ENERGY OR NUTRIENT REGULATION OF DECOMPOSITION: IMPLICATIONS FOR THE MINERALIZATION–IMMOBILIZATION RESPONSE TO PERTURBATIONS

Ernesto Bosatta and Frank Berendse

Department of Ecology and Environmental Research, Swedish University of Agricultural Sciences, S-750 07 Uppsala, Sweden and Department of Landscape Ecology and Nature Management, University of Utrecht, Opaalweg 20, NL-3523 RP Utrecht, The Netherlands

Summary—A model developed previously to describe the turnover of forest soil nitrogen is modified here to explain the effects of carbon and nitrogen additions on their dynamics. The model, which is structurally very simple, seems to explain correctly, among other phenomena, the negative correlation between N mineralization and CO_2 evolution observed in many experimental situations. An important variable used to explain this behaviour is the deficiency factor, which is related to the critical C-to-nutrient ratio and which gives a measure of the C or nutrient deficiency in the substrate with respect to the needs of the decomposers. Ways are discussed in which the model output can be used to explain the observed retention in the soil of fertilizer N added to mature forest soils.

INTRODUCTION

Mineralization of plant nutrients is a key process controlling primary production in many ecosystems. Even if understanding of the mechanisms behind the mineralization–immobilization process is far from complete, an acceptable level of description of its dynamics under unperturbed conditions is available today (Swift *et al.*, 1979).

For N, Aber and Melillo (1979), Staaf and Berg (1982) and others have found that, in a great number of decomposing litter materials, two distinct phases can be distinguished in the turnover. A period of N accumulation, the duration and magnitude of which depends on the substrate, is followed by a period of net N release. An explanation of this behaviour has already been provided by Waksman and Tenney (1927). During the accumulation phase the N in the decomposing material is in short supply with respect to the needs of the microorganisms which, consequently, must import nitrogen from the surroundings: the material is N-deficient (immobilization predominates over mineralization). On the other hand, during the release phase, the material is C- or energy-deficient (mineralization predominates over immobilization).

According to Swift *et al.* (1979) the same general trends of the mineralization–immobilization dynamics should also apply to other nutrient elements, and they claim that the carbon-to-element ratio in resource and in decomposer biomass are main factors determining the presence or the lack of an accumulation phase of the nutrient in the material. Very little is understood of the processses involved in perturbed situations but they may be more complex.

It has often been found that N mineralization from soils is stimulated by the additions of nitrogen fertilizers (Johnson and Guenzi, 1963; Broadbent and Nakashima, 1971). The same effect has been observed in the laboratory by Johnson *et al.* (1980) following the addition of urea to control soils. The interesting point, however, is that C mineralization seems to be negatively correlated to N mineralization, viz., both in laboratory and field experiments, the CO_2 evolution decreases following N fertilization (Johnson *et al.*, 1980; Bååth *et al.*, 1981). The common idea that the priming effect of N additions on N mineralization is due to enhanced microbial activity (e.g. Westerman and Tucker, 1974) seems to be challenged by this observed negative correlation. Another perturbation phenomenon that is not yet understood is the retention of N in the soil organic matter following N-fertilization of forest soils (Ingestad *et al.*, 1981).

The aim of our paper is two-fold. First, a model previously developed (Bosatta and Staaf, 1982) is modified here in order to study the effects of C and N additions to the mineralization–immobilization dynamics. Second, to show that the deficiency factor (a variable measuring the status of the decomposing material as being energy or nutrient deficient) is of primary importance in explaining the responses of the mineralization–immobilization dynamics to perturbations.

A GENERAL MODEL FOR MINERALIZATION–IMMOBILIZATION. THE DEFICIENCY FACTOR

The mineralization–immobilization process is intimately associated with the activity of the decomposers. Suppose that an amount, B, of living microbial biomass is growing in a certain amount of a homogeneous decomposing substrate producing new biomass at a rate P and with a given concentration of C, f_c, and N, f_n. (Throughout this chapter, the word "nitrogen" could equally well be substituted by the word "nutrient").

