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Soil biodiversity for agricultural sustainability

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Abstract

We critically highlight some evidence for the importance of soil biodiversity to sustaining (agro-)ecosystem functioning and explore directions for future research. We first deal with resistance and resilience against abiotic disturbance and stress. There is evidence that soil biodiversity does confer stability to stress and disturbance, but the mechanism is not yet fully understood. It appears to depend on the kind of stress and disturbance and on the combination of stress and disturbance effects. Alternatively, community structure may play a role. Both possible explanations will guide further research. We then discuss biotic stress. There is evidence that soil microbial diversity confers protection against soil-borne disease, but crop and soil type and management also play a role. Their relative importance as well as the role of biodiversity in multitrophic interactions warrant further study. Henceforth, we focus on the effects of plant and soil biodiversity on nutrient and water use efficiencies as important ecological functions in agroecosystems. The available evidence suggests that mycorrhizal diversity positively contributes to nutrient and, possibly, water use efficiency. Soil fauna effects on nutrient and water use efficiencies are also apparent, but diversity effects may be indirect, through effects on soil structure. We present a conceptual diagram relating plant and soil biodiversity with soil structure and water and nutrient use efficiencies as a framework for future studies. We then consider how cropping systems design and management are interrelated and how management options might be interfaced with farmers' knowledge in taking management decisions. Finally, we attempt to express some economic benefits of soil biodiversity to society as part of a wider strategy of conserving and using agrobiodiversity.

Keywords: Agroecosystem; Disturbance; Economic benefit; Ecosystem functioning; Environmental services; Nutrient use efficiency; Soil biodiversity; Stress; Sustainability; Water use efficiency

1. Introduction

Agricultural production depends on the availability and management of resources, such as labour (human and animal), capital, machinery, fuel, soil, seeds, water, nutrients, crop residues, manure and pesticides. Agricultural sustainability is related to the time frame within which non-declining plant and animal production is desired; the time frame within which the resources are renewed or remain available at levels to attain such production; and the time frame within which agriculture remains financially sufficiently profitable to support the farmers' livelihoods. Is biodiversity meaningful to farmers in this context and where does it come in?

Biodiversity comprises the ''planned biodiversity'', i.e. the crops and/or livestock the farmer wishes to produce, but also to the ''unplanned'' biodiversity, i.e. all other biota in, and entering the system. That biota may be considered beneficial, such as insects pollinating the crop, or harmful, such as pathogens, pests and weeds. The ''unplanned'' biodiversity may become ''planned'' in the sense of being managed for or against. Such management is directed to elimination or promotion of population processes (e.g. pest control) or ecosystem processes (e.g. N fixation), which are associated with species diversity and functional group diversity, respectively.

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Most of the biodiversity of agricultural systems resides in soil. Food web interactions among the soil biota (including plant roots) have large effects on the quality of crops (affecting human and animal nutrition or other utility), the incidence of soil-borne plant and animal pests and diseases (affecting production levels), and the beneficial organisms that, e.g. cycle nutrients or are predators of the pest species. This is because the availability of water, nutrients and certain microorganisms at the root surface is mediated by such interactions. Farmers manage, consciously or inadvertently, soil biodiversity in the face of unpredictable disturbances and stress agents.

Four challenges are driving research on soil biodiversity and agricultural sustainability:

1. Understanding the ''importance'' of soil biodiversity for the resistance and resilience against stress and disturbance. The relationships between (soil) biodiversity and ecosystem functioning are not straightforward (Chapin et al., 2000; Brussaard et al., 2004). It is perhaps therefore that the insurance hypothesis (Loreau and Yachi, 1999) which suggests that ''high'' biodiversity confers an insurance against ecosystem malfunctioning under stress or disturbance, is receiving much attention.
2. Understanding the ''importance'' of soil biodiversity for the sustainable use of resources. If soil biodiversity confers resistance and resilience (see 1), it may also well be related to efficient use of natural resources, such as water and nutrients. This holds promise for relieving pressure from agriculture on natural areas in agricultural landscapes and beyond, and even for providing habitats for species with conservation value from ''natural'' areas.
3. Managing soil biodiversity. Whereas aboveground biodiversity is widely managed by choosing livestock and livestock breeds, crