The Potential for Nitrification and Nitrate Uptake in the Rhizosphere of Wetland Plants: A Modelling Study

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● *Background and Aims* It has recently found that lowland rice grown hydroponically is exceptionally efficient in absorbing NO_3^-, raising the possibility that rice and other wetland plants growing in flooded soil may absorb significant amounts of NO_3^- formed by nitrification of NH_4^+ in the rhizosphere. This is important because (*a*) this NO_3^- is otherwise lost through denitrification in the soil bulk; and (*b*) plant growth and yield are generally improved when plants absorb their nitrogen as a mixture of NO_3^- and NH_4^+ compared with growth on either N source on its own. A mathematical model is developed here with which to assess the extent of NO_3^- absorption from the rhizosphere by wetland plants growing in flooded soil, considering the important plant and soil processes operating.
● *Methods* The model considers rates of O_2 transport away from an individual root and simultaneous O_2 consumption in microbial and non-microbial processes; transport of NH_4^+ towards the root and its consumption in nitrification and uptake at the root surface; and transport of NO_3^- formed from NH_4^+ towards the root and its consumption in denitrification and uptake by the root. The sensitivity of the model's predictions to its input parameters is tested over the range of conditions in which wetland plants grow.
● *Key Results* The model calculations show that substantial quantities of NO_3^- can be produced in the rhizosphere of wetland plants through nitrification and taken up by the roots under field conditions. The rates of NO_3^- uptake can be comparable with those of NH_4^+. The model also shows that rates of denitrification and subsequent loss of N from the soil remain small even where NO_3^- production and uptake are considerable.
● *Conclusions* Nitrate uptake by wetland plants may be far more important than thought hitherto. This has implications for managing wetland soils and water, as discussed in this paper.

Key words: Ammonium, flooded soil, modelling, nitrate, nitrification–denitrification, rice, rhizosphere, root aeration, soil aeration, wetland plants.

INTRODUCTION

In flooded soils, NO_3^- added to the soil or formed by nitrification of NH_4^+ in aerobic zones near roots or at the soil surface tends to be rapidly lost through denitrification in the anoxic soil bulk, and it is therefore generally assumed that wetland plants take up little NO_3^- compared with NH_4^+. However, in experiments using the radiotracer ^{13}N and hydroponically grown seedlings of rice, it was found that a widely grown variety of lowland rice was exceptionally efficient in absorbing and assimilating NO_3^- compared with NH_4^+, and compared with other plant species (Kronzucker *et al.*, 1999, 2000). This suggests a particular adaptation of rice to NO_3^- and raises the possibility that NO_3^- absorption by rice and perhaps other wetland plants is more important than generally thought. Since growth and yield of most plant species are superior under mixed NO_3^-–NH_4^+ nutrition (Taiz and Zeiger, 2002), this possibility is intriguing and warrants further investigation.

Three lines of evidence from Kronzucker *et al.* suggest unusually efficient NO_3^- absorption. First, in the Michaelis–Menten relationships fitted to N influx data over an ecologically and agronomically relevant range of N supply, and plants of identical N status, V_{max} for steady-state N influx was 40 % greater for NO_3^- than for NH_4^+, and K_M was 50 % smaller. Secondly, NO_3^- absorption was inducible and, in plants deprived of NO_3^- for 24 h, the induction of NO_3^- uptake was exceptionally rapid, peaking within 2 h; in comparison, in barley, which is considered a highly efficient NO_3^- user, full induction requires up to 24 h, and in white spruce, which is considered poor at using NO_3^-, full induction takes several days (references in Kronzucker *et al.*, 1995, 1997, 2000). Thirdly, from the subcellular distribution of N absorbed by plants fed either NO_3^- or NH_4^+, estimated from the kinetics of ^{13}N efflux from labelled roots, the proportion of NO_3^- translocated to the shoot was 50 % larger, and that lost through efflux back out of the roots 50 % smaller. When NO_3^- and NH_4^+ were provided together at the same total N concentration as in the single N species experiments, absorption and assimilation of NO_3^- were repressed, but those of NH_4^+ were stimulated to the extent that net N influx was doubled compared with plants fed solely on NH_4^+. Because very little free NH_4^+ is translocated to the shoot in rice (Kronzucker *et al.*, 1998), this indicates that NO_3^- enhances NH_4^+ assimilation in some way, possibly through the NO_3^--specific induction of additional pathways for NH_4^+ assimilation (Kronzucker *et al.*, 1999; Britto and Kronzucker, 2004).

The extent of NO_3^- uptake by roots in flooded soil will depend on its rate of formation from NH_4^+ near root surfaces, its rate of transport to and absorption by the root, and its rate of transport away from the root and loss through denitrification. The rates of NO_3^- formation and subsequent

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denitrification will depend on reducing conditions in the soil and sinks for O_2 other than nitrification. The sinks include microbial and non-microbial processes.

In this paper, a mathematical model of these processes is developed with which to calculate rates of formation, uptake and loss of NO_3^- over the range of conditions in which wetland plants grow.

