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Soil Biota and Global Change

Global change, soil biodiversity, and nitrogen cycling in terrestrial ecosystems: three case studies

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Abstract

The relative contribution of different soil organism groups to nutrient cycling has been quantified for a number of ecosystems. Some functions, particularly within the N-cycle, are carried out by very specific organisms. Others, including those of decomposition and nutrient release from organic inputs are, however, mediated by a diverse group of bacteria, protozoa, fungi and invertebrate animals. Many authors have hypothesized that there is a high degree of equivalence and flexibility in function within this decomposer community and thence a substantial extent of redundancy in species richness and resilience in functional capacity. Three case studies are presented to examine the relationship between soil biodiversity and nitrogen cycling under global change in ecosystem types from three latitudes, i.e. tundra, temperate grassland and tropical rainforest.

In all three ecosystems evidence exists for the potential impact of global change factors (temperature change, CO_2 enrichment, land-use-change) on the composition and diversity of the soil community as well as on various aspects of the nitrogen and other cycles. There is, however, very little unequivocal evidence of direct causal linkage between species richness and nutrient cycling efficiency. Most of the changes detected are shifts in the influence of major functional groups of the soil biota (e.g. between microflora and fauna in decomposition). There seem to be few data, however, from which to judge the significance of changes in diversity within functional groups. Nonetheless the soil biota are hypothesized to be a sensitive link between plant detritus and the availability of nutrients to plant uptake. Any factors affecting the quantity or quality of plant detritus is likely to change this link. Rigorous experimentation on the relationships between soil species richness and the regulation or resilience of nutrient cycles under global change thus remains a high priority.

Keywords: biodiversity, decomposition, ecosystem comparison, N-cycle, soil food-web

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Introduction

The contribution of soil organisms to nutrient cycling in terrestrial ecosystems is well established. The responsible community is highly diverse but can conveniently be categorized as a number of functional groups. In this paper we concentrate on the responses of functional groups of soil organisms to global change and the consequent effects on nutrient cycling. Our review is largely confined to the nitrogen cycle, the element most strongly influenced by biological activities.

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The nutrient cycle functions performed by some members of the soil biota are highly specific whilst others are rather general. Three functional groups in the former category are the *N-fixers*, the *nitrifiers* and the *denitrifiers*. These functions are largely confined to a few genera of bacteria. The *mycorrhizal fungi* are similarly a very specific functional group but with a high internal diversity. The *decomposers* are a very diverse group comprising bacteria, fungi, and a wide range of invertebrate phyla. For detailed analysis this group must be subdivided but no universally accepted scheme for this exists. The most common approach is to group the decomposers by body size as *microorganisms*, *mesofauna*, and *macrofauna* (Swift *et al.* 1979). Two groups of the macrofauna, the termites and the earthworms are commonly grouped together as a separate functional group, the *ecosystem engineers*. In some ecosystems, ecosystem engineers can determine to a considerable extent the soil physico-chemical environment in which the nutrient cycle takes place. Engineer populations differ among ecosystems and they may or may not belong to the detrital food web.

The approach adopted in this paper is to try and identify the ways in which global change may affect the nitrogen cycle through its effect on these functional groups and/or specific member organisms. Global change comprises a range of factors such as rising CO_2, increasing UVB-radiation, changes in land use, pollution and changes in temperature and water balance. The relative importance of these components differs among ecosystems and the case-studies presented below have been selected to show this. The impacts on soil organisms of global change are not always direct. For example, CO_2 fertilization may influence C allocation within plants and consequently the chemical composition of plant litter, thence triggering changes in soil populations. Indeed many of the impacts of global change are mediated through the organic matter or detritus which includes above- and below-ground litter, root exudates, excreta, corpses, and soil organic matter. The proportions and the quality characteristics of these nutrient sources varies among ecosystems.

Changes in biodiversity may occur within functional groups or in the balance between functional groups within the soil community. In determining the effects of global change on soil biodiversity it is thus important to determine whether the effect of global change is (a) merely a change in physico-biochemical rate (e.g. due to a shift in temperature); (b) induced via a biomass change (e.g. by reduction of mesofauna abundance); (c) operates by the organisms present changing their strategy (e.g. anabiosis in earthworms); or (d) through a shift in the balance of organisms in the community (e.g. extinction or immigration of species). Schimel & Gulledge (1998, this issue) discuss in more detail the distinction between direct global change effects and global change effects that are mediated via biodiversity change. It is also necessary to consider how biotic shifts are likely to occur. This refers to the tolerance limits, reproduction strategies, and colonization abilities of the organisms.

In the following sections, three case studies are presented of ecosystems that form a sequence with respect to decreasing soil organic matter content and increasing nutrient cycling efficiency. Simultaneously, the selected examples demonstrate differing susceptibility to aspects of global change: Arctic ecosystems are cold limited and particularly sensitive to global warming; temperate grasslands are nutrient limited and susceptible to increased CO_2 and N-deposition; whereas tropical rainforests rely on tightly closed nutrient cycles and are for the foreseeable future more likely to be affected by land-use change than by any other component of global change.

Tundra: an example of harsh climate and low diversity

Introduction

The soil organic matter of terrestrial ecosystems represents a carbon (C) pool three times larger than that of the atmospheric (GCTE 1996). Soils in tundra systems contain a major part of the terrestrial C, the accumulation of soil organic matter resulting largely from climatic limitation of the rate of decomposition (Swift *et al.* 1979). Arctic systems tend to have low biodiversity. It is often assumed that low diversity creates a less stable ecosystem, because as each function is performed by a low number of species the disappearance of a species compromises function. It has also been argued that high diversity gives a higher probability for continued function when conditions change (Andrén *et al.* 1995). However, one may also argue that if a property X (such as drought resistance) is needed, then a hundred drought-susceptible species are as useless as one. There is a growing mass of evidence indicating that biodiversity per se does not matter much for ecosystem processes, and 'there is no convincing evidence that ecosystem processes are crucially dependent on higher levels of biodiversity' (Grime 1997). It is alternatively possible that the species which comprise a low-diversity ecosystem such as tundra may be the most tolerant to a wide range of conditions, having been selected to survive in a strongly fluctuating environment and commonly with a wide niche breadth (i.e. cryotolerant rather than cryophilous).

