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1973 PROGRESS REPORT

A NITROGEN SUBMODEL

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**US/IBP DESERT BIOME
RESEARCH MEMORANDUM 74-62**

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INTRODUCTION

The nitrogen submodel deals with the nitrogen transformation in soil caused by microorganisms. In addition to those biological processes, it includes an option for ammonium volatilization because of its importance in desert conditions. As in the decomposition submodel (Parnas and Radford, 1974), all the biological transformations are

proportional to the growth rate of the particular microbial population which is responsible for that process. The model includes most of the possible nitrogen transformations, even those which are very small in magnitude in desert conditions. The purpose is to keep the submodel as general as possible.

PROCESSES INCLUDED IN THE NITROGEN SUBMODEL

In order to understand the way in which some of the processes are handled in this subroutine it is important to mention here that one of the assumptions in the nitrogen and the decomposition submodels is that all the constituents of a living microorganism are not available to plants or to any other source. Only through death does the microbial biomass become available.

SYMBIOTIC FIXATION OF N_2

Symbiotic fixation causes enrichment of the symbiotic roots with some of the fixed nitrogen, and that of the symbiotic microflora with some of the root carbon. In the submodel the only way in which the soil organic matter will be enriched with the fixed nitrogen is by the death of the symbiotic microflora, which in this case is the same as death of the symbiotic roots. Thus, symbiotic microbes are considered part of the root tissue. Plants know how much carbon to allow roots in order to account for microbial growth because the microbial biomass value is continually calculated and communicated to the plant submodel (or at least back to the SOILS calling program).

HETEROTROPHIC FIXATION OF N_2

Some heterotrophic types of bacteria fix N_2 . Soil organic matter will be enriched by that fixed nitrogen only after the death of the fixers.

AUTOTROPHIC FIXATION OF N_2

Autotrophic fixation of N_2 is accomplished mainly by the blue-green algae on the soil surface. The same rule as in symbiotic and heterotrophic fixations holds here also. Growth of autotrophs is actually calculated elsewhere

(e.g., by a plant submodel), as is death. Nitrogen fixation itself depends on growth but is calculated here.

NH_4^+ OXIDATION TO NO_2^-

The basic equations of this process are those of McLaren (1971). The process includes use of NH_4^+ as a source of energy for maintenance and growth. In addition, some external oxidation of NH_4^+ to NO_2^- occurs. This last process is not agreed upon by other authors. NH_4^+ oxidation to NO_2^- is accomplished mainly by the *Nitrosomonas* population.

NO_2^- OXIDATION TO NO_3^-

The basic process is the same as above (only the source for energy is NO_2^-) and is based on the same work (McLaren, 1971). This process is accomplished mainly by the *Nitrobacter* population.

DENITRIFICATION

In the submodel this process is accomplished by the same basic population which is responsible for decomposition (Parnas and Radford, 1974). Denitrification can happen in anaerobic conditions. It requires very high moisture or even flood in the upper horizons, which of course is not typical to arid conditions. Nevertheless, denitrification is included for purposes of generality of the submodel.

NH_3 VOLATILIZATION

NH_3 volatilization occurs under warm and alkaline conditions. This may optionally be handled outside the nitrogen submodel.

STRUCTURE OF THE SUBROUTINE

The processes mentioned are calculated by soil horizons only. For each process, the growth rate of the corresponding population in a given horizon is calculated. In addition to the growth rate, the death rate for each type of population is calculated. The substrate which limits growth is different

for each type of population; so is the cause of death. Usually, if the source of energy for that specific population drops to zero, a higher rate of death will occur. When the source of energy is available, a smaller rate of death takes place. NH_4^+ , NO_2^- and NO_3^- concentrations are calculated

separately and used in a combined pool which is the total mineral nitrogen. This last pool is the source of mineral nitrogen for immobilization and for the N_2 fixers. Preference coefficients are given to the different constituents of the mineral nitrogen in order to determine the immobilization of a specific type of nitrogen.

The input to this subroutine requires initial concentrations of the various pools, the various microbial biomass concentrations, and maximal growth rate for each type of population. Again as in the decomposition submodel

(Parnas and Radford, 1974), the product microbial biomass times maximal growth rate can be replaced by "potential activity" if biomass cannot be measured meaningfully.

APPLICABILITY

The model can be applied to many ecosystems at various environmental conditions. The reason is its generality, as has been discussed in the decomposition submodel (Parnas and Radford, 1974).

VERBAL AND GRAPHICAL DESCRIPTION OF PROCESSES

SYSTEM DIAGRAM

The system modelled and some of the necessary connecting flows to related submodels are shown in Figure 1.

VERBAL DESCRIPTION OF PROCESSES

GROWTH RATE OF THE VARIOUS MICROBIAL POPULATIONS

The growth rate is a function of maximal growth rate of the specific population, environmental coefficients in the different horizons and of the growth-limiting nutrient. In

most cases the growth-limiting nutrient will be the source of energy. In this way the growth-limiting factor for the *Nitrosomonas* will be the NH_4^+ concentration, and for *Nitrobacter* the NO_2^- concentration. For the N_2 fixers, the growth-limiting factor will be the carbon source (in roots, in dead material) or the light intensity (for the autotrophic fixers). The function which describes the growth rate as a function of the limiting nutrient is that of Michaelis-Menton.