THEORY

Consider the movements of O_2, NH_4^+ and NO_3^- in anoxic flooded soil near a cylindrical root that simultaneously releases O_2 and absorbs NH_4^+ and NO_3^-. The microbial sinks for O_2 include both autotrophic processes, such as oxidation of NH_4^+, S^{2-} and CH_4, and heterotrophic processes (Conrad and Frenzel, 2002; Kirk, 2004). The non-microbial sinks include oxidation of inorganic reductants in the soil, such as Fe(II), which may be both mobile and immobile (Howeler and Bouldin, 1971; Reddy *et al.*, 1980; Kirk and Solivas, 1994).

In initially anoxic soil, populations of aerobic microbes will be small, and therefore non-microbial processes consuming O_2 will initially tend to dominate. As inorganic reductants close to the roots become exhausted, the rate of non-microbial O_2 consumption will decline. Concomitantly, the rate of microbial O_2 consumption will increase as aerobic populations develop. Hence the system will be complex and dynamic. We have some understanding of the kinetics of the non-microbial processes (Ahmad and Nye, 1990; Kirk *et al.*, 1990; Kirk and Solivas, 1994), but only a weak understanding of the microbial processes and the complex interactions they involve (Bodelier *et al.*, 2000, 2004; Brune *et al.*, 2000; van Bodegum *et al.*, 2001). Therefore, a very elaborate treatment of the O_2-consuming processes, dissecting out the various contributors, is unjustified at this stage of our understanding, and, in our model, we therefore combine microbial and non-microbial processes. Likewise, our understanding of growth rates and activities of NH_4^+-oxidizing microbes in the rhizosphere of wetland plants and interactions with nutrients, toxins and competing substrates is insufficient for a very elaborate treatment, and hence we apply the simplest realistic treatment, with the maximum rate of nitrification as a proportion of the maximum rate of overall O_2 consumption.

The following sections give the equations we use to describe the system. The symbols used are defined in Table 1.

Oxygen

The transport of O_2 away from the root and its simultaneous consumption in soil processes is described by the equation

$$\frac{\partial [O_2]}{\partial t} = \frac{1}{r}\frac{\partial}{\partial r}\left[rD_{LO}\theta f\frac{\partial [O_2]_L}{\partial r} + av[O_2]_L\right] - R_O \quad (1)$$

where R_O is the rate of consumption in soil processes. The whole-soil concentration of O_2 is related to the concentration in solution by $[O_2] = \theta[O_2]_L$. Following the reasoning above, we lump together microbial and

TABLE 1. *List of symbols*

Symbol	Meaning	Dimensions*
a	Root radius	Length
b	Radius of zone of root influence	Length
b_{NH4}	Buffer power for NH_4^+, $d[NH_4^+]/d[NH_4^+]_L$	Volume$_L$ volume^{-1}
D_L	Solute diffusion coefficient in water, subscripted A, N or O for NH_4^+, NO_3^- and O_2	Area time^{-1}
F_{mNH4}	Maximum influx of NH_4^+ into roots	Mass area^{-1} time^{-1}
F_{mNO3}	Maximum influx of NO_3^- into roots	Mass area^{-1} time^{-1}
f	Soil diffusion impedance factor	
I_{Denit}	Inhibition function for denitrification	
K_{MDenit}	Michaelis constant for denitrification	Mass volume$_L^{-1}$
K_{MNH4}	Michaelis constant for NH_4^+ uptake	Mass volume$_L^{-1}$
K_{MNit1}	Michaelis constant for nitrification (re O_2)	Mass volume$_L^{-1}$
K_{MNit2}	Michaelis constant for nitrification (re NH_4^+)	Mass volume$_L^{-1}$
K_{MNO3}	Michaelis constant for NO_3^- uptake	Mass volume$_L^{-1}$
K_{MO}	Michaelis constant for O_2 consumption	Mass volume$_L^{-1}$
L_V	Root length density	Length volume^{-1}
$[NH_4^+]_L$	Concentration of NH_4^+ in soil solution	Mass volume$_L^{-1}$
$[NO_3^-]_L$	Concentration of NO_3^- in soil solution	Mass volume$_L^{-1}$
$[O_2]_L$	Moncentration of O_2 in soil solution	Mass volume$_L^{-1}$
V_{mDenit}	Maximum rate of denitrification	Mass volume^{-1} time^{-1}
V_{mNit}	Maximum rate of nitrification	Mass volume^{-1} time^{-1}
V_{mO}	Maximum rate of O_2 consumption	Mass volume^{-1} time^{-1}
v	Water flux into root	Length time^{-1}
λ	Root wall permeability factor	Length time^{-1}
θ	Soil water fraction by volume	Volume$_L$ volume^{-1}

* Subscript L indicates soil solution; no subscript indicates whole soil.