Tundra is commonly defined as areas with permafrost, but a simpler definition is that it is beyond the climatic limit of tree growth, roughly coinciding with an annual mean temperature below 0 °C. The tundra can be divided into polar and alpine, with climate determined by latitude or altitude, respectively. A common characteristic is that temperature severely limits species diversity, production, decomposition and evapotranspiration. High soil acidity and waterlogging, but also drought due to inaccessibility of frozen water, as well as high summer insolation and surface temperatures, also limit both the presence and the activities of organisms.

Tundra is not just a deep-frozen or waterlogged environment however, and may be classified into dry, moist and wet. In summer the tundra (particularly that which is less wet) may have fairly high surface soil temperatures and the surface can become very dry. The long days during summer, with possibilities for 24 h sunshine and the absence of trees, make irradiation a major component in increasing the soil temperature, even if the air temperature remains low. Similarly, during the long winter snow cover can isolate the soil from the low air temperatures. Snow patch distribution may have a greater influence on winter soil temperature than air temperature (see French 1974; Rosswall & Heal 1975; Bliss *et al.* 1981; Chapin & Korner 1995).

In conclusion, the conditions in tundra soil may be extreme, but it is the combination of the factors of low temperature, too high or too low moisture and high acidity rather than any one of them which characterizes the zone. It has been suggested that the C stores in tundra will be particularly responsive to climate change, with temperature and moisture controlling the activity of the soil biota, and thus the dynamics of soil organic matter (Tinker & Ineson 1990; Shaver *et al.* 1992). Therefore, in the present context of global change and biodiversity, we use tundra as an example of a species-poor, severely climate-limited system.

Soil organisms

Organisms in tundra are in general those that can endure the winters. Perhaps one can also say that the larger the organisms, the more special adaptations are necessary. Among microorganisms, many taxa readily survive, but among mammals this is confined to real specialists. The diversity of microorganisms in Arctic systems is assumed to be low and the composition to differ from that of the temperate zone. The decomposition rate in tundra is also low and dependent on fungal and bacterial species active at very low temperatures. During summer when the temperature is fluctuating, microorganisms with varying temperature optima and versatile enzyme capabilities predominate. It has been shown that specific fungal species may have different enzyme production at low and high temperatures (e.g. optimum for pectinase at 20 °C but for cellulase at 5 °C; Flanagan & Veum 1974). The ecological consequences of such flexibility are obvious. The fungi may operate both in the cold and the warmer environments but decompose different compounds.

According to Chernov (1995), the soil fauna of tundra is species-poor with only 10–15% of the species numbers found in the temperate zone. For insects it is generally less than 1% but an exception may be Collembola, where 7–8% of the temperate zone species number is found in tundra. Earthworms occur sparsely in the Eurasian tundra zone (five species), but seem to be lacking from American tundras. Nematodes are found even in the polar deserts, where up to 50 species have been recorded, although only three were found in a recent study of dry valleys in the Antartic (Freckman, pers. comm.). Rotifers and tardigrades, although not well investigated, also exist under the harshest conditions. Finally, no less than 54 species of Protozoa have been recorded in an Antarctic investigation (Smith 1972). Concerning enchytraeids, the few species found in the North are spread over a wide range of latitude, which indicates a large degree of tolerance of physical conditions.

In the event of global warming in Arctic systems, an increase in diversity is likely unless there is also an associated increase in the frequency of catastrophic events, such as extremely cold (or warm and dry) summers. For example, artificially elevated summer temperatures in polar semidesert and tundra heath did not affect oribatid mites, but collembola density decreased in heated semidesert (Coulson *et al.* 1996). The year-to-year variation in climate had an equal or greater effect on microarthropod density than the artificial heating. On the other hand, low temperatures during summer, when the animals had reduced their supercooling ability, was also harmful to soil microarthropods (Coulson *et al.* 1995).

Special emphasis may be placed on the Enchytraeidae for two reasons: first, they have comparatively high abundance and activity in Arctic and Subarctic regions in tundra (Lundkvist 1973; MacLean 1974), taiga (Lundkvist 1982, 1983), moorlands and montane grasslands (Coulson & Whittaker 1978) and agricultural land in the taiga zone (Lagerlöf *et al.* 1989); second, they are a species-poor group and could therefore be lacking in buffering against species losses under global change. Enchytraeids, which may partly occupy the often vacant earthworm niche in tundra organic soils, are frequently concentrated in the upper horizons (Springett *et al.* 1970) where organic matter accumulates and the majority of the absorptive roots occur. But they also occur in deeper layers where temporary increases in their numbers are attributed either to vertical migration in response to adverse conditions (for example, Nielsen 1955; Nurminen 1967; and Abrahamsen 1972) or to the accessibility of litter at deeper layers, e.g. after ploughing (Lagerlöf *et al.* 1989). They do not survive for long if the soil water content is less than 10% of field capacity (Abrahamsen 1971). Consequently, summer droughts and frosts (which also create drought) could result in severe reductions in total numbers (Nielsen 1955; O'Connor 1957; Kasprzak 1982).

Thus, changes in temperature and water regimes, as forecast under future climate scenarios, could certainly influence the population sizes. A transplant experiment (Briones *et al.* 1997a) indicated that temperature is the main factor influencing cocoon formation and hatching and that mobility determines the adult worm's ability to survive. The temperature response was highly species dependent, resulting in greater numbers of the more tolerant species, migrations to other microhabitats or layers and extinction when temperature increased too much. Vertical migration seemed to be a successful strategy for some species to avoid adverse climatic conditions, but readily available organic matter was concentrated in the top 10 cm of these peaty soils, limiting the downward movement. In a tundra soil with a shallow active layer on top of the permafrost, downward movement would be even more restricted. Cold- and drought-tolerant enchytraeids can also survive as a species by laying resistant egg cocoons (Lagerlöf & Strandh 1997). Even if the adults do not survive the winter, the eggs will hatch in the spring, and rapidly growing juveniles will replace their parents. This strategy could be sensitive to climate change: if the summer temperature sum becomes lower, the life cycle from egg to juvenile to egg-laying adults may not be completed. Additionally, asexual reproduction through fragmentation, as found in *Cognettia sphagnetorum* (Christensen 1959; Lundkvist 1982, 1983), may be an even more successful strategy.