The environmental coefficients are calculated by use of trapezoidal functions as described in Figure 3 of the decomposition submodel (Parnas and Radford, 1974).

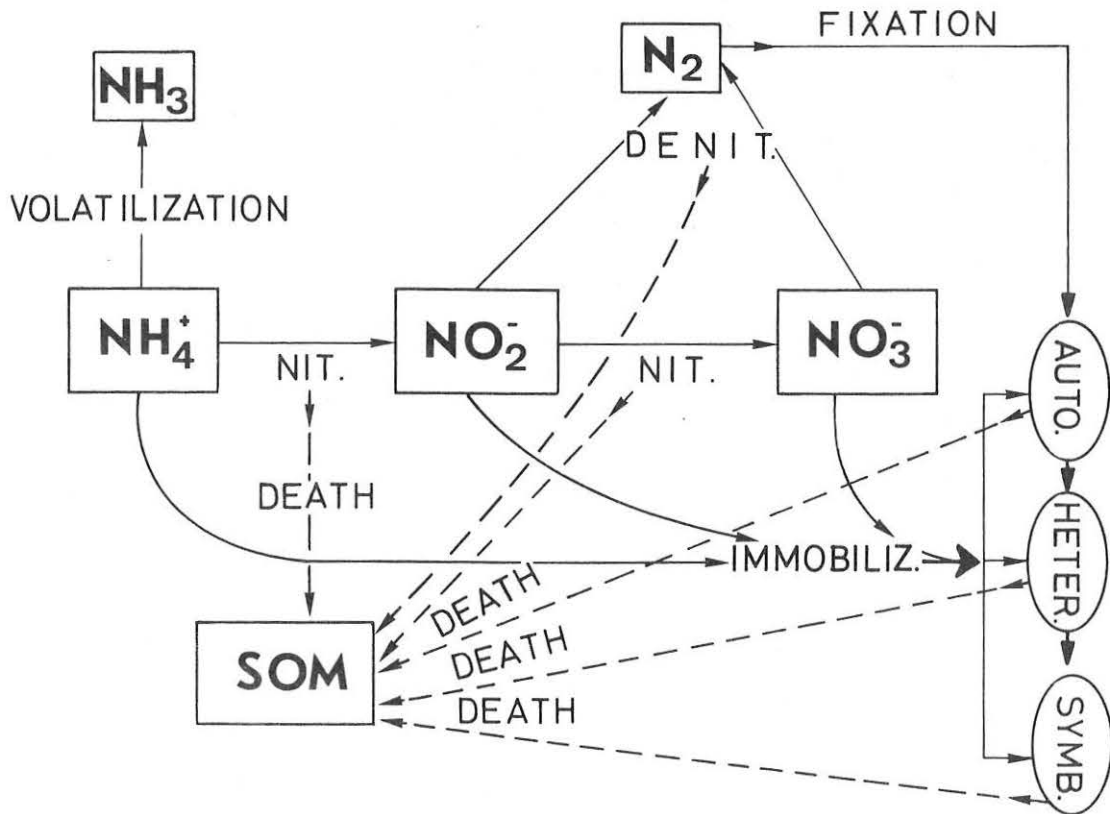


Figure 1. Decomposition submodel with connecting flows to related submodels.

DEATH RATE OF THE VARIOUS MICROBIAL POPULATIONS

Calculation of the death rate is, in principle, the same for all the populations, but the cause for death is different. For each population at each horizon, two values for death rate are given. One (the normal one) is the death rate when the specific energy source is available. This death happens along with growth at a constant rate. When a starvation conditions exists (the energy source is not available), growth stops and death proceeds at a higher rate than at normal conditions. Since the energy source is different for different types of populations, the cause for death will vary from population to population and it is calculated separately for each of them. For the autotrophic N_2 fixers where the source of energy is light, the death rate (calculated outside the nitrogen submodel) usually depends on the size of the fixer's biomass. The idea is that when the microbial biomass reaches a certain maximal value the light intensity per cell decreases because of the shadow effect. When the population is very dense the lower levels of the population will not accept any light at all; conditions which are similar to starvation.

SYMBIOTIC N_2 FIXATION

The symbiotic N_2 fixation is dependent on the microbial biomass of the fixers, and on the host plant root carbon. This fixation is inhibited in a regular competitive way by inorganic nitrogen. The N_2 that is being fixed serves the microbial population and the symbiotic roots. The biomass of the symbiotic fixers and the symbiotic roots is considered essentially as one biomass for purposes of death. The two types of biomass are calculated separately for fixation rate calculations. By the death of the combined biomass (root death), they are attacked by the decomposers and so become part of the soil organic matter. Carbon dioxide evolution accompanies the growth of the symbiotic fixers. Symbiotic fixation can happen in all horizons. The amount of plant carbon allocated to symbiotic roots (calculated elsewhere, as is CO_2 evolution) depends upon symbiotic microbe biomass (calculated here). In the general process of symbiotic N_2 fixation, the following processes are included: (1) N_2 fixation, an increasing function of microbial biomass and of root carbon -- decreasing function of inorganic nitrogen concentration; (2) increase in fixers' biomass; (3) death of the fixers and root biomass -- this last process is responsible for the enrichment of soil organic matter by organic nitrogen.