Let S_c and S_n denote the amounts of C and N in the substrate respectively and B_c and B_n the corresponding amounts of the same elements in the microbial biomass. By definition, $C = S_c + B_c$ and $N = S_n + B_n$ will be the total amounts of C and N in the substrate-microbe complex. To set up a general model for the dynamics of C and N, the rates of change of C and N are given by the rates of respiration, R and mineralization, m, respectively.

The rate of respiration is the difference between the rate at which C is taken up from the substrate, $f_c P/e$, and the rate at which it is incorporated into biomass, $f_c P$, i.e.

$$R = \frac{f_c}{e} P - f_c P \qquad (1)$$

where e is the production-to-assimilation ratio. In this model, e, f_c and f_n are constant magnitudes (parameters).

N uptake is equal to the product of C uptake and the substrate N-to-C ratio and so, the rate of net mineralization is

$$m = \frac{f_c}{e} P \frac{S_n}{S_c} - f_n P \qquad (2)$$

where $f_n P$ is the rate at which the N is incorporated into biomass.

In our previous model (Bosatta and Staaf, 1982) it was assumed that living and dead microbial biomass had the same C-to-N ratio. The present derivation is more general, since that assumption is not used here.

The amount of living microbial biomass is usually a small fraction of the whole decomposing litter. Berg and Söderström (1979) found that the total amount of fungal biomass after 1 yr was about 1% of the weight of the total litter at that time. Thus, we assume that the C-to-N ratio of the substrate (S_c/S_n) can be approximated by the C-to-N ratio, r, of the substrate–microbe complex, i.e.

$$r = C/N \cong S_c/S_n. \qquad (3)$$

The critical C-to-N ratio, r_c, is defined as (Parnas, 1975):

$$r_c = f_c/(f_n e). \qquad (4)$$

Introducing equations (3) and (4) into (2) we obtain a net mineralization rate:

$$m \cong \left(\frac{r_c}{r} - 1\right) f_n P. \qquad (5)$$

We now define the deficiency factor as:

$$\gamma = \frac{r_c}{r}. \qquad (6)$$

If the substrate is C deficient $r_c > r$ (i.e. $\gamma > 1$), then $m > 0$, i.e. mineralization will predominate. On the other hand, for a N deficient substrate $r > r_c (\gamma < 1)$ then $m < 0$ and immobilization will predominate.

From equations (1) and (5), we can now obtain dynamic equations for the total amounts of C and N, namely:

$$\dot{C} = -R = -(1 - e) f_c P/e; \qquad (7a)$$

$$\dot{N} = -m = -\left(\frac{r_c}{r} - 1\right) f_n P. \qquad (7b)$$

A series of relevant results can be deduced from this model without making any assumption whatsoever about the nature of the microbial production P (except, of course, that $P \geqslant 0$). Using this, the definition of e and equation (7a) we see that C behaves as a monotonously decreasing function of time.

To find the behaviour of N, we first take the time derivative of the C-to-N ratio and introduce equation (7) into it to obtain:

$$\dot{r} = \frac{P}{N} (f_c - f_n r). \qquad (8)$$

Let C_0, N_0 and $r_0 = C_0/N_0$ be the amounts of C, N and the C-to-N ratio at some time t = 0. Since P/N is a positive quantity, r will either decrease or increase in time depending on whether $r_0 > f_c/f_n$ or $r_0 < f_c/f_n$ until it reaches the final value f_c/f_n.

Two situations are of practical interest. Assume first that the substrate is initially C deficient, i.e. $r_c > r_0 > f_c/f_n$. Under these conditions, $m > 0$ all the time, and N will decay steadily in time. The other situation is that for which $r_0 > r_c > f_c/f_n$, i.e. the substrate is N-deficient. From equation (5), $m < 0$ and N will increase from its starting value N_0. But, from equation (8), r decays in time and when it reaches the value r_c, m equals zero and N reaches a maximum. Thereafter, the substrate becomes C-deficient and a net release of N begins.

The conclusion is that, regardless of the definition adopted for P, the equations (7a) and (7b) predict the accumulation and release phases of N in the decomposing substrate.