Carbon and nutrient cycling in Tundra

There is a growing body of experimental data from heating experiments concerning the effects of a temperature rise on nutrient cycling in tundra. The results are to some extent conflicting, but usually experimental warming increases litter decomposition rates and nutrient mineralization (Hobbie 1996), although the mineralised nutrients may rapidly become immobilized in microbial biomass (Jonasson *et al.* 1993). The effects on tundra plants of an increased nutrient availability (NPK fertilization) also seems to be highly variable (Shaver & Chapin 1995), so nutrient limitation is probably less common in tundra than in most other systems. If a temperature and CO_2 increase affects the species composition in tundra, great differences in carbon and nutrient release rates can occur, since different plant species and their components show very different decomposability (Table 1). CO_2 increases can also directly affect the decomposability of plant litter, through changes in their chemical composition (see the grassland example for discussion).

Table 1 Litter decomposition rate constants (k,% d^{-1}) at 4 °C of common tundra plants. (From Hobbie 1996; NA = not applicable)

Plant species	Leaf	Stem	Root
Carex bigelowii	0.15	0.17	0.18
Eriophorum vaginatum	0.16	0.24	0.10
Betula nana	0.09	0.03	0.05
Ledum palustre	0.15	0.04	0.01
Vaccinium vitis-idaea	0.11	0.05	0.01
Hylocomium splendens	0.01	NA	NA
Sphagnum spp.	0.02	NA	NA

For processes such as N_2O losses from the soil (part of denitrification losses), changes in precipitation may change the fluxes more than changes in temperature. It has been calculated that an increase of 20% in temperature will not affect N_2O emission from tundra (– 1%), whereas a 20% increase in rainfall would increase the emission by 11% (Smith 1997).

For a large part of the year, tundra soil is frozen. This has the consequence that, in relative terms, the activity during frozen periods contributes significantly to the total annual activity. In some areas, up to 30% of annual C mineralization can occur under frozen conditions (J. Schimel, pers. comm.; Clein & Schimel 1995). It is likely therefore that even a small increase in soil temperature (due to increased irradiation, air temperature or reduced snow cover) can have substantial effects. The relatively uncommon cryophilic organisms (those that need low temperatures) might suffer, but cryotolerant organisms (those that can also be active at low temperatures, but are more active at higher), should increase their activity.

In general, the responses to temperature changes below + 5 °C are governed by the cryotolerance of the organisms. As temperature decreases, more and more organisms and their enzymes become inactive. Thus, the Q_{10} concept does not work well in this range, since as organisms switch on from almost zero activity, the Q_{10} can approach infinity. Instead, detailed knowledge of the critical switching points should be used. If that information is not available, a linear interpolation between the Q_{10}-predicted activity at +5 °C and zero activity at a temperature close to 0 °C can be used. Alternatively, other more flexible functions can be used for the temperature response (Diaz-Ravina *et al.* 1994). A possible consequence of this discontinuous response to temperature may be that the temperature sensitivity of decomposition processes in tundra is much greater than that of net primary production, which occurs in summer only. It has been suggested that a 1 °C increase in temperature could ultimately lead to a loss of over 10% of the soil organic C in regions with an annual mean temperature of 5 °C, whereas the same temperature increase would lead to a loss of only 3% in soil organic C for a soil at 30 °C (Kirschbaum 1995). These predictions were based on a model which links temperature to Q_{10} using a unique 'optimal temperature for the process'. Results from the VAMOS project, dealing with C-mineralization potential of soils originating from a North to South coniferous forest transect, indicate that there are different optimal temperatures for C mineralization with a lower value (16 °C) for soil from 64°N compared with 30 °C for soil at latitude 43°N.

We can also speculate about the response to moisture change in the tundra. A radical temperature increase that would thaw permafrost would mainly influence activity in the soil through increased availability of water through thawing. The general effect of water availability is an increase in activity from dry to mesic conditions, and a decrease as water-logging and oxygen deficiency occurs (Flanagan & Veum 1974; Wilson & Griffin 1975). Since water is closely linked to anaerobic conditions, such processes as peat bog formation and methane production are linked to water availability.

The combined effects of temperature increase and drying can be studied in soil heating experiments. Harte *et al.* (1995, 1996) measured mesofaunal diversity in response to heating. In most cases, diversity expressed by the Shannon–Weaver index and by the number of species found increased with heating, except in very dry conditions, where it was the reverse. It may be questioned however, whether it is acceptable to extrapolate sudden changes which occur under heating or transplanting experiments to a progressive change, with temporary setbacks, as is expected under global warming?

Even if the rate of processes is slow, the fluxes may not necessarily be low. Thus, in tundra, although the SOM is slow to decompose, the pool size can be very large. Annual nutrient mineralization from this pool may thus still be sufficient to maintain a significant plant production. Andrén & Kätterer (1997) have discussed this issue of SOM pool sizes in relation to input and decomposition. Nitrification in tundra is limited by the low pH, as also in most of the taiga zone. Global warming may have a direct effect on ammonification processes, since the rate will increase with increasing temperature.

In spite of the dominance of Enchytraeidae in cold soils, only few data on their contribution to ecosystem processes within these systems are available. Enchytraeids have been reported to consume more than 10% of the annual carbon input to a Swedish arable soil (Lagerlöf *et al.* 1989; Andrén *et al.* 1990; Paustian *et al.* 1990), and to have a strong influence on both respiration and nutrient leaching in coniferous forest soils (Williams & Griffiths 1989; Setälä *et al.* 1991; Haimi & Boucelham 1991) particularly in increasing mineralization of N and P. There is also a growing realization of previously unknown or ignored fluxes of organic forms of N and P, particularly in nutrient-poor soils, with mycorrhizae being associated with plant uptake of organic forms of major nutrients (Michelsen *et al.* 1996).

In a microcosm experiment, Briones *et al.* (1997b) showed that enchytraeids (*Cognettia sphagnetorum*) increased nutrient release from several soil layers, having the greatest effect in the upper layers. Leachate concentrations of both inorganic N and P increased in the presence of animals, which agrees well with the results of others (for example, Anderson *et al.* 1983; Huhta *et al.* 1988; Setälä *et al.* 1990 and Forster *et al.* 1995). Dissolved organic carbon, dissolved organic nitrogen and dissolved organic phosphorous leaching were significantly enhanced by the presence of the enchytraeids, indicating that organic matter turnover was accelerated by the presence of these organisms. The mechanisms by which soil fauna and especially enchytraeids may affect nutrient cycling are varied and may be attributable to direct (e.g. excretory products, such as NH_4^+) or indirect effects (e.g. creating a soil structure and liberating nutrients that enhance microbial mineralization, Anderson & Ineson 1984). These mechanisms should be especially effective in nutrient-poor systems (Couteaux *et al.* 1991).