non-microbial sinks for O_2 and describe net O_2 consumption using Michaelis–Menten kinetics:

$$R_O = V_{mO}\frac{[O_2]_L}{K_{MO} + [O_2]_L} \quad (2)$$

The boundary conditions for eqn (1) are as follows. The flux of O_2 across the root surface, $r = a$, depends on the rate of delivery of O_2 through the root, the external sink for O_2 in the soil and the permeability of the root wall separating the soil solution from the root gas spaces. Following Armstrong and Beckett (1987), we define a root wall permeability factor, λ, relating the flux across the root wall to the difference in O_2 concentration across it. The flux across the root wall is equal to the flux into the soil at $r = a$. Hence

$$D_{LO}\theta f\frac{\partial [O_2]_L}{\partial r} + v[O_2]_L = \lambda\left([O_2]_{Lc} - [O_2]_{La}\right) \quad r = a, \quad t \geqslant 0$$

$$(3)$$

where subscripts c and a indicate the root cortical tissue and the soil at the root surface, respectively. Armstrong and Beckett give values of λ derived from experiments with polarographic electrodes (see Parameter Values, below). At the other boundary where the zones of influence of adjacent roots overlap, there is no transfer of O_2. Thus

$$D_{LO}\theta f\frac{\partial [O_2]_L}{\partial r} + \frac{av}{b}[O_2]_L = 0 \quad r = b, \quad t \geqslant 0 \quad (4)$$

Ammonium

The transport of NH_4^+ towards the root and its simultaneous consumption in nitrification is described by the equation

$$\frac{\partial [NH_4^+]}{\partial t} = \frac{1}{r}\frac{\partial}{\partial r}\left[rD_{LA}\theta f\frac{\partial [NH_4^+]_L}{\partial r} + av[NH_4^+]_L\right] - R_{Nit}$$

(5)

The whole-soil concentration of NH_4^+ is related to the concentration in solution by the soil NH_4^+ buffer power: $b_{NH4} = d[NH_4^+]/d[NH_4^+]_L$. The rate of nitrification will depend on the concentrations of O_2 and NH_4^+, and we describe this using dual-substrate Michaelis–Menten kinetics (see McConnaughey and Bouldin, 1985, for NO_3^- reduction, or Arah and Stephen, 1998, for CH_4 oxidation):

$$R_{Nit} = V_{mNit}\frac{[O_2]_L}{K_{MNit1} + [O_2]_L}\frac{[NH_4^+]_L}{K_{MNit2} + [NH_4^+]_L}$$

(6)

where V_{mNit} is the rate in the absence of substrate limitation and K_{MNit1} and K_{MNit2} are Michaelis constants. The boundary conditions for eqn (5) are as follows. The flux of NH_4^+ into the root will depend on the concentration of NH_4^+ in solution at the root surface and the root NH_4^+ absorption properties. In accordance with conventional practice (Kronzucker *et al.*, 1997, 2000), we describe this with a Michaelis–Menten equation:

$$D_{LA}\theta f\frac{\partial [NH_4^+]_L}{\partial r} + v[NH_4^+]_L = F_{mNH4}\frac{[NH_4^+]_{La}}{K_{MNH4} + [NH_4^+]_{La}}$$
$$r = a, t \geq 0$$

(7)

The quantities F_{mNH4} and K_{MNH4} are not constant during plant growth but vary with the plant's N status and other factors. However, we treat them as constants and test the model's sensitivity to them. At the other boundary, we assume there is no transfer of NH_4^+. Thus

$$D_{LA}\theta f\frac{\partial [NH_4^+]_L}{\partial r} + \frac{av}{b}[NH_4^+]_L = 0 \quad r = b, \quad t \geq 0$$

(8)

Nitrate

The transport of NO_3^- towards the root and its simultaneous production in nitrification and consumption in denitrification is described by the equation

$$\frac{\partial [NO_3^-]}{\partial t} = \frac{1}{r}\frac{\partial}{\partial r}\left[rD_{LN}\theta f\frac{\partial [NO_3^-]_L}{\partial r} + av[NO_3^-]_L\right]$$
$$+ R_{Nit} - R_{Denit}$$

(9)

Because NO_3^- is not adsorbed on the soil solid, its concentration in the whole soil is simply related to the concentration in solution by $[NO_3^-] = \theta[NO_3^-]_L$. The rate of denitrification will depend on $[NO_3^-]_L$ and also on the concentration of O_2, which is the preferred electron acceptor.