HETEROTROPHIC N_2 FIXATION

The growth-limiting substrate for the heterotrophic fixers is the soil organic carbon by horizon. The heterotrophic N_2 fixation is also inhibited by the available inorganic nitrogen. The growth rate of this population is determined by the usual components, that is, maximal growth rate, environmental coefficients by horizon, organic carbon concentration by horizon, and the microbial biomass

by horizon. The death constant by horizon will be dependent on presence of soil organic carbon. By their death they are subject to decomposition and the soil organic matter is enriched in organic nitrogen (among other constituents). The enrichment of soil organic matter by organic nitrogen is proportional to the fraction of nitrogen in the microbial cells which is around 5-12% of the cell biomass.

AUTOTROPHIC N_2 FIXATION

It is assumed that the main autotrophic fixation is done by the blue-green algae on the soil surface. The growth rate of the autotrophic fixers depends on light intensity and the length of the day. In addition, their growth rate is dependent, as in the other cases, on environmental conditions and the concentration of their biomass. The actual growth of these surface autotrophs is calculated by a plant submodel or elsewhere. This nitrogen submodel receives the information about the amount of carbon fixation and autotroph growth and proceeds to calculate how much nitrogen assimilation occurs and, of this nitrogen, how much is inorganic soil nitrogen (as is determined for the nitrogen fixers in general). As in symbiotic and heterotrophic N_2 fixations, the enrichment of soil organic matter by the organic nitrogen of the free fixers occurs only by the death of the autotrophic population. Their fixation is also inhibited by the presence of inorganic nitrogen.

OXIDATION OF NH_4^+ TO NO_2^-

Oxidation of NH_4^+ to NO_2^- can happen in all horizons. The source of energy for growth and maintenance of the corresponding population is NH_4^+ ; NO_2^- is the oxidation product. The disappearance of NH_4^+ is proportional to three subprocesses: (1) Growth rate of the oxidizers, multiplied by (1/efficiency). The growth rate, as always, is proportional to the maximal growth rate, microbial biomass concentration and NH_4^+ concentration. The efficiency describes the amount of NH_4^+ assimilated divided by the amount of NH_4^+ used for growth. (2) Maintenance requirement--the specific maintenance energy is a constant independent of growth rate, per unit biomass. It has to be multiplied by the microbial biomass. Its units are $time^{-1}$. (3) In addition to the processes (1 and 2 above) which are connected with microbial growth, some external oxidation happens. This process is proportional to the external enzymes present which are due to that waste metabolism. The rate of the waste metabolism has also the general form of a Michaelis-Menton equation. It means it also has some maximal value and is dependent on NH_4^+ concentration. According to McLaren (1971), this is the major process in NH_4^+ oxidation, but not all the authors agree on this. In some cases a very good agreement to laboratory conditions could be shown without considering at all the waste metabolism.

The formation of NO_2^- is of course proportional to the loss

in NH_4^+ . For keeping the right balance, the free NO_2^- which is evolved should be calculated by taking into consideration the efficiency of this reaction. The efficiency, which is very low in this case ($\sim 6\%$), gives the amount of NH_4^+ which is attached to the microbial cell. In this case, and not as in the fixation process, the NO_2^- formation is a direct product of this transformation. In addition, the death of this population contributes to the soil organic matter.

OXIDATION OF NO_2^- TO NO_3^-

This process is completely analogous to oxidation of NH_4^+ to NO_2^- . The only difference is that the source of energy is NO_2^- and the oxidation product is NO_3^- . This process is faster than the first oxidation; therefore, we don't expect any accumulation of NO_2^- which is really the case in field conditions. The two processes have slightly different sensitivity to pH and temperature. Nitrification as a whole requires higher moisture level than does ammonification. It means that in dry conditions NH_4^+ could be accumulated. It is not accumulated because of volatilization.

DENITRIFICATION

Denitrification can happen in more than one way. In any case the rate of denitrification will be a function of growth rate of the denitrifiers, which in turn will be an increasing function of nitrate, nitrite and organic carbon concentrations and a decreasing function of oxygen. pH and temperature will affect the denitrification in the usual way. The biomass which is responsible for denitrification is part of the decomposers' population. At anaerobic conditions they will use NO_3^- as a competitive electron acceptor. The rate equation for denitrification includes competitive inhibition of NO_3^- use by the presence of O_2 . Oxygen amount is indicated by soil water potential here. In later models, actual O_2 concentration may be calculated and used. The death of denitrifiers, as that of the decomposers, is caused by carbon starvation in that horizon. In normal conditions the death rate will be lower than the starvation rate, and death and growth will happen simultaneously.

MATHEMATICAL DESCRIPTION

See the section on MAIN Calling Program in the 1973 Desert Biome Progress Report, Volume 1, for explanation of symbolism conventions.

NITROGEN EXCHANGES WITH THE ATMOSPHERE

$$\dot{X}_{01,11} = \sum_h \left[\sum_{i \in F} \left(\frac{Z_{1ih} \cdot Z_{2ih}}{Z_{4h}} \right) \cdot P_{21} - \sum_{j \in N} Z_{3jh} - Z_s \right] \quad (1)$$

NH_3 VOLATILIZATION

The rate of volatilization is an increasing function of NH_4^+ concentration, pH and temperature, and a decreasing function of soil plant cover. The dependency of the rate of volatilization upon pH and temperature is shown in Figure 2.