CARBON OR NITROGEN LIMITATIONS TO MICROBIAL GROWTH. THE EFFECTS OF C AND N ADDITIONS

To analyze the effects of C and N additions on mineralization and respiration we must define P in some explicit way.

If μ (day^{-1}) is the relative growth rate of the microbial biomass B when no element is limiting growth, we define productivity as:

$$P = \mu B. \qquad (9)$$

If some element is limiting growth, we introduce a reduction factor, ρ,

$$P = \rho \mu B \qquad (10)$$

such that $0 < \rho < 1$.

In N-poor systems, i.e. systems in which N is limiting growth ($r > r_c$), the reduction factor coincides with the deficiency factor defined in equation (6) (Berendse and Bosatta, 1984, to be published), i.e.

$$\rho_N = r_c/r. \qquad (11)$$

Now, we assume that if C is limiting growth ($r < r_c$), the reduction factor is:

$$\rho_c = r/r_c. \qquad (12)$$

From equations (11) and (12), growth will be at a maximum when $r = r_c$, a result already observed by Parnas (1976) in culture experiments. The next assumption is that B is a constant fraction, α, of the total C in the substrate (Bosatta and Staaf, 1982), i.e.

$$B = \alpha C. \qquad (13)$$

Finally, the effect of perturbations must be compared to some reference state. This is generated here by driving the system to a steady state (ss) by means of an external input of carbon at a rate I (mg day^{-1}) having a N-to-C ratio w.

With this, and introducing (10) and (13) into equations (7) we get

$$\dot{C} = -k\rho C + I \qquad (14a)$$

$$\dot{N} = -k_n\rho N + b\rho C + wI, \qquad (14b)$$

where

$$k = \frac{1-e}{e} f_c\mu\alpha \qquad (15)$$

$$k_n = \frac{f_c}{e}\mu\alpha \qquad (16)$$

and

$$b = f_n\mu\alpha. \qquad (17)$$

If ρ is set to $\rho_c = C/N/r_c$ the system (14) reaches ss in which

$$(N/C)^* = r_c^{-1} + w(1-e) \qquad (18)$$

and so $r^* < r_c$. This means that the ss is carbon deficient and a net release of nitrogen is produced from the substrate in this state, namely

$$m^* = wI. \qquad (19)$$

For the N-limited case, ρ in equations (14) must be substituted with ρ_N (equation 11). Trivially, no N-deficient ss can be generated from equations (14a and b) if a net input of N is given to the system.

A N-deficient ss can be achieved, on the other hand, if an output of N (such that output $> wI$) is subtracted from equation (14b). If we use the litter layer as an image of a N-deficient system, we could regard this output as a transfer of nitrogen related to the humification process. The easiest way to mimic N

losses is by giving w a negative value, and, in this way, equation (18) can be used again to calculate the (N/C)*. So, putting w to a negative value, we get $r^* > r_c$ and the substrate has a net immobilization.

An analysis of the characteristic roots of equations (14) in the neighborhood of both ss points shows that:

—the C-limited ss is stable for any choice of parameter values;

—the N-limited ss will be stable only if:

$$\frac{|w|f_c(1-e)}{ef_n} < \tfrac{1}{2}. \qquad (20)$$

Furthermore, when the following relationship is fulfilled

$$\frac{|w|f_c(1-e)}{ef_n} + \frac{1}{2[1-(1-e)^{1/2}]} > 1 \qquad (21)$$

the variables in the N-limited system will, as a response to the perturbation, oscillate in their return to equilibrium.

As a conclusion, a qualitatively different response to same perturbation can be expected depending on whether the system is C- or N-deficient. This is depicted in Fig. 1.

The values of f_c and f_n agree with values found by Bååth and Söderström (1979) in fungal biomass from different forest soils. The values given to e has been used before (Bosatta et al., 1980) as an estimate of the production efficiency in the same kind of systems.