Following McConnaughey and Bouldin (1985), we describe this with a modified Michaelis–Menten equation:

$$R_{Denit} = I_{Denit}V_{mDenit}\frac{[NO_3^-]_L}{K_{MDenit} + [NO_3^-]_L}$$

(10)

where I_{Denit} is a function for inhibition by O_2. We take inhibition to be linear up to a threshold concentration equal to the Michaelis constant for O_2 consumption (Arah and Vinten, 1995):

$$\text{for } [O_2]_L \geq K_{MO}, I_{Denit} = 0,$$

(11)

$$\text{for } [O_2]_L < K_{MO}, I_{Denit} = 1 - \frac{[O_2]_L}{K_{MO}}$$

(12)

As for NH_4^+, we use a Michaelis–Menten equation for the relationship between the flux of NO_3^- into the root and the concentration in solution at the root surface:

$$D_{LN}\theta f\frac{\partial [NO_3^-]_L}{\partial r} + v[NO_3^-]_L$$
$$= F_{mNO3}\frac{[NO_3^-]_{La}}{K_{MNO3} + [NO_3^-]_{La}} \quad r = a, t \geq 0$$

(13)

At the other boundary, we assume there is no transfer of NO_3^-. Thus

$$D_{LN}\theta f\frac{\partial [NO_3^-]_L}{\partial r} + \frac{av}{b}[NO_3^-]_L = 0 \quad r = b, t \geq 0$$

(14)

Numerical solutions

We expressed eqns (1)–(14) in finite-difference form using Crank–Nicholson approximations and solved the resulting sets of equations by standard numerical methods (Smith, 1985). With time steps of 0·1 h and distance steps of 0·1 mm, mass balances for all solute were conserved to within 1 % for simulations up to 10 d. Copies of the computer program for the numerical solutions, written in Fortran, are available from the first author.

PARAMETER VALUES

The standard set of parameter values used in the calculations are given in Table 2. Our reasons for choosing these values are as follows.

Rate of O₂ release

The O_2 budget of an individual root depends both on the rate of O_2 movement and consumption within the root—which varies with position along the root and between main roots and laterals—and on the rate of O_2 consumption in the surrounding soil. Measurements of rates of release, therefore, need to allow for differences across the root and its laterals and must be made under O_2 sink conditions that are realistic for roots in soil. In practice, it is difficult to satisfy these conditions, and consequently reported rates of release for whole root systems vary by more than two orders of

TABLE 2. *Standard parameter values*

Parameter	Value	Reference
a	0·1 mm	Matsuo and Hoshikawa (1993)
b	2 mm	Matsuo and Hoshikawa (1993)
b_{NH4}	50 cm^3 cm^{-3}	Kirk (2004)
$D_{LA,N,O}$	2×10^{-5} cm^2 s^{-1}	Kirk (2004)
F_{mNH4}	5 pmol cm^{-2} s^{-1}	Kronzucker *et al.* (1999)
F_{mNO3}	25 pmol cm^{-2} s^{-1}	Kronzucker *et al.* (1999)
f	0·4	Kirk *et al.* (2003)
K_{MDenit}	1 μM	See text
K_{MNH4}	50 μM	Kronzucker *et al.* (1999)
K_{MNit1}	1 μM	See text
K_{MNit2}	200 μM	See text
K_{MNO3}	10 μM	Kronzucker *et al.* (1999)
K_{MO}	1 μM	See text
$[NH_4^+]_{t=0}$	5 μmol cm^{-3}	Kirk (2004)
$[O_2]_{Lc}$	0·18 μM	See text
V_{mDenit}	2 pmol cm^{-3} s^{-1}	See text
V_{mNit}/V_{mO}	0·25	See text
V_{mO}	500 pmol cm^{-3} s^{-1}	See text
v	0 cm s^{-1}	See text
λ	1×10^{-4} cm s^{-1}	Armstrong and Beckett (1987)
θ	0·6 cm^3 cm^{-3}	Kirk (2004)

magnitude (Bedford *et al.*, 1991; Begg *et al.*, 1994; Sorrel and Armstrong, 1994).

However, mathematical models of root aeration show that rates of release at the upper end of the measured range can be sustained by rice roots with typical characteristics (Armstrong and Beckett, 1987; Kirk, 2003). Kirk (2003) developed a model of the steady-state diffusion of O$_2$ through a primary rice root and its laterals and the simultaneous consumption of O$_2$ in root respiration and loss to the soil. A sensitivity analysis showed that the basic architecture of rice root systems, i.e. a system of coarse, aerenchymatous, primary roots with gas-impermeable walls conducting O$_2$ to short, fine, gas-permeable laterals, provides the greatest absorbing surface per unit aerated root mass. With this architecture and typical rates of root respiration, rates of O$_2$ loss to the soil from the laterals and primary root tip can be at the upper end measured experimentally, equivalent to a flux of up to 25 pmol cm^{-2} (root surface) s^{-1}.

Based on this and trial runs with the present model, we use as standard a root wall permeability factor, $\lambda = 10^{-4}$ cm s^{-1} and we specify the O$_2$ concentration in the root cortex {[O$_2$]$_{Lc}$ in eqn (3)} as equal to half that in air [8·75 mol cm^{-3} (gas space) at s.t.p.].

Rate of O$_2$ consumption

For ten soils with a wide range of organic matter and reducible Fe contents, Howeler and Bouldin (1971, Table 4) found steady-state rates of O$_2$ consumption by reduced soil cores exposed to O$_2$ equivalent to 100–1000 pmol cm^{-3} s^{-1} (mean value 500 pmol cm^{-3} s^{-1}). Roughly 50 % of this was microbial. We therefore take $V_{mO} = 500$ pmol cm^{-3} s^{-1} as our standard value. Heterotrophic aerobes will operate efficiently at sub micromolar O$_2$ concentrations (Conrad and Frenzel, 2002) and we take as standard $K_{MO} = 1$ μM.