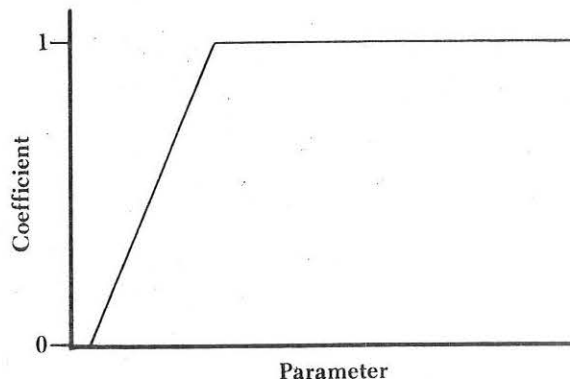


Figure 2. Coefficient of NH_3 volatilization as a function of environmental conditions.

ASSUMPTIONS

1. The rate of any biological transformation is proportional to the growth rate of the population responsible for that transformation.
2. The growth rate is described by a Michaelis-Menton equation. It includes maximal growth rate, and is proportional to the concentration of the substrate which is growth-limiting.
3. The environmental coefficients affect the maximal growth rate.
4. The living microbial biomass is not available to the plants. It becomes available only after death and mineralization.
5. Death constants for each type of population can have one out of two values. The lower one is the normal rate constant which takes place while growth is happening. The second and higher one takes place when no source of energy is available.

where:

- $\sum_h \sum_{i \in f} \sum_{j \in N}$ = Summations over all horizons h , over the set of nitrogen fixing biomasses or activities i , over the set of types of mineral N_j , respectively
- Z_{1ih} = Instantaneous growth rate of biomass/activity type i in horizon h as in (2)
- Z_{2ih} = Quantity of biomass or activity as in (4)

- Z_{3jh} = Uptake of mineral N type j by N-fixing organisms as in (10)
 Z_{4h} = Denitrification as in (13)
 Z_5 = Volatilization of NH_3 as in (8)
 P_{21} = Normal units of N of fixers per unit biomass

INSTANTANEOUS GROWTH RATE OF NITROGEN TRANSFORMING ACTIVITY i (Z_{1ih})

$$Z_{1ih} = Z_{6ih} \cdot (Z_{7ih} / (P_{1i} + Z_{7ih})) \quad (2)$$

where:

- Z_{6ih} = Maximal growth rate adjusted to the physical environment in horizon h , as in (5)
 Z_{7ih} = Total host root carbon for symbionts, total soil dead material carbon for heterotrophs and denitrifiers, ammonium for ammonium oxidizers, nitrite for nitrite oxidizers
 P_{1i} = A Michaelis constant

INSTANTANEOUS DEATH RATE OF NITROGEN TRANSFORMATION ACTIVITIES (Z_{8ih})

$$Z_{8ih} = P_{2i}, \text{ if } Z_{7ih} \leq 0 \\ = P_{3i}, \text{ if } Z_{7ih} > 0 \quad (3)$$

where:

- Z_{7ih} = As in (2)
 P_{2i}, P_{3i} = Different death rates for the conditions imposed (concerning Z_{7ih}), for biomass/activity i

BIOMASS/ACTIVITY (Z_{2ih})

$$Z_{2ih,t} = Z_{2ih,t-1} \cdot \exp(Z_{1ih} - Z_{8ih}) \quad (4)$$

where:

- $t, t-1$ = The value of Z_{2ih} is for the present (t) or preceding ($t-1$) simulation time unit
 Z_{1ih} = Growth rate for biomass/activity i of horizon h as in (2)
 Z_{8ih} = Death rate for biomass/activity i of horizon h as in (3)

MAXIMAL GROWTH RATE ADJUSTED TO PHYSICAL ENVIRONMENT (Z_{6ih})

$$Z_{6ih} = (P_{4i} \cdot Z_{9ih} \cdot Z_{10ih} \cdot Z_{11ih} \cdot Z_{12ih}) \cdot Z_{13ih} \quad (5)$$

where:

- P_{4i} = Maximum instantaneous growth rate for biomass/activity type i , under ideal conditions
 Z_{9ih} = A temperature coefficient specific to horizon h temperature and biomass/activity type i -- calculated in OPT
 Z_{10ih} = A pH coefficient -- calculated in the OPT subroutine
 Z_{11ih} = A salinity coefficient -- see OPT
 Z_{12ih} = A moisture coefficient -- see OPT
 Z_{13ih} = As in (6)

MULTIPLICATION FACTOR (Z_{13ih})

$$Z_{13ih} = 1, \text{ for } i \leq 4 \\ = (X_{24h3} + X_{24h4}) \cdot P_5 / ((X_{24h3} + X_{24h4} + P_{15}) \cdot (P_5 + Z_{14h})), \text{ for } i=5 \quad (6)$$

where:

- X_{24h3}, X_{24h4} = Nitrite and nitrate, respectively
 P_5 = An inhibition constant for the inhibition of the use of ($\text{NO}_2^- + \text{NO}_3^-$) as oxygen source, by oxygen present
 Z_{14h} = Soil water potential (negative bars), as calculated elsewhere and passed from SOILS
 P_{15} = A Michaelis constant