As can be seen from equations (20) and (21) the qualitative pattern of behaviour is not affected by the choice of μ: this choice can only speed or slow down the whole dynamics. The value given to α is based in the observation of Berg and Söderström (1979) previously mentioned (see discussion preceeding equation 3). With this election of parameter values, the critical C-to-N ratio is $r_c = 62.5$.
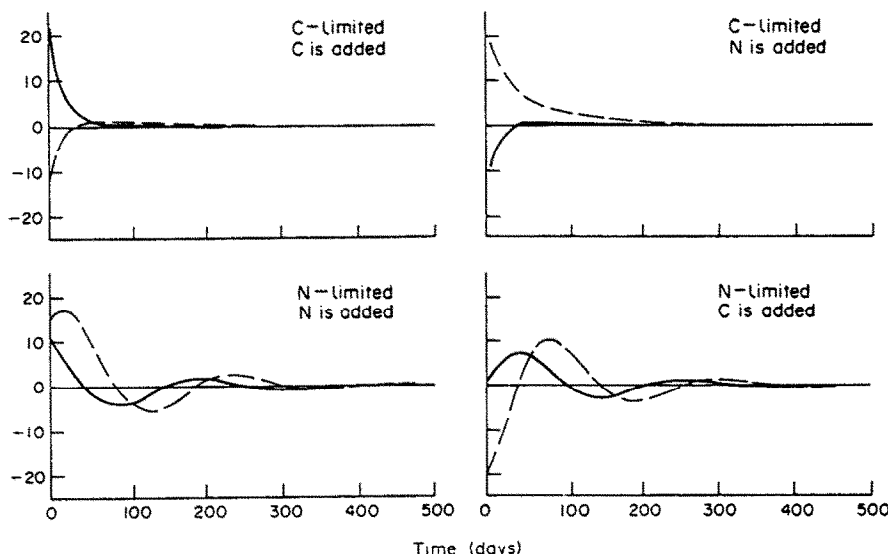

Fig. 1. The changes (in %) with respect to steady state of rates of respiration (——) and net nitrogen mineralization (- - - -). In all cases, the amounts added are 10% of the steady state values. The curves are calculated assuming that $e = 0.2$, $f_c = 0.5$, $f_n = 0.04$, $\mu = 2$. day^{-1}, $\alpha = 0.01$ and $I = 1$ mg day^{-1}.
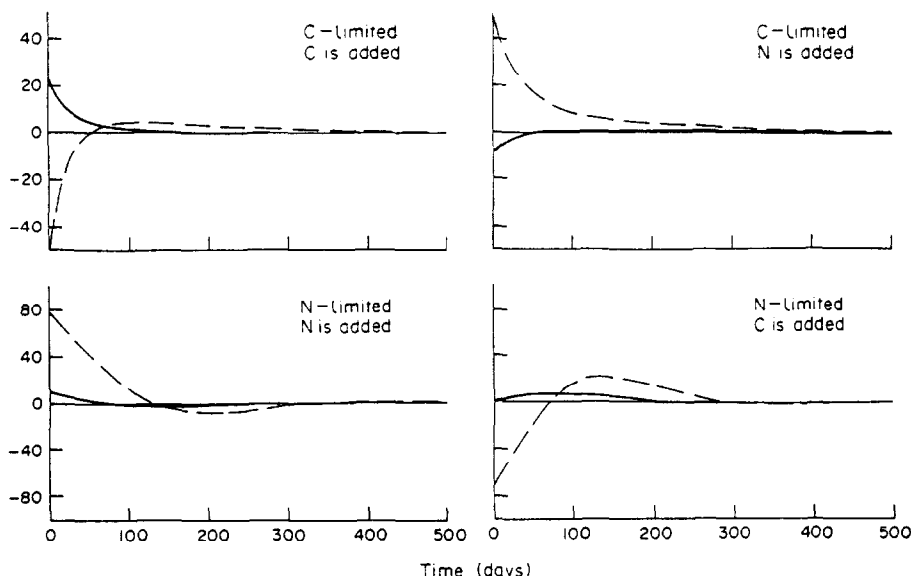
Fig. 2. Changes in the rates of respiration and net nitrogen mineralization when the production-to-assimilation ratio, e, is set to 0.4. The remaining parameters are the same as in Fig. 1.