Rate of nitrification

The maximum rate of nitrification is taken as a proportion of the maximum overall rate of microbial O$_2$ consumption. From the stoichiometry of nitrification, 2 mol of O$_2$ are consumed per mol of NO$_3^-$ formed:

$$NH_4^+ + 2O_2 \rightarrow NO_3^- + 2H^+ + H_2O$$

Therefore, an upper limit on the rate of nitrification is half the net rate of microbial O$_2$ consumption, i.e. $V_{mNit}/V_{mO} = 0.5$. We take as standard $V_{mNit}/V_{mO} = 0.25$. Also we take as standard $K_{MNit1} = K_{MO} = 1$ μM and $K_{MNit2} = 200$ μM based on typical concentrations of NH$_4^+$ in solution in rice soils.

Rate of denitrification

Experiments in which NO$_3^-$ fertilizer is added to flooded soils under field conditions indicate maximum rates of N$_2$ + N$_2$O loss through denitrification of a few kg of N ha^{-1} d^{-1} (e.g. Lindau *et al.*, 1990; Samson *et al.*, 1990). Assuming denitrification to be distributed over a soil depth of 10 cm, this is equivalent to a rate of denitrification per unit soil volume of a few pmol cm^{-3} s^{-1}. We therefore take as standard $V_{mDenit} = 2$ pmol cm^{-3} s^{-1}. Measured concentrations of NO$_3^-$ in flooded soils rarely exceed a few micromolar, unless the soil is fertilized with NO$_3^-$ (Arth and Frenzel, 2000; Liesack *et al.*, 2000), and therefore denitrifier populations must operate at concentrations less than this. We assign as standard $K_{MDenit} = 1$ μM.

The ratio of nitrous oxide to nitrogen gas formed in denitrification will depend on the relative abundance of NO$_3^-$ and organic substrates and on other factors influencing the rates of the sequential steps in denitrification (Kirk, 2004). Small concentrations of NO$_3^-$ relative to organic substrates, as expected near the roots of wetland plants, will favour complete reduction to N$_2$. Also, the slow escape of any N$_2$O formed in flooded soil will favour its further reduction to N$_2$. Hence, reported denitrification losses from rice fields as N$_2$O are at least two orders of magnitude smaller than losses as N$_2$ (Galbally and Chalk, 1987; Mosier *et al.*, 1989; Buresh *et al.*, 1991; Bronson *et al.*, 1997).

Root NH$_4^+$ and NO$_3^-$ uptake properties

Up to a certain point, plants can regulate the inflow of N across their roots according to their need for N, and the inflow for a given external N concentration therefore depends on the plant's past supply of N. Hence, Wang *et al.* (1993) found for rice grown for 4 weeks in 2, 100 and 1000 μM NH$_4^+$ solutions, the respective values of V_{max} (μmol g^{-1} h^{-1}) and K_M (μM) were: 12·8 and 32·2; 8·2 and 90·2; and 3·4 and 122·1, i.e. V_{max} was 6-fold smaller and K_M 4-fold larger for 2 μM compared with 1000 μM NH$_4^+$. For rice grown in 100 μM N solutions, Kronzucker *et al.* (1999) found that V_{max} values were 8·1 and 5·7 μmol g^{-1} h^{-1} for NO$_3^-$- and NH$_4^+$-fed plants, respectively, and K_M values were 26 and 51 μM. Given that external NO$_3^-$ concentrations at the root surface will be far smaller than NH$_4^+$ concentrations, NO$_3^-$ uptake will be 'upregulated' to a greater extent than NH$_4^+$ uptake, and we take as standard
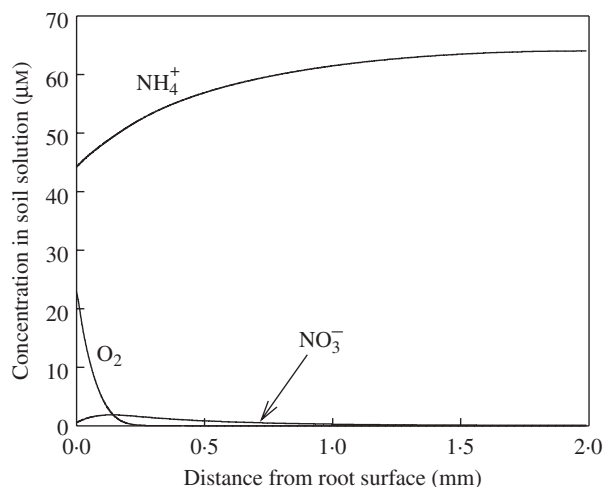
FIG. 1. Calculated concentration–distance profiles of O_2, NO_3^- and NH_4^+ in the soil near a root after 10 d of root–soil contact. Parameter values as in Table 2.
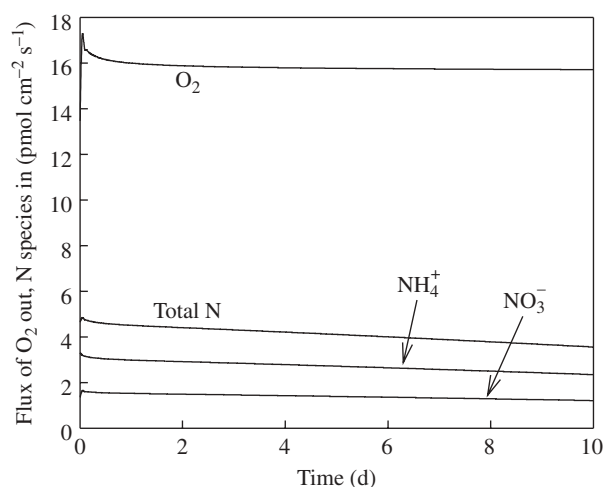