In view of these results and those mentioned above, we can expect that global warming in organic soils could result in an increase in the abundance of enchytraeids, leading to an increase in their contributions to organic matter turnover. In conclusion, we emphasize the linkages between soil fauna, particularly enchytraeids, and ecosystem functioning in tundra, and the need for more integrative studies to understand possible linkages and their influence on our predictions of tundra response to global change.

Temperate grasslands: effects of CO_2 increase at different levels of nitrogen availability

Introduction

Grasslands cover a wide ecological gradient with above-ground productivities ranging from 2 to 20 Mg ha^{-1} y^{-1}. Low productivity in grasslands may be attributed to low availability of nutrients, high relative below-ground allocation of the net primary production, high C:N ratio of litter inputs and a relatively higher degree of accumulation than decomposition of soil organic matter. The question whether or not grassland soils will be a net sink or source of carbon explains the current interest in the effects of elevated CO_2 on these ecosystems. The magnitude of such effects will largely depend on the nitrogen inputs, which mainly come from N fertilizers and atmospheric deposition.

Studies on carbon and nutrient cycling in Lolium perenne

Considerable research has been done with the perennial rye grass, *Lolium perenne,* as a test species which provides a useful case-study. Recent studies have shown a variety of effects of elevated CO_2 on the productivity of *L. perenne* and hence on the amounts and nature of inputs to the soil system[1]:

1 Gross photosynthesis increases under elevated CO_2, relatively less so at low N (equivalent to 130 kg N ha^{-1} y^{-1}) than at high N (equivalent to 530 kg N ha^{-1} y^{-1}) (Casella & Soussana 1997);

2 Primary production (predominantly as root biomass) increases considerably under elevated CO_2 (Van Ginkel *et al.* 1996; N equivalent to 135 kg N ha^{-1}) relatively more so at low N than at high N fertilization (Casella *et al.* 1996; for figures of low and high N: see above);

3 The C:N ratio of the grass and of coarse litter increases under elevated CO_2 at both low and high levels of N fertilization (Gorissen *et al.* 1995; Casella & Soussana 1997);

4 Water soluble carbohydrates increase in the grass under elevated CO_2, but the Neutral Detergent Fibre remains the same, with no change in hemicellulose and lignin content (Soussana *et al.*, unpubl. data); however, in addition to higher soluble carbohydrate and lower cellulose contents, Van Ginkel *et al.* (1996) found higher lignin contents of roots under elevated CO_2, contributing to a higher C:N ratio and a lower N content at high N (equivalent to 400 kg N ha^{-1}), but not at low N (equivalent to 20 kg N ha^{-1}).

The decomposition of leaves of *L. perenne* produced under elevated or ambient CO_2 has received little attention, possibly due to the fact that the above-ground production is usually grazed or harvested. In one study, however, Magid *et al.* (1995), found that the decomposition of rye grass shoots grown under elevated CO_2, resulting in a C:N ratio of 37, was significantly retarded between Day 4 and Day 45 in comparison with the decomposition of shoots grown under ambient CO_2, resulting in a C:N ratio of 18. After 100 days there was no further difference.

In a four-year experiment under field conditions, Loiseau & Soussana (unpubl. data) produced ^{13}C-labelled root and stubble under ambient CO_2 during the first 18 months. The decomposition of this stubble and root material was henceforth studied over 27 months under ambient and elevated CO_2 and was found to be promoted under elevated CO_2. In ^{13}C-labelled stubbles and roots freshly produced under elevated CO_2 in the period following the first 18 months, both the production and decomposition rates of root and stubble materials were enhanced. The rate of production increased to a higher extent than the decomposition rate however, resulting in a net C accumulation in the nonharvested phytomass and in the free macro-organic matter.

In a two year incubation study under field conditions, the decomposition of root litter produced under elevated CO_2 was retarded in comparison with root litter produced under ambient CO_2 after one year, irrespective of the N availability during the production of the root material and irrespective of the CO_2 concentration during decomposition (Van Ginkel *et al.* 1996). These results confirm those of Gorissen *et al.* (1995) in a short-term (9 weeks) experiment. After two years, there was still a significant retardation of decomposition in the root material, produced at low N (equivalent to 20 kg N ha^{-1} y^{-1}), but not in the root material produced at high N equivalent to 400 kg N ha^{-1} y^{-1} (Van Ginkel *et al.* 1996). In an experiment with ^{14}C-labelled plant material, Van Ginkel *et al.* (1997) found no effect of elevated CO_2 on the decomposition of native soil organic matter, neither at low N (equivalent to 68 kg N ha^{-1}), nor at high N (equivalent to 193 kg N ha^{-1}).

Hence, the available evidence suggests that the increased production, and the retardation of the decomposition of stubbles and roots render *Lolium perenne* grasslands net sinks of carbon under elevated CO_2. Long-term studies are needed, however, to confirm this.

Biomass, composition and activity of the soil biota under L. perenne

As high CO_2 does not change the litter composition in a way that is likely to stimulate the decomposition process, one hypothesis explaining the enhanced decomposition of recently produced below-ground material as described above (Loiseau & Soussana, unpubl. data) lies in the increase in the volume of rhizosphere soil, due to the stimulation of the root mass and length. Decomposition could also be favoured by an increase in biotic activity in the rhizosphere, due to the stimulation of exudate production. In the first year of the experiment an improved water use efficiency was shown which could prolong the time period during which the soil moisture is favourable for microbial activity. During the second year however, the increase in transpiration, due to the CO_2-induced increase of the LAI, did not result in an increase of the soil moisture (Casella *et al.* 1996). These results are consistent with those of Rice *et al.* (1994), who found significantly increased microbial biomass C and N under elevated CO_2 (at the $P < 0.10$ level) in a year with raised soil moisture, but not when soil moisture was not raised. Added N increased microbial C and N under CO_2 enrichment. Microbial activity was higher under elevated

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[1] Unless otherwise stated, ambient CO_2 means 350 mL L^{-1} and elevated CO_2 means 700 mL L^{-1}.

CO_2, presumably due to better soil water conditions and was further stimulated by added N (Rice *et al.* 1994).