The C-to-N ratio of Scots pine litter is about 100 (Staaf and Berg, 1982). So, the C-limited steady state is generated by choosing $w = 0.01$, and, in this way, $r^* = 41.7$. The N-deficient ss is generated by placing $w = -0.006$ and, in this way, $r^* = 91.2$. The efficiency in producing new biomass, e, is probably the most uncertain parameter. According to McGill et al. (1981), its value can lie between 0.2 and 0.6. Also, as can be seen from equations (20) and (21), changes on e can drastically change the qualitative properties of the system.

In the example in Fig. 2, e has been set to 0.4. Comparing this figure with Fig. 1, the conclusion can be drawn that N is more sensitive than C to changes in this parameter. It should be noticed that the concentration of N in the ss of Fig. 2 is higher than in the corresponding ss of Fig. 1.

DISCUSSION

From the results of Fig. 1, C-limited or nutrient-limited systems will react in very different ways when perturbed. This indicates that the "primary effect" explanation must be used with care, and that consideration must be made of the deficiency status of the system.

The priming effect is introduced here in equation (10) through the reduction factor ρ. As can be seen in equation (12), for example, this factor will increase if C is added to a C-deficient system, thus increasing the productivity of microorganisms. The status of a system is given here by the deficiency factor (equation 6), which has previously also been found to be a variable of major importance in explaining the dynamics of co-existence between plants and decomposers (Bosatta, 1981). The easiest way to define the deficiency factor in an experimental way is, perhaps, to measure whether the substrate is releasing or accumulating nutrient *before* the perturbation is applied. Also, if the specific decomposition rate of the material is known, the critical C-to-N ratio can be estimated with the regression model of Bosatta and Staaf (1982).

The negative correlation between respiration and mineralization for the C-limited case supplied with N in Fig. 1 agrees well with the experimental results of Söderström et al. (unpublished), Johnson et al. (1980) for forest soils, and Kowalenko et al. (1978) for agricultural soils. Foster et al. (1980) also observed a decrease in respiration when they added N to soil sample consisting of a mixture of L and F horizons from a pine stand, and they attributed this decrease to toxic effects of the added N. They claimed that the high C-to-N ratio (~ 43) will make this substrate N-limited with respect to microbial growth. Instead, an alternative explanation could be that their material was C-limited, a reasonable assumption for this range of C-to-N (e.g. Berg and Staaf, 1981).

Figure 1 shows that a C-limited system amended with C will increase respiration and immobilization (net mineralization decreases in respect to ss). This is in agreement with experimental results of Johnson and Edwards (1979) on N mineralization and CO_2 evolution from a girdled stand when sucrose was added to it.

Nömmik and Möller (1981) had, among others, observed an increased retention of N in forest soils after fertilization. The litter layer of a forest soil can be considered N-limited and thus will be steadily immobilizing N (Staaf and Berg, 1977). It can be speculated that the addition of nitrogen to the N-limited L-layer stimulates microbial immobilization and this, combined with the humification process, will make the N less mobile in the soil. Some support for increased immobilization speculated upon here can be found in Fig. 1; after a certain period immobilization increases with respect to steady state if N is added to a N-limited system.

REFERENCES

Aber J. D. and Melillo J. M. (1979) Litter decomposition: measuring relative contributions of organic matter and nitrogen to forest soils. *Canadian Journal of Botany* **58**, 416–421.

Bååth E. and Söderström B. (1979) Fungal biomass and fungal immobilization of plant nutrients in Swedish coniferous forest soils. *Revue d'Ecologie et de Biologie du Sol* **16**, 477–489.

Bååth E., Lundgren B. and Söderström B. (1981) Effects of nitrogen fertilization on the activity and biomass of fungi and bacteria in a podzolic soil. *Zentralblatt für Bakteriologie, Parasitenkunde, Infektionskrankheiten und Hygiene, Abt. I., Orig. C* **2**, 90–98.

Berg B. and Söderström B. (1979) Fungal biomass and nitrogen in decomposing Scots pine needle litter. *Soil Biology & Biochemistry* **11**, 339–341.

Berg B. and Staaf H. (1981) Leaching, accumulation and release of nitrogen in decomposing forest litter. In *Terrestrial Nitrogen Cycles* (Clark F. E. and Rosswall T., Eds). *Ecological Bulletins (Stockholm)* **33**, 163–178.