CHANGES IN AMMONIUM (\dot{X}_{24h2})

$$\dot{X}_{24h2} = -Z_5 - Z_{15h} - Z_{31h}, \text{ for } h = 1 \\ = -Z_{15h} - Z_{31h}, \text{ for } h > 1 \quad (7)$$

where:

- Z_5 = Volatilization as in (8)
 Z_{15h} = Oxidation to NO_2^- as in (9)
 Z_{31h} = Uptake by fixers as in (10)

**VOLATILIZATION OF AMMONIUM FROM
HORIZON 1 (Z_5)**

$$Z_5 = [Z_{16} \cdot Z_{17} \cdot Z_{18} \cdot P_6] \cdot X_{24_{12}} \quad (8)$$

where:

- Z_{16} = A temperature coefficient as calculated by RAMP subroutine
 Z_{17} = A pH coefficient as calculated by RAMP
 Z_{18} = A soil cover coefficient as calculated by DCLIN subroutine
 P_6 = Maximal rate of volatilization under optimal conditions, units per unit present per time
 $X_{24_{12}}$ = Quantity of ammonium in horizon 1

OXIDATION OF NH_4^+ TO NO_2^- (Z_{15h})

$$Z_{15h} = (P_7 \cdot Z_{13h} + P_8 + P_9 \cdot P_{10} \cdot X_{24h2} / (X_{24h2} + P_{11})) \cdot Z_{23h} \quad (9)$$

where:

- P_7 = 1/efficiency or NH_4^+ transformed to NO_2^- divided by amount of that transformed that is assimilated by transformers
 Z_{13h} = The growth rate of biomass/activity type 3 in horizon h as in (2)
 P_8 = Units NH_4^+ required for transformer maintenance per unit transformer biomass per unit time
 P_9 = A rate constant for waste metabolism connected to NH_4^+ oxidizers
 P_{10} = External enzyme concentration per unit NH_4^+ oxidizer biomass
 X_{24h2} = Ammonium as in (7)
 P_{11} = A Michaelis constant for waste product metabolism
 Z_{23h} = Biomass/activity quantity for type 3, horizon h as in (4)

**UPTAKE OF MINERAL NITROGEN TYPE i BY FIXERS
(Z_{3ih})**

$$Z_{3ih} = Z_{19h} \cdot P_{12i} \cdot X_{24hi} \quad (10)$$

where:

- Z_{19h} = Mineral N demand of all fixers in horizon h , as in (11)
 P_{12i} = A "preference" factor, units type i taken up per unit mineral N demand

X_{24hi} = Amount of type i nitrogen in horizon h

**TOTAL MINERAL N DEMAND BY FIXERS
(Z_{19h})**

$$Z_{19h} = \sum_{i \in F} (Z_{1ih} \cdot Z_{2ih}) / (\sum_{j \in N} X_{24hj} + P_{16}) \quad (11)$$

where:

- $\sum_{i \in F, j \in N}$ = Respectively, summation over fixer biomass/activity types j , summation over nitrogen types j
 Z_{1ih} = Growth rate of fixer i , horizon h as in (2)
 Z_{2ih} = Biomass/activity of fixer type i , horizon h as in (4)
 X_{24hj} = Nitrogen type j in horizon h
 P_{16} = A Michaelis constant

CHANGES IN NO_2^- (\dot{X}_{24h3})

$$\dot{X}_{24h3} = Z_{15h} - (Z_{13h} \cdot P_{21} \cdot Z_{23h} / P_7) - Z_{32h} - Z_{4h} \cdot (X_{24h3} / (X_{24h3} + X_{24h4})) - Z_{20h} \quad (12)$$

where:

- P_7 = Efficiency of conversion of NH_4^+ to NO_2^- as in (9)
 Z_{13h} = Oxidizer growth rate as in (2)
 Z_{15h} = NH_4^+ oxidation as in (9)
 Z_{23h} = Oxidizer biomass as in (4)
 Z_{32h} = Uptake of N_2 by fixers as in (10)
 Z_{4h} = Denitrification of NO_2^- , NO_3^- as in (13)
 X_{24h3} and X_{24h4} = NO_2^- , NO_3^-
 P_{21} = As in (16)
 Z_{20h} = NO_2^- oxidation to NO_3^- as in (14)

DENITRIFICATION (Z_{4h})

$$Z_{4h} = P_{14} \cdot Z_{15h} \cdot Z_{25h} \quad (13)$$

where:

- P_{14} = Units ($\text{NO}_2^- + \text{NO}_3^-$) required as oxygen source per unit growth
 Z_{15h} = Growth rate of denitrifiers as in (2)
 Z_{25h} = Biomass/activity type 5 (denitrifiers) in horizon h as in (4)

OXIDATION OF NO_2^- TO NO_3^- (Z_{20h})

$$Z_{20h} = (P_{15} \cdot Z_{14h} + P_{16} + P_{17} \cdot P_{18} \cdot X_{24h3} / (X_{24h3} + P_{19})) \cdot Z_{2h4} \quad (14)$$

where:

- P_{15} = 1/efficiency or NO_2^- transformed to NO_3^- per unit NO_2^- assimilated by transformers
 Z_{14h} = Growth rate of oxidizers as in (2)
 P_{16} = NO_2^- required for maintenance per unit biomass of NO_2^- oxidizers
 P_{17} = Rate constant for waste metabolism connected to NO_2^- oxidation
 P_{18} = External enzyme concentrations per unit microbial biomass of the NO_2^- oxidizers
 X_{24h3} = NO_2^- as in (12)
 P_{19} = A Michaelis constant
 Z_{24h} = Biomass/activity of oxidizers in horizon h as in (4)

CHANGES IN NO_3^- NITROGEN (\dot{X}_{24h4})

$$\dot{X}_{24h4} = Z_{20h} - (Z_{14h} \cdot P_{21} \cdot Z_{24h}/P_{15}) - Z_{33h} - Z_{4h} \cdot (X_{24h4}/(X_{24h3} + X_{24h4})) \quad (15)$$

where:

- P_{15} = Efficiency as in (14)
 Z_{20h} = NO_2^- oxidized as in (14)
 Z_{33h} = Uptake of NO_3^- by fixers in horizon h
 Z_{24h} = Biomass of NO_2^- oxidizers as in (4)
 Z_{4h} = Denitrification of NO_2^- , NO_3^- as in (13)
 Z_{14h} = Growth rate of NO_2^- oxidizers as in (2)
 X_{24h3} and X_{24h4} = NO_2^- , NO_3^- nitrogen
 P_{21} = As in (16)

CHANGES IN SOIL ORGANIC MATTER (\dot{X}_{22hf})

$$\dot{X}_{22hf} = + \left[\sum_{i \in D} Z_{21ih} \right] \cdot P_{21}, \text{ for } f = 1 \quad (16)$$

$$= - \sum_{i \in D} (P_{20if} \cdot Z_{22ih}), \text{ for } f > 1$$

where:

- $\sum_{i \in D}$ = Summation over non-symbiotic types
 Z_{21ih} = Death as in (17)
 P_{21} = N fraction of biomass
 P_{20if} = Requirement of biomass type i for constituent f for growth

Z_{22ih} = Change in biomass i of horizon h as in (18)

DEATH OF BIOMASS/ACTIVITY i (Z_{21ih})

$$Z_{21ih} = Z_{2ih} \cdot (1 - 1/\exp(Z_{8ih})) \quad (17)$$

where:

- Z_{2ih} = Quantity of biomass/activity as in (4)
 Z_{8ih} = Instantaneous death rate as in (3)

CHANGE IN BIOMASS TYPE i IN HORIZON h (Z_{22ih})

$$Z_{22ih} = Z_{2ih,t} - Z_{2ih,t-1} \quad (18)$$

where:

- Z_{2ih} = Biomass/activity at present (t) or previous time unit ($t-1$) as in (4)

DUMMY BIOMASS EQUIVALENT CHANGES (\dot{X}_{21Df})

$$\dot{X}_{21Df} = + \sum_h (Z_{12h} \cdot Z_{22h} - \sum_{i \in D} Z_{21ih} + Z_{13h} \cdot Z_{23h}/P_7 + Z_{14h} \cdot Z_{24h}/P_{15}) \cdot P_{21}, \text{ for } f = 1 \quad (19)$$

$$= + \sum_h \sum_{i \in D} (P_{20if} \cdot Z_{22ih}), \text{ for } f > 1$$

where:

- $\sum_h, \sum_{i \in D}$ = Summation over all horizons, summation over non-symbiotic types
 $Z_{1ih} \cdot Z_{2ih}$ = As in (1)
 Z_{21ih} = Death as in (17)
 P_7, P_{15} = Inverse efficiencies as in (9) and (14)
 P_{20if}, P_{21} = As in (16)
 Z_{22ih} = Change in biomass i as in (18)

CHANGE IN DENITRIFYING DECOMPOSERS (\dot{Z}_{25h})

$$\dot{Z}_{25h} = (\exp(Z_{15h} - Z_{85h}) - 1) \cdot Z_{25h}/P_{22} \quad (20)$$

where:

- Z_{15h}, Z_{25h} = Growth rate (2) and biomass
 Z_{85h} = Death rate as in (3)
 P_{22} = Units of Z_{25h} biomass not involved in denitrification per unit involved

