure 4).

The magnitude of the N_2/N_2O ratio was highly variable among soils (Figures 6b, 7c, and 7d). Higher ratios in the intact clays than the intact loams can be explained by gas diffusivity. Lower gas diffusion rates in the intact clays contribute to anoxia and increase the residence time of N_2O in the soil, thus increasing the probability that N_2O from denitrification will be reduced to N_2 in the soil. The repacked soils showed higher ratios in sand than clay, and the response of N_2/N_2O to the model inputs was more variable than in the intact soils, suggesting that disturbance strongly affects soil properties that influence the N_2/N_2O ratio.

6. Conclusions

The denitrification model shows that simple functions based on soil water, nitrate, respiration, and texture can be combined to model nitrogen gas emission from soil. The model performed well with the nondisturbed soils used for model building and testing. However, N gas flux rates were underestimated in the disturbed soils. The model needs to be tested with soils from diverse biomes.

Model results (Figure 8) and comparisons of stratified and unstratified data (Table 4) support the assumption that denitrification rates are controlled by the molecular species (NO_3 or labile C) or environmental condition (O_2 availability) that is most limiting. The data used for model building suggest that general NO_3 and CO_2 functions apply to diverse soils and that the water curve for N gas emission from denitrification can vary with respiration in nondisturbed soils. High CO_2 respiration not only indicates high labile C availability but also contributes to microsite anoxia in unsaturated fine textured soils. Daily variations in soil NO_3, CO_2, and WFPS may adequately explain daily variability of N_2/N_2O at a given site, but average ratios vary by up to a factor of 10 among soils. Thus a single function cannot be used to model the N_2/N_2O ratio.

Model parameters related to soil properties that affect gas diffusivity showed opposite trends in response to texture in the intact and repacked soils. The intact clays became anaerobic at lower WFPS and had higher N_2/N_2O ratios than the intact loams. Both observations suggest than the intact clays contain a higher volume of anoxic microsites at a given water content than the loams. However, the repacked clay required higher WFPS for denitrification and showed lower N_2/N_2O ratios than the repacked loamy or sandy soils. Disturbance appears to enhance gas diffusivity in fine textured soils and to decrease aeration in coarse soils. Disturbance also decreases the ability of NO_3/CO_2 and WFPS to predict the N_2/N_2O ratio (Figures 8c-8d). The data show that in nondisturbed soil cores the response of total N gas flux from denitrification and the N_2/N_2O ratio vary among soils and that differences in response may be explained by soil physical properties related to gas diffusivity. These results support the hypothesis that disturbance significantly alters the effect of soil water content on denitrification. Further work is needed to better predict how soil factors related to particle size distribution and aggregate structure interact with water and respiration to control O_2 availability and potential N gas emission rates from denitrification.

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S. J. Del Grosso, D. S. Ojima, and W. J. Parton, Natural Resources Ecology Laboratory, Colorado State University, Fort Collins, CO 80523-1499. (delgro@nrel.colostate.edu; dennis@nrel.colostate.edu; billp@nrel.colostate.edu)

A. E. Kulmala, Agriculture Research Center of Finland, FIN-31600, JOK101NEM, Finland.

A. R. Mosier, Agriculture Research Service, U. S. Department of Agriculture, Fort Collins, CO 80523. (amosier@lamar.colostate.edu).

S. Phongpan, Thailand Department of Agriculture, Bangkok, Thailand.

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