Bosatta E. (1981) A qualitative analysis of the stability of the root-microorganisms soil system. 1. Carbon-nitrogen status and nitrogen mineralization. *Ecological Modelling* **13**, 223–236.

Bosatta E. and Staaf H. (1982) The control of nitrogen turnover in forest litter. *Oikos* **39**, 143–151.

Bosatta E., Bringmark L. and Staaf H. (1980) Nitrogen transformations in a Scots pine forest mor-model analysis of mineralization, uptake by roots and leaching. In *Structure and Function of Northern Coniferous Forests— An Ecosystem Study* (T. Persson, Ed.). *Ecological Bulletins (Stockholm)* **32**, 565–589.

Broadbent F. E. and Nakashima T. (1971) Effects of added salts on nitrogen mineralization in three California soils. *Soil Science Society of America Proceedings* **35**, 457–460.

Foster N. W., Beauchamp E. G. and Corke C. T. (1980) Microbial activity in a *Pinus banksiana* Lamb. forest floor amended with nitrogen and carbon. *Canadian Journal Soil Science* **60**, 199–209.

Ingestad T., Aronsson A. and Ågren G. I. (1981) Nutrient flux density model of mineral nutrition in conifer ecosystems. *Studia Forestalia Suecia* **160**, 61–71.

Johnson D. D. and Guenzi W. D. (1963) Influence of salts on ammonium oxidation and carbon dioxide evolution from soil. *Soil Science Society of America Proceedings* **27**, 663–666.

Johnson D. W. and Edwards N. T. (1979) The effects of stem girdling on biogeochemical cycles within a mixed deciduous forest in Eastern Tennessee II. Soil nitrogen mineralization and nitrification rates. *Oecologia* **40**, 259–271.

Johnson D. W., Edwards N. T. and Todd D. E. (1980) Nitrogen mineralization immobilization and nitrification following urea fertilization of a forest soil under field and laboratory conditions. *Soil Science Society of America Journal* **44**, 610–616.

Kowalenko C. G., Ivarson K. C. and Cameron D. R. (1978) Effect of moisture content, temperature and nitrogen fertilization on carbon dioxide evolution from field soils. *Soil Biology & Biochemistry* **10**, 417–423.

McGill W. B., Hunt H. W., Woodmansee R. G. and Reuss J. O. (1981) PHOENIX, a model of the dynamics of carbon and nitrogen in grassland soil. In *Terrestrial Nitrogen Cycles*. (F. E. Clark and T. Rosswall, Eds). *Ecological Bulletins (Stockholm)* **33**, 49–115.

Nömmik H. and Möller Gö (1981) Nitrogen recovery in soils and needle biomass after fertilization of a Scots pine stand, and growth responses obtained. *Studia Forestalia Suecia* **159**, 5–37.

Parnas H. (1975) Model for decomposition of organic material by microorganisms. *Soil Biology & Biochemistry* **7**, 161–169.

Parnas H. (1976) A theoretical explanation of the priming effect based on microbial growth with two limiting substrates. *Soil Biology & Biochemistry* **8**, 139–144.

Staaf H. and Berg B. (1977) Mobilization of plant nutrients in a Scots pine forest mor in central Sweden. *Silva Fennica* **11**, 210–217.

Staaf H. and Berg B. (1982) Accumulation and release of plant nutrients in decomposing Scots pine needle litter. Long-term decomposition in a Scots pine forest II. *Canadian Journal of Botany* **60**, 1561–1568.

Swift M. J., Heal O. W. and Anderson J. M. (1979) *Decomposition in Terrestrial Ecosystems*. Studies in Ecology, Vol. 5. Blackwell, Oxford.

Waksman S. A. and Tenney F. G. (1927) The composition of natural organic materials and their decomposition in the soil: II influence of age of plant upon the rapidity and nature of its decomposition—Rye plants. *Soil Science* **24**, 317–333.

Westerman R. L. and Tucker T. C. (1974) Effects of salts plus nitrogen-15-labelled ammonium chloride on mineralization of soil nitrogen, nitrification and immobilization. *Soil Science Society of America Proceedings* **38**, 602–605.