TABLE OF SYMBOLS FOR MATHEMATICAL
EQUATIONS

Symbol	FORTTRAN	Eq. Where Defined	Units	Sym.	FORTTRAN	Eq.	Units	Example
X_{01rf}	AGAIN(R,F)	1	g/ha·time	P_{1i}	CM(I)	2	g/ha	1000.
X_{21Df}	CLIT (LDUM,F)	19	g/ha	P_{2i}	D1(I)	3	1/time	.02
X_{22hf}	CORG(H,F)	16	g/ha	P_{3i}	D2(I)	3	1/time	.002
X_{24hf}	SMIN(H,F)	7, etc.	g/ha	P_{4i}	GM(I)	5	1/time	.7
Z_{1ih}	GR(I)	2	1/time	P_5	CION	6	-bars	-10.
Z_{2ih}	BIOM(I,N), CBIO(N)	4	g/ha	P_6	FVNH4	8	1/time	.01
Z_{3ih}	V11NH4, V11NO2, V11NO3	10	g/ha·time	P_7	A3	9	dimensionless	16.
Z_{4h}	V8	13	g/ha·time	P_8	MAIN3	9	1/time	.00005
Z_5	V10	8	g/ha·time	P_9	K3	9	1/time	1.0
Z_{6ih}	G(I), GG	5	1/time	P_{10}	B3	9	dimensionless	.0005
Z_{7ih}	CI(N), TOTO, C, SMIN(H,*)	2	g/ha	P_{11}	KM3	9	g/ha	1.0
Z_{8ih}	D(I)	3	1/time	P_{12i}	BNH4,	10	dimensionless	1.0
Z_{9ih}	TC	5	dimensionless		BNO2,	10		.1
Z_{10ih}	PHC	5	dimensionless		BNO3	10		.3
Z_{11ih}	SC	5	dimensionless	P_{14}	A5	13	dimensionless	.5
Z_{12ih}	WC	5	dimensionless	P_{15}	A4	14	dimensionless	16.0
Z_{13ih}	—	6	dimensionless	P_{16}	MAIN4	14	1/time	.00005
Z_{14h}	WATPOT(H)	6	-bars	P_{17}	K4	14	1/time	1.0
Z_{15h}	V6	9	g/ha·time	P_{18}	B4	14	dimensionless	.0005
Z_{16}	TC8	8	dimensionless	P_{19}	KM4	14	g/ha	1.0
Z_{17}	PHC8	8	dimensionless	P_{20if}	CFEPCT(I,F)	16	dimensionless	.10, etc.
Z_{18}	SOCOC	8	dimensionless	P_{21}	BN	16	dimensionless	.10
Z_{19h}	V11	11	g/ha·time	P_{22}	CBFAC	20	dimensionless	2.
Z_{20h}	V7	14	g/ha·time					
Z_{21ih}	—	17	g/ha·time					
Z_{22ih}	CHANGE	18	g/ha					

COMPUTER IMPLEMENTATION

DATA REQUIREMENTS AND EXECUTION CHARACTERISTICS

CLIT(LDUM,*) is a dummy storage type which can have an arbitrary value but must be at least as great as actual total equivalent amount of constituent * in all three biomasses (free fixers, two oxidizers) included and over-all horizons. CBFAC must be non-zero. Linkages to other programs are B1(N) (symbionts in plant roots of horizon N); SYMNIT(N) (symbiotic growth requirement for N -- not all fixed necessarily); CI(N) (total host root carbon of horizon N); AUTNIT and AUTGRO (growth requirement for N and input growth of autotrophs as calculated elsewhere). Logical switches must be on or off as desired. TNC(N) is the sum of inorganic types of N and must be summed in some external place. There must always be unique places to store all the different types of N (don't use them summed under something like "total inorganic N"). This is why SMIN is used in place of CMIN. For purposes of a major simulation, plant and animal submodels may not be able to use the different types of N at all and would have to have a "total

mineral N" type constituent in CMIN. If they do contribute or take from this category, the distribution of such activity over types of SMIN will have to be determined (happy interfacing!). A flow chart of the submodel is provided in Figure 3.

PARAMETER DEFINITIONS

- A3
1/Eff. or NH_4^+ disappeared/ NH_4^+ assimilated by the oxidizers (NH_4^+ to NO_2^-).
- A4
1/Eff. or NO_2^- disappeared/ NO_2^- assimilated by the oxidizers.
- A5
The units of ($\text{NO}_2^- + \text{NO}_3^-$) required (as oxygen source) per unit growth.
- AUTGRO
Growth of autotrophic fixers. Growth rate times biomass, as calculated in plant or other submodel.
- BIOM(I,N)
Some measure of total biomass of microbial population I in horizon N. I = 1 for symbionts, I = 2 for heterotrophes, I = 3 for NH_4^+ oxidizers, I = 4 for NO_2^- oxidizers.
- BN
Nitrogen in biomass populations in general, units N per unit microbial biomass.
- BNH4
Preference coefficient for use of NH_4^+ as source of nitrogen for microbial growth.
- BNO2
Preference coefficient for use of NO_2^- as source of nitrogen for microbial growth.
- BNO3
Preference coefficient for use of NO_3^- as source of nitrogen for microbial growth.
- B3
External enzyme concentration per unit microbial biomass of the NH_4^+ oxidizers.
- B4
External enzyme concentration per unit microbial biomass of the NO_2^- oxidizers.
- CBFAC
The inverse of CBFAC ($1/\text{CBFAC}$) is the fraction of CBIO(N) which is involved in denitrification.
- CBIO(N)
Some measure of decomposer biomass in horizon N as calculated mainly in the DECOMP subroutine.
- CFEPCT(I,K)
Units constituent k normally found in biomass type i per unit total biomass type i (dry weight as stored in CLIT(NDUM,*)).

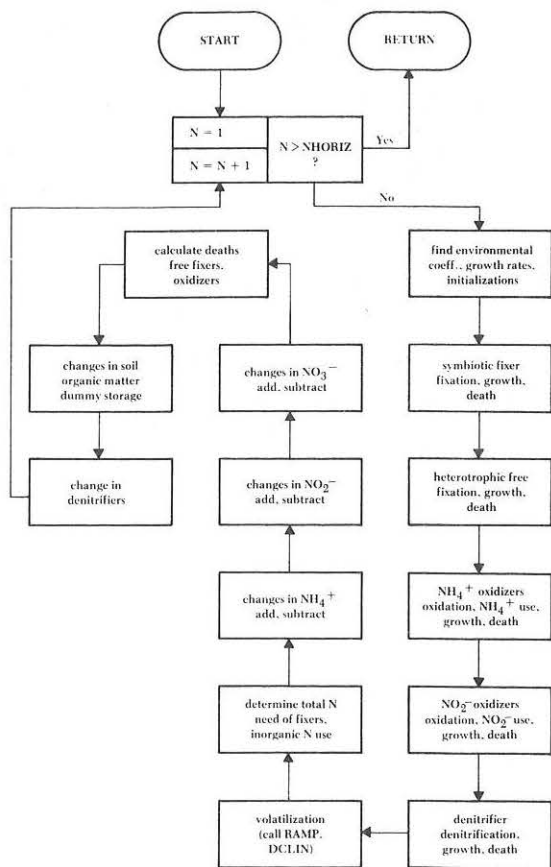


Figure 3. Program flow chart.