In their study of root decomposition under field conditions, Van Ginkel *et al.* (1996) did indeed find a higher microbial biomass in soil with roots produced under elevated CO_2 at low and high N, in spite of a slower decomposition rate. Soussana *et al.* (1996), found no consistent pattern in the effects of elevated CO_2 on the size of the microbial biomass in a long-term field study, although there was a positive effect of elevated CO_2 on the total soil respiration, i.e. the respiration of (roots + microbial biomass). Van Ginkel *et al.* (1997) likewise found an increase in plant-derived (soil + root) respiration in their study of C and N allocation of *L. perenne* under different CO_2 and N and no effect of elevated CO_2 on the size of the soil microbial biomass or microbial immobilization. Most of the increased respiration was due to enhanced root activity. The amount of available N, immobilized in the microbial biomass, was low (≈ 17% of N available to plants + microbes) under all conditions of CO_2 and N (van Ginkel *et al.* 1997). These results are consistent with those of Niklaus & Körner (1996) in alpine grasslands, fertilized with 45 kg ha^{-1} y^{-1}. In their study microbial N pools were not enhanced in nonfertilized plots under elevated CO_2. Unpublished data from Loiseau & Soussana suggest that under elevated CO_2 less of the harvested N is derived from soil than under ambient CO_2. They also suggested higher microbial N immobilization was at variance with the nonconsistent effects of elevated CO_2 on the size of the microbial biomass.

The inconsistencies of effects of below-ground materials on the size and activity (in terms of N immobilization) of the soil microbial biomass call for detailed studies of the chemical composition of the microbial substrates and of microbial diversity as related to the ability to degrade such substrates. No such data seem to be available yet for grasslands. In a study on microbial communities in soil with *Populus grandidentata*, grown under ambient or elevated CO_2, Zak *et al.* (1996) found significant increases in labile organic carbon and microbial biomass C in the rhizosphere soil and of microbial biomass C in the nonrhizosphere soil. These increases were, however, approximately proportional to the increase in root biomass. However, they found no significant differences when using phospholipid fatty acid analysis to characterize the soil microbial communities under ambient and elevated CO_2. They conclude that longer-term studies with both above-ground and below-ground litter are needed. Also, further study is needed of the nature of the substrates produced, not only in terms of C:N or lignin:N ratios, but also in terms of secondary metabolites and contents of other nutrients than N (Gorissen 1996).

Studies with slow- and fast-growing grasses

The results mentioned above have almost all been obtained in grasslands that were sufficiently nitrogen-rich to sustain the growth of *L. perenne*. Below a threshold level of above-ground productivity of about 6 Mg ha^{-1} y^{-1} the composition of plant species shifts from a few, light-limited, to many, nutrient-limited, species (Olff & Bakker 1991). Such a drop in productivity was shown in a study of yearly mown grasslands that had been taken out of production for 2, 6, 19 and 45 years, respectively. A clear change in plant species was observed together with a different spectrum of representation of life-history strategies among the species, showing a shift from rapidly germinating, fast-growing species in the productive grasslands to slowly germinating, slow-growing species in the less productive grasslands (Olff *et al.* 1994b). Concomitant with the drop in above-ground and total productivity, below-ground standing biomass increased from the most productive to the least productive grassland, due both to increase in the fine root (intermediate stages) and rhizome biomass (least productive stage). These changes corresponded with a decrease in N mineralization in the field (Olff *et al.* 1994a).

Land-use change may alter N-availability in grasslands (e.g. from fertilized – for production – to nonfertilized – when offtake of production is needed to increase biodiversity of the vegetation). N-availability may also differ because of different atmospheric nitrogen loads: for instance, the atmospheric N deposition in the Netherlands may range from 20 to 500 kg ha^{-1} y^{-1} (average 42) (Houdijk & Roelofs 1991). In a greenhouse experiment with six plant species, among which the slow-growing grass *Molinia caerulea* and the fast-growing grass *Arrhenatherum elatius*, representing natural habitats with a low and a high nutrient richness, respectively, Arp *et al.* (1997) demonstrated a small response to elevated CO_2 (560 mL L^{-1}) at low N-availability (equivalent to 40 kg ha^{-1}) irrespective of the moisture status of the soil (optimal for ambient CO_2 or 70% of that). At high nitrogen availability (equivalent to 160 kg ha^{-1}) there was a large increase in production. Most of the increase in biomass was in the production of fine roots.

Cotrufo & Gorissen (in prep.) also compared slow- and fast- growing plant species under ambient and elevated CO_2: *Lolium perenne*, *Agrostis tenuis* and *Festuca ovina*. *F. ovina* reacted similar to *M. caerulea* in the study of Arp *et al.* (in prep.), while the other two species reacted in a similar way to *A. elatius*. The size of soil microbial biomass was increased under elevated CO_2, but that was correlated with the increased root biomass. When expressed per unit root biomass, there was no effect of CO_2 on the size of the microbial biomass. When comparing the slow-growing *Molinia* and the fast-growing *Arrhenatherum*,

Arrhenatherum showed a relatively larger effect of CO_2 at high N, whereas the CO_2 effect was relatively larger in *Molinia* at low N. These results suggest that elevated CO_2 tends to favour the species that are already best adapted to their environment (Arp *et al.* 1997).

Felske *et al.* (1997) found considerable differences in the soil microflora between the four successional stages of grasslands mentioned above, using Temperature Gradient Gel Electrophoresis. Brussaard *et al.* (unpubl.) observed changes in the soil fauna in these grasslands: nematode density and diversity decreased, with average sizes of plant-parasitic nematodes also decreasing; soil mite density increased, with fungivorous grazers and browsers increasing at the expense of herbivorous grazers; and earthworm numbers and biomass decreased with litter-dwelling species increasing at the expense of soil-dwelling species.