FIG. 2. Fluxes of O_2, NH_4^+, NO_3^- and total N across the root over time. Parameter values as in Table 2.

F_{max} = 5 pmol cm^{-2} s^{-1} (calculated from V_{max} in µmol g^{-1} h^{-1} using root density = 1 g cm^{-3} and a = 0·1 mm) and K_M = 50 µM for NH_4^+ uptake, and F_{max} = 25 pmol cm^{-2} s^{-1} and K_M = 10 µM for NO_3^- uptake.

Root geometry

The root system of rice plants in flooded soils comprises coarse primary roots, 0·3–1 mm in diameter, supporting a dense system of fine laterals, 50–150 µm in diameter (Matsuo and Hoshikawa, 1993). Total root length densities averaged over the 15–20 cm deep puddled soil layer may be as high as 20–30 cm cm^{-3}. Calculations with the above parameters for root NH_4^+ absorption properties and measured concentrations of NH_4^+ in soil solutions indicate that almost the whole of this root length is required to account for measured rates of N uptake by rice in flooded soils (Kirk and Solivas, 1997).

The corresponding mean inter-root distance is calculated as follows. With a regular parallel array of roots, if each root is assigned a cylinder of influence such that the whole soil volume is divided equally between roots, the radius, b, of the cylinder is given by

$$b = \frac{1}{\sqrt{\pi L_V}} \qquad (15)$$

where L_V is the root length density. The value b = 3 mm, which is realistic for half the distance between neighbouring primary roots, corresponds to L_V = 3·5 cm cm^{-3}; b = 1 mm, which is realistic for half the distance between laterals, corresponds to L_V = 31·8 cm cm^{-3}.

MODEL PREDICTIONS

Predicted concentration profiles, fluxes and rates of nitrification–denitrification

Figure 1 shows the concentration profiles of O_2, NH_4^+ and NO_3^- in the soil calculated with the standard set of parameter

values over 10 d of root–soil contact, and Fig. 2 gives the fluxes of O_2 and N species across the root over time. Figure 1 shows that only very small concentrations of NO_3^- in the soil solution develop: approx. 1–2 µM within <0·5 mm of the root and 0 µM at >1 mm from the root, i.e. given the radial geometry, all but undetectable averaged over the inter-root distance. Nonetheless, the fluxes of NO_3^- into the root shown in Fig. 2 are substantial. The accumulated uptake of nitrogen over 10 d is 1·61 µmol cm^{-3} of soil, or 33 % of the initial NH_4^+ content of the soil (= 5 µmol cm^{-3}, equivalent to 105 kg of N ha^{-1} over a 15 cm depth), and the concentration of NH_4^+ in solution in the soil bulk concomitantly falls from 100 to 64 µM. Nitrate uptake accounted for 34 % of total N uptake, and nitrification accounted for 14 % of the total O_2 consumption in 10 d. The ratio of N denitrified to total N uptake was 0·20 or 6·6 % of the NH_4^+ initially in the soil.

To gauge how realistic these results are, we compare the calculated rates of denitrification with published values. Measurements of denitrification in flooded rice fields made by following the emission of $^{15}N_2$ and $^{15}N_2O$ following addition of N-fertilizer strongly labelled with ^{15}N indicate losses in the range 1–5 % of applied ammoniacal-N over the range of soils and management conditions considered (Buresh and Austin, 1988; Mosier *et al.*, 1989; Reddy *et al.*, 1989; Buresh *et al.*, 1991). Arth *et al.* (1998) directly measured N_2 and N_2O emitted by rice plants grown in chambers with an atmosphere of O_2 and helium. This gave denitrification losses of the order of 6 % of added urea-N in 10 d and mean N_2 + N_2O emission rates of approx. 30 nmol (N) cm^{-2} (soil surface) h^{-1}. The mean emission rate calculated here with the standard parameters is 14 nmol (N) cm^{-2} (soil surface) h^{-1} assuming 10 cm soil depth. We conclude that our calculated losses are realistic.