- CI(N)
Total symbiotic host root carbon in horizon *n*.
- CI(N)
Inhibition constant for the inhibition of the use of ($\text{NO}_3^- + \text{NO}_2^-$) as source of oxygen, by the oxygen present.
- CM
Michaelis constant for the limiting substrate in each reaction.
- D1(I)
Death rate under starvation conditions for biomass type *i*. This is used in the EXP exponential function.
- D2(I)
Death rate under normal conditions (energy source is available) for biomass type *i*.
- FVNH4
Maximal rate of NH_3 volatilization independent of NH_3 concentration, at optimal conditions for volatilization, units volatilized per unit present.
- GM(I)
Maximal growth rate (substrate concentration is high, environmental conditions are optimal) for biomass type *i*.
- HETFIX
Logical switch. Set to .TRUE. if free heterotrophic fixation is to be modelled.
- IAGN
Nitrogen constituent number in the AGAIN array.
- ICO2
Carbon constituent number in the AGAIN array.
- INH4
Ammonium constituent number in the SMIN array.
- INIT
Organic nitrogen constituent number in the CORG or CLIT or SMIN array.
- INO2
Nitrite position in SMIN (usually 3).
- INO3
Nitrate position in SMIN (usually 4).
- IR
Number of biomasses or of types of transformers involved (usually 5).
- KA
Atmospheric route of exchange number in AGAIN.
- KM3
Michaelis constant for waste metabolism connected to NH_4^+ oxidation.
- KM4
Michaelis constant for waste metabolism connected to NO_2^- oxidation.
- K3
Rate constant for waste metabolism connected to NH_4^+ oxidation.
- K4
Rate constant for waste metabolism connected to NO_2^- oxidation.
- LDUM
Position in CLIT array reserved for the dummy biomass equivalent to the sum of BIOM in all horizons.
- MAIN3
 NH_4^+ required for maintenance per unit biomass of NH_4^+ oxidizers.
- MAIN4
 NO_2^- required for maintenance per unit biomass of NO_2^- oxidizers.
- NNAMLS
Integer switch. If .GT.O, NITRO's namelist (HANNA) if printed out.
- PHK(I,J)
pH points for the various types of biomass (I), J = 1 minimum pH below which the pH coefficient is zero, J = 2,3 two maximal pH points between which the pH coefficient is one, J = 4 maximum pH above which the pH coefficient is one.
- PHMAX
Maximal pH for NH_3 volatilization above which the pH coefficient is one.
- PHMIN
Minimal pH for NH_3 volatilization below which the pH coefficient is zero.
- SA(I,J)
Salinity points for the various types of biomass (I); J = 1 minimum salinity below which the salinity coefficient is zero, J = 2,3 two maximal salinity concentrations between which the salinity coefficient equals 1; J = 4 max salinity above which the salinity coefficient is zero.
- SMIN(N,K)
Soil mineral nitrogen pools, including NO_3^- , NO_2^- and NH_4^+ .
- SYMFIX
Logical switch. If .TRUE., symbiotic fixation is calculated by NITRO.
- T(I,J)
Temperature points for various types of biomass (I); J = 1 minimum temperature below which the temperature coefficient is zero, J = 2,3 two maximal points between which the temperature coefficient is one, J = 4 maximum temperature above which the temperature coefficient is zero.
- TMAX
Maximal temperature for NH_3 volatilization above which the temperature coefficient is one.
- TMIN
Minimal temperature for NH_3 volatilization below which the temperature coefficient is zero.
- VMAX
Maximal plant cover of soil above which the cover coefficient for NH_3 volatilization is one.
- VOLATL
Logical switch. If .TRUE., volatilization of NH_3 is calculated here in NITRO.
- W(I,J)
Water potential (in negative bars) points for various

types of biomass (I), includes the requirements for moisture and oxygen; $J = 1$ minimum water potential below which the water coefficient is zero, $J = 2,3$ maximal water potential values between which the water coefficient is one, $J = 4$ maximal water potential above which the water coefficient is zero.

LITERATURE CITED

- McLAREN, A. D. 1971. Kinetics of nitrification in soil: growth of the nitrifiers. *Soil Sci. Soc. Amer. Proc.* 35(1):91-95.
- PARNAS, H., and J. RADFORD. 1974. A decomposition submodel. US/IBP Desert Biome Res. Memo. 76-63. 23 pp.

Listings of the programs which handle both nitrogen and decomposition appear as Appendix 1 to Research Memorandum 74-63 -- *A decomposition submodel*. An example of input/output follows the program listing (Appendix 2).