An important question is whether these changes in the soil biota and possible changes in their activity follow changes in the vegetation or the other way round. Most probably the feedbacks between vegetation and soil biota govern the direction and rate of changes in both soil species composition and carbon and nutrient fluxes. Most illuminating here are a few studies on soil organisms that live in symbiosis with plants: mycorrhizas and N-fixing bacteria. In a growth chamber study with the shortgrass steppe grass *Bouteloua gracilis*, Morgan *et al.* (1994) found that plants grown under elevated CO_2 not only produced 35% and 65% more total and root biomass, but also had twice the level of arbuscular mycorrhizal infection (19.8% vs. 10.8%). Plant P uptake, however, appeared little influenced by CO_2 regime, while N uptake was reduced. In a study of symbiotic N_2 fixation by *Trifolium repens* under elevated CO_2 (560 mL L^{-1}) in open top chambers the total N yield was increased and, using the ^{15}N isotope dilution method, it was established that all additional plant N was derived from symbiotic N_2 fixation, not from soil (Zanetti *et al.* 1996). In a mixture of *Trifolium repens* and *Lolium perenne* an increased amount of symbiotically fixed N was introduced into the system. Increased N_2 fixation under elevated CO_2 may give *T. repens* a competitive advantage in mixed swards with pasture grasses and it may counteract a rise in C:N ratio of organic matter added to soil. Very little work has been done on the effect of elevated CO_2 on the free-living biota of grasslands, e.g. Freckman *et al.* (1991) found no difference in nematode community structure in intact grassland cores after two years of exposure to elevated CO_2.

Policy measures aimed at reduction of the CO_2 increase in the atmosphere, reduction of nitrogen deposition and taking land out of production will have to be evaluated in terms of effects on biodiversity and carbon and nutrient fluxes. In the above-mentioned studies it was recognized that feedbacks in the ecosystem, leading, for example, to changes in competition between plants, changes in plant species composition and changes in amounts and qualities of litter, modulate the effects observed in single species investigations. This calls for a full understanding of the feedbacks in ecosystems under global change.

Research priorities

The main patterns in plant responses to elevated CO_2 and nitrogen are becoming clear. Elucidation of the various biotic feedbacks in the plant–soil system, both in studies with one plant species and in mixed-species ecosystems under change, should now have a high priority. This should include both evaluation of the effects of global change on the species composition and carbon and nutrient fluxes in temperate grasslands and also in developing measures to mitigate undesirable effects. Whilst ensuring adequate assessment of the influence of varying soil conditions, the following areas of research have a high priority: chemical composition (resource quality) and quantity of above-ground and below-ground materials produced under ambient or elevated CO_2 and entering the soil system as organic inputs; root symbiotic relationships, affected by elevated CO_2; size of the soil microbial biomass degrading the substrates entering the soil; activity of the soil microbial biomass in terms of mineralization and immobilization turnover of nitrogen and other major nutrients; composition of the microbial and animal community in soil as related to the ability and rate of degradation of the major compounds of the organic substrate; biotic feedbacks, both at the plant level and at the plant community level, between plant-derived organic inputs and soil microorganisms and animals.

Humid tropical forest environment: effects of conversion to agriculture

Introduction

Humid tropical forests can broadly be defined as those with a constant high temperature, an annual precipitation greater than 1500 mm and less than four dry (i.e. less than 100 mm of rainfall) months. A major proportion of such forests are situated on soils of low to moderate fertility (ultisols or oxisols), although soils of much higher nutrient status are also known and figure disproportionately in research reports. The high biomass, often with high root/shoot ratios, sequesters a high proportion of the available nutrient and nutrient cycling is generally described as highly efficient (Vitousek & Sanford 1986). The productivity of such forests is therefore thought to be nutrient limited under the majority of circumstances although Vitousek & Sanford (1986) have also cautioned against generalization in this respect.

The tropical rainforests are generally accepted as highly biodiverse in all components although the basis of this diversity remains a matter of rich debate (e.g. see Lugo 1988). Regrettably the below-ground biota is the least well described component. Where however, detailed studies have been made, for instance with the termites (Eggleton *et al.* 1995), earthworms or fungi (Rambelli *et al.* 1983) taxonomic richness can be extremely high. Very significant variation in below-ground biomass and densities for major groups of macrofauna has also been observed between different forest sites and types within the same region (Collins 1980). Despite the limited evidence it seems a reasonable working hypothesis that the diversity of soil organisms is also maximal in this environment. Swift *et al.* (1979) hypothesized that the relative contribution of the macrofauna to decomposition and nutrient cycling would also be highest in this biome. Recent studies of the earthworms and termites (the ecosystem engineers) serve to confirm this.

Global change in tropical forest environments

Current rates of clearing of tropical rain forest are extremely high (e.g. see Whitmore & Sayer 1992) making land-use change the most important feature of global change in this environment, both in terms of direct effects on biodiversity and also with respect to consequent contributions to global warming through emissions of greenhouse gases. These are estimated to account for 23% of the global total from terrestrial ecosystems of which 80% is attributable to conversion for agricultural purposes. A significant fraction of such conversion has been occurring as a result of human migration into forest environments often as a response to government-sponsored large-scale agricultural development schemes. Traditionally agriculture in rainforest environments has been based on long periods of fallow between short (one to three year) cropping cycles. In modern times, and particularly in migration areas, more intensive types of agriculture are practised. There are a great variety of pathways of intensification but three different endpoints may be mentioned here as providing contrasts with respect to the impact on soil biodiversity: conversion to continuous arable (i.e. food crop) cultivation such as upland rice; to plantation crops such as oil palm, rubber or cocoa; and to pasture. Because of the nutrient limitation other features of global change such as CO_2 fertilization are unlikely to have an effect on tropical rain forest. Smith (1997) has, however, estimated that a 20% increase in temperature could decrease N_2O, emissions by 18%. A similar increase in rainfall would have little effect.

Major changes in the abundance and composition of the soil biota as a result of conversion to agricultural practice have been shown at a number of different sites. The majority of these studies have been confined to elements of the macrofauna, particularly the two main groups of 'ecosystem engineers', the earthworms and termites. For example, clearing forest (Eggleton *et al.* 1995) and conversion to arable agriculture (Lavelle & Pashanasi 1989) can result in highly significant declines in taxonomic richness and changes in composition of termites and other groups of macrofauna (Table 2). Both sets of authors show however, that conversion to plantations or pastures may have less drastic effects (see also Gilot *et al.* 1995) especially during periods which may be described as of intermediate disturbance.