We know of no published direct measurements of rates of NO_3^- uptake by wetland plants in flooded soil under field conditions. Because the NO_3^- is rapidly assimilated, direct measurements of uptake are difficult.
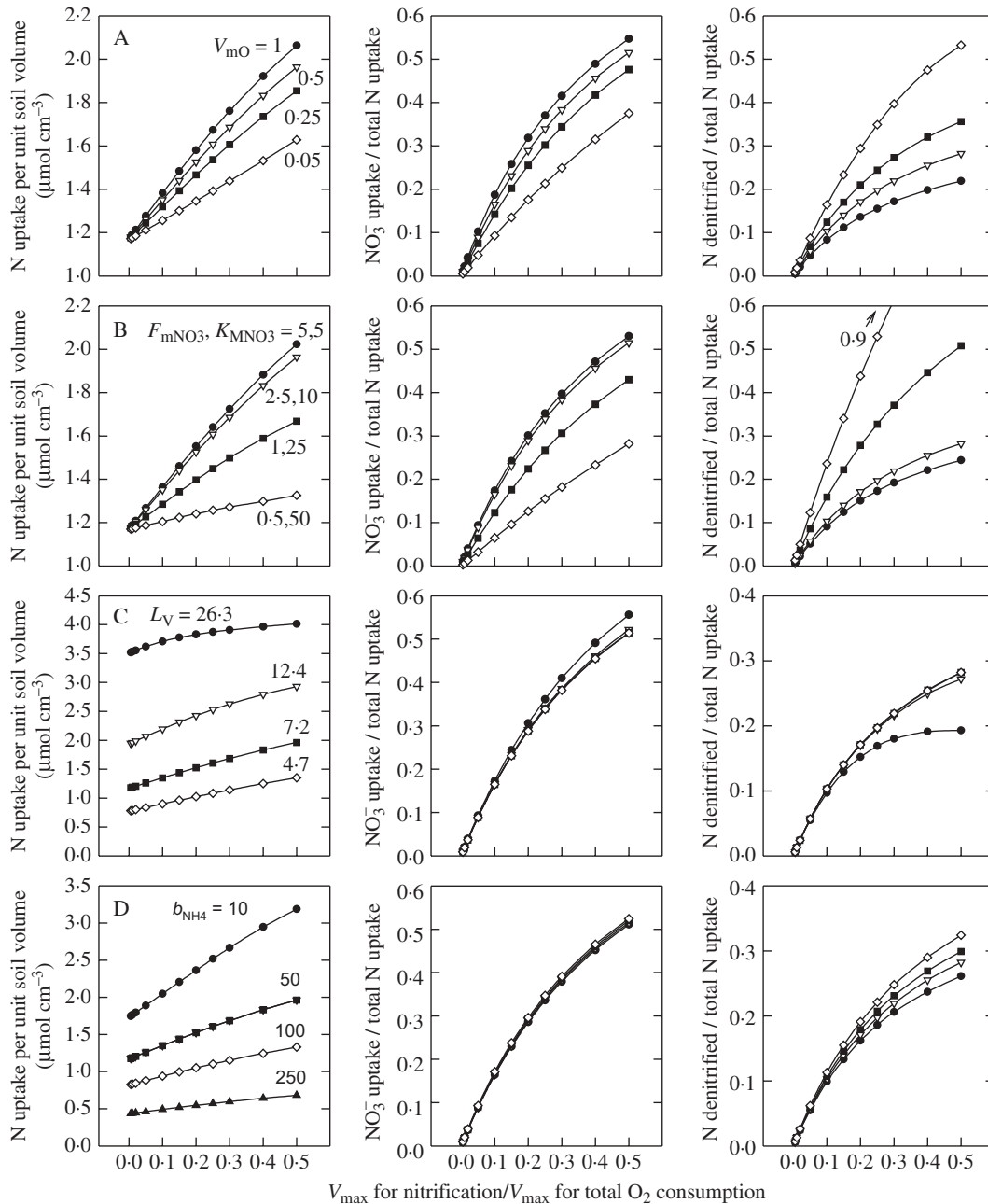
FIG. 3. Sensitivity of total N uptake, uptake of NO_3^- as a proportion of total N uptake and denitrification as a proportion of total N uptake to model parameter values. (**A**) The top three graphs indicate sensitivity to V_{max} for total O_2 consumption [V_{mO} in eqn (2); numbers on curves are values in nmol cm^{-3} s^{-1}]; (**B**) the upper middle three graphs indicate sensitivity to parameters for root NO_3^- uptake [F_m, K_M in eqn (13); numbers on curves are values in nmol cm^{-3} s^{-1}, μM]; (**C**) the lower middle three graphs indicate sensitivity to root length density [L_V in eqn (15); numbers on curves are values in cm cm^{-3}]; and (**D**) the bottom three graphs indicate sensitivity to the soil NH_4^+ buffer power (b_{NH4}; numbers on curves are values in cm^3 cm^{-3}). Ten d of root–soil contact. Other parameter values as in Table 2.