Land use change from primary or secondary forest to agriculture also results in both qualitative and quantitative changes to nutrient cycles. The major effects are clearly due to the massive disruption caused by clearing, removing and in many cases burning the forest biomass leading to decreases in soil carbon and losses of N and S by volatilization. The composition and abundance of the soil biota is also likely to be strongly affected by each of the practices associated with land clearance but no comprehensive study of these changes has been made. Conversion to cultivation also results in a very significant decrease in the amount of nutrient returned annually to soil in plant residues. Nutrient cycles within the agricultural systems therefore operate at a lower equilibrium of stocks, and also suffer periodic removal of nutrient in harvest. This is illustrated by the well documented changes in the stocks of C and N in the soil (e.g. Greenland 1980). The lower extent of plant cover, in many cases including seasonal periods of bare ground, also results in enhanced output by leaching and volatilization. Within such a massive change is there any evidence that the changes in diversity of the soil biota have any contributory effects on nutrient cycling?

Soil biodiversity and nutrient cycling

A series of studies at Ibadan, Nigeria, on a relatively fertile Alfisol provide a case study that can give a partial answer to the above question. Critchley *et al.* (1979), Swift *et al.* (1980, 1981), Ingram & Swift (1989) and Tian *et al.* (1997) report on a series of investigations comparing forest fallow and agricultural systems with respect to soil biodiversity and the processes of decomposition and nutrient cycling. Conversion of the fallow to cultivation of cowpea (*Vigna unguiculata*) resulted in marked changes in the composition of the soil fauna (Table 3).

Detritus food webs and their roles in nutrient cycling are not well defined for humid tropical environments. The decomposition of plant materials in litter bags of different mesh size has been described however, for a

Table 2 Taxonomic richness, mean abundance and biomass of macro-invertebrates in different types of land-use at Yurimaguas, Peru (Lavelle & Pashanasi 1989)

Types of land-use	No. of taxonomic units*	Mean population density (m^{-2})	Mean biomass (g fm m^{-2})
Forests			
Primary forest	41	4304	53.9
Secondary forest (15 years)	27	4099	24.1
Crops (1st crop)			
High input maize	20	730	3.1
Low input rice	24	3683	8.5
Traditional cassava	18	1197	7.6
Pastures			
Improved *Bracharia–Desmodium* system	27	922	159.2
Traditional 'moist' pasture	23	1768	121.1
Traditional 'dry' pasture	20	1347	82.3
Fallows			
Six-months *Centrosema* after pasture	22	1546	111.9
Six-months Kudzu (*Pueraria phaseoloides*) after high input crop	23	2214	15.5
Peach-palm + Kudzu cover	32	1858	93.9

*defined as orders or families.

Table 3 Mean population densities of Acari and Collembola in an Alfisol at Ibadan, Nigeria for the 0–5 cm and 5–10 cm soil depth (number m^{-2}) (from Critchley *et al.* 1979; quoted in Tian *et al.* 1997)

Soil depth	Bush plot	Cultivated plot
0–5 cm		
Acari		
Cryptostigmata	17 403	1991
Prostigmata	8477	9839
Mesostigmata	3557	1121
Astigmata	1372	708
Collembola		
Isotomidae	6963	1425
Entomobryidae	2421	754
Onychiuridae	1628	243
Sminthuridae	1128	620
Poduridae	665	54
5–10 cm		
Acari		
Cryptostigmata	7695	2230
Prostigmata	6353	7862
Mesostigmata	1013	766
Astigmata	237	17
Collembola		
Isotomidae	3644	733
Entomobryidae	355	425
Onychiuridae	364	105
Sminthuridae	280	322
Poduridae	200	9

variety of forest and agricultural sites in the humid zone [see Anderson & Swift (1982) and Swift & Anderson (1989) for reviews of earlier literature]. Such studies permit evaluation of the contribution of different size classes and functional groups of soil organisms to decomposition and nutrient release. In the forest environment the results of litter bag studies are consistent with the concept of fungi as the primary decomposers of plant litter at the soil surface, with surface-active macro- and meso-detritivores (earthworms, millipedes, gryllids, termites) and microbivorous microarthropods (collembola and mites) entering the food web after an interval of a few days to several weeks, dependent on the resource quality of the litter.

Swift *et al.* (1981) described the patterns of decomposition in an eight-year-old regenerating bush fallow and compared them with those in agricultural plots cultivated with cowpea (Swift *et al.* 1980; Ingram & Swift 1989). Little difference was found between the rate of decomposition of cowpea litter on the surface of the cultivated plots when compared to that of forest litter within the fallow plots (Table 4) despite the fact that the environment at the surface of cultivated plots is much harsher for biological activity than that in fallow or forest. For instance peak soil surface temperatures frequently reached 35 or 40 °C in the former but rarely exceeded 25 °C in fallow (Swift *et al.* 1979). Comparison between litter bags of different mesh sizes however, showed that there had been a shift in the relative roles of key functional groups with the contribution of the fauna relative to the microflora reduced in the cultivated plots as compared with the bush fallow (Table 4), a result which is consistent with the decrease in the populations of most of the microarthropod groups (Table 3). A later study by Tian

Table 4 Partitioning of initial (four week) weight loss to different sources in decomposition for leaf litters in bush-fallow and cultivated systems (Swift *et al.* 1980)

	Bush Surface	Cowpea Surface	Buried
Total loss %	60	65	90
Loss to leaching %	15	25	25
(as % of total loss)	(25)	(38)	(28)
Taken by animal %	30	20	20
(as % of total loss)	(50)	(31)	(22)
Microbial decomposition %	15	20	45
(as % of total loss)	(25)	(31)	(50)

et al. (1997) gave a different outcome however. Rates of decomposition of standard litter of *Senna siamea* were significantly lower in maize–cassava cropping systems than in a neighbouring bush fallow and the relative role of microarthropods was enhanced rather than reduced under cultivation (Table 5).

Both these studies clearly demonstrate the effects of changes in land-use on the relative role of different functional groups in decomposition and nutrient cycling. The contrast in the direction of the effect however, shows that the operational factors are probably not the same. Whilst there is no clear evidence for the mechanisms involved, the differences in the circumstances of the two studies offer some hypotheses. There is an interaction with resource quality: whilst the later study compared a standard litter (*Senna siamea*) in the two environments, that of Swift *et al.* (1980) compared tree leaf litter in the bush with cowpea litter in the cultivated plots. No data are available for lignin or polyphenol contents but the C:N ratio of the mixed bush litter used in the experiment was 29 as compared with that of 17 for the cowpea leaves. It may therefore be hypothesized that the lack of difference in decomposition rate between the two environments was due to that in the fallow being limited by resource quality whereas that in the cultivated plots was limited by high temperature and low moisture availability. The same interaction of factors could have influenced the relative activities of fauna and microflora. Shifts in the resource quality spectrum are likely to affect the relative activities of different groups of the biota with consequent feedback effects on the relationship between diversity and ecosystem function. Tian *et al.* (1997) showed that ecosystem engineers such as earthworms or millipedes have more impact on decomposition of low quality residues than they do on high quality litters. These fauna would have been able to obtain some access to the 10 mm mesh bags used in the experiment of Swift *et al.* (1980) – as would termites – but would have been excluded from the 0.5 mm mesh bags used by Tian *et al.* (1997). The animal activity in the latter was therefore largely attributed to microarthropods (i.e. collembola and mites) and interpreted as demonstrating their high adaptability to moisture and temperature stress.

Table 5 Effect of litter bag mesh-size on plant residue decomposition rate constants (*k* week^{-1}) under bush-fallow and cropping conditions and calculated contribution of soil microarthropods to decomposition (Tian *et al.* 1997)

	Plant residue decomposition constants (*k* week^{-1}) litter bag mesh size		Soil microarthropod-mediated Treatments decomposition (%)
	0.08 mm	0.5 mm	
Cropped plots			
Continuous	0.030	0.048	
Cropping			38
With *Leucaena*	0.041	0.052	21
With *Pueraria*	0.054	0.065	17
Bush-fallow plots			
3 month fallow	0.070	0.080	13
15 month fallow	0.075	0.083	10
27 month fallow	0.083	0.088	6

$LSD_{.05}$ for decomposition rate constants between mesh-size for the same treatment: 0.013.

[1] Unless otherwise stated, ambient CO_2 means 350 mL L^{-1} and elevated CO_2 means 700 mL L^{-1}.

The difference between these two superficially similar studies emphasizes the need for detailed dissection of the interaction between the different factors regulating decomposition and nutrient release (i.e. physico-chemical environment, resource quality and biotic community, Swift *et al.* 1979) in any examination of the relationship between decomposer diversity and nutrient cycling.

The preceding discussion relates almost entirely to the activities of the detrital food web. Conversion of forest to agriculture also disrupts nutrient cycles in other ways. The composition of populations of N-fixing bacteria and mycorrhizal fungi are often inadequate to serve the functions necessary in the derived ecosystem. Considerable research has been devoted to establishing effective populations by inoculation or other means. Tropical forests are very substantial sources of N_2O emissions so conversion to agricultural land may result in a decrease, but derived tropical pastures emit even higher levels than the forest (Luizao *et al.* 1989). In contrast, forests are generally sinks for methane but agricultural lands, particularly those under rice cultivation, are significant sources. Both these situations indicate shifts in bacterial population dominance (e.g. between methanotrophs and methanogens) as a result of land use change.

Conclusions

The contribution of soil organisms to nutrient cycles are firmly established. Detailed food webs with quantification of the relative contribution of different functional or taxonomic groups have been drawn up for a number of ecosystems (e.g. Hunt *et al.* 1987; De Ruiter *et al.* 1993). Some functions, particularly within the N-cycle, are carried out by very specific organisms. Others, including those of decomposition and nutrient mineralization and immobilization, are mediated by the interactions within a diverse community of organisms. Most authors have assumed that there is a high degree of equivalency of function within this decomposer community and thence a substantial degree of redundancy in species richness and resilience in functional capacity.

In all three case studies described above clear evidence exists for the potential impact of global change factors (temperature change, CO_2 enrichment and land-use change, respectively) on the composition and diversity of the soil community as well as on various aspects of the nitrogen and other cycles.

- In tropical rainforest land-use change produces very significant changes in soil biodiversity and consequent shifts in the relative importance of different functional groups. These are effects which are probably general to all such land conversions irrespective of ecological zone.
- In temperate grasslands, increased concentration of atmospheric CO_2 is predicted to stimulate both primary production and decomposition, the net effect being an increase in soil organic matter. There is little evidence for the impact this will have on the soil community but it is hypothesized that the changes in the quantity and quality of the food resource are likely to promote significant functional shifts. These effects are also likely to occur in other types of ecosystem susceptible to CO_2 fertilization.
- The grassland studies also show that microsymbionts such as mycorrhiza, or the Rhizobium associates of pasture legumes, are highly sensitive to the effects of high CO_2 on their hosts, with consequent effects on nutrient aquisition rates. These organisms, with very specific functions, could provide a rewarding target for studies of feed-back effects between global change impacts and nutrient cycling.
- In tundra the impact of increased temperature may increase decomposition and mineralization rates with consequent effects on soil biotic activities and shifts in the relative importance of different physiological and functional groups. The interactions between temperature and moisture and nutrient limitation may be equally important in determining the outcome.

A number of general conclusions may be drawn from these case studies:

- there is little unequivocal evidence for directly linking effects between global change factors, soil biodiversity and nutrient cycling;
- nonetheless, as the above summary shows there are strong indications that functional shifts within the soil community are likely to occur under the influence of global change; the quantitative significance of these shifts to nutrient cycles remains to be documented;
- the soil community responds differentially to different global change factors; the responses are most likely to be interactive rather than direct or unidirectional;
- the soil biota represent a sensitive link between plant detritus and plant-available nutrient; factors which influence detrital quality and quantity are likely to be of high significance.

There is an urgent need for rigorous experimentation to address the question of the significance of species richness, as well as other components of biodiversity, to decomposer function. The experiments of Couteaux *et al.* (1991) on decomposition of sweet chestnut litter produced under elevated CO_2 are instructive in this respect. They showed a negative feedback on decomposition rate when the soil fauna was represented by only a few groups but a positive feedback when the soil fauna was more diverse. These results were obtained in microcosm experiments in the laboratory but they point the way forward in this area. Relatively species-poor ecosystems such as tundra or agroecosystems may serve such experimentation best. The elegant studies of Coleman and his coworkers on agroecosystems provide an instructive starting point for such work (Coleman *et al.* 1994). A key question of considerable practical significance in agriculture is whether there are diversity thresholds below which essential functions are impaired (the so-called rivet-popper analogy, Ehrlich & Ehrlich 1981). Whilst the conventional practice in agriculture has been to by-pass the biological regulation of nutrient cycles with fertilizers, current concerns with pollution and sustainable development have turned attention back to the organic base of agricultural production. Within this context questions such as the minimum extent of biodiversity to optimalise nutrient cycling occupy an important status (Swift & Anderson 1993).

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