Sensitivity analysis

Figure 3 shows the sensitivity of the calculated total N and NO_3^- uptakes and denitrification to model parameter values over what we consider to be realistic ranges for wetland plants. As discussed above, we have some understanding of total rates of O_2 consumption in flooded soils, but a much weaker understanding of the growth rates and activities of nitrifying microbes under different circum-

stances. We therefore show the sensitivity to different parameters in interaction with a varying nitrification potential as represented by V_{max} for nitrification as a proportion of V_{max} for total O_2 consumption (V_{mNit}/V_{mO}).

Effect of nitrification and denitrification rates. Figure 3A shows the sensitivity to the maximum total rate of O_2 consumption (V_{mO}). At a given V_{mNit}/V_{mO}, with increases in V_{mO} the proportion of N uptake as NO_3^- increases and

total N uptake increases correspondingly. Also, the ratio of N denitrified to total N uptake decreases. This is because with a greater O_2 sink, the spread of the oxygenated zone around the root is smaller and nitrification occurs closer to the root. Therefore, the concentration gradient of NO_3^- towards the root is steeper and a greater proportion of the NO_3^- is taken up. The effect of V_{mO} varies with V_{mNit}/V_{mO}: when V_{mNit}/V_{mO} is large, denitrification losses decrease more rapidly with increases in V_{mO}.

Effect of root NO_3^- uptake properties. As F_{mNO3} increases and K_{MNO3} decreases, an increasing proportion of N is taken up as NO_3^- and a decreasing proportion of the NO_3^- formed is denitrified (Fig. 3B). Over the range of F_{mNO3} and K_{MNO3} values shown in Fig. 3B, and other parameter values as standard, NO_3^- accounts for 15 to nearly 40 % of N uptake. Denitrification losses increase sharply as root NO_3^- uptake decreases.

Effect of root geometry. Figure 3C shows interactions between root geometry and rates of NO_3^- uptake and denitrification. As root length density (L_V) increases, the rates of total N uptake and depletion of soil N increase. Simultaneously, with increasing L_V, the inter-root distance decreases and therefore the proportion of the inter-root zone that is oxygenated increases, and so nitrification and NO_3^- uptake increase. Superimposed on this is the effect of root radius. With large inter-root distances, increasing the root radius tends to increase the capture of NO_3^- and decrease denitrification (data not shown). However, with small inter-root distances, denitrification rates are small and the capture of NO_3^- increases as the root radius decreases.

Effect of soil NH_4^+ buffer power. Figure 3D shows that uptake increases sharply as b_{NH4} decreases, but the proportion of uptake as NO_3^- is little influenced. As b_{NH4} decreases, for a given total concentration of NH_4^+ in the soil, the concentration of NH_4^+ in solution increases, and hence the uptake of NH_4^+ tends to increase. Simultaneously, nitrification tends to increase as NH_4^+ in solution increases, and hence the rate of NO_3^- uptake increases. Thus, the sensitivity of N uptake to V_{mNit}/V_{mO} increases as b_{NH4} decreases. There is a corresponding decrease in denitrification relative to N uptake, because the gradient of NH_4^+ near the root is shallower at smaller b_{NH4}, and hence a greater proportion of nitrification occurs close to the root.

Effect of mass flow of the soil solution. Mass flow of solution towards the root in the transpiration stream tends to compress the zones of oxygenation and nitrification and extend the zone of NH_4^+ depletion. The above calculations were made with $v = 0$. The model shows that a rapid flux of water across the root surface ($v = 10^{-5}$ cm s^{-1}) slightly compresses the profile of NH_4^+ but has a negligible effect on the profiles of O_2 and NO_3^- and rates of NO_3^- uptake and denitrification (data not shown). Approximate solutions of eqn (5) indicate that the fractional increase in NH_4^+ influx resulting from mass flow is about $av/(0{\cdot}5D_{LA}\theta f)$ (Kirk and Solivas, 1997), or approx. 2 % for the standard parameter values and $v = 10^{-5}$ cm s^{-1}. Hence, for practical purposes, the effect of mass flow can be ignored.

CONCLUDING REMARKS

Our calculations show that wetland plants growing in flooded soil can take up a large part of their nitrogen as NO_3^- formed from NH_4^+ in the rhizosphere, without excessive losses of N through denitrification. The extent of this will vary greatly between soils and management regimes, being sensitive to reducing conditions in the soil and the sinks for O_2 other than nitrification. Water regimes will particularly influence this. It is expected that in future rice will have to be produced with far less water across Asia as water resources are increasingly diverted to non-agricultural uses (IRRI, 2003). Therefore, water-saving irrigation methods, such as maintaining a minimal depth of standing water in the field and intermittently draining water from the field, will be increasingly widespread. This will favour increased NO_3^- formation, and it will be important to manage conditions to maximize the capture of NO_3^- by the crop and minimize denitrification.

We have focused on lowland rice, but it is probable that other wetland plants are similarly efficient in capturing NO_3^- formed in the rhizosphere. This would have implications for the selection of plants for waste-water treatment in artificial wetlands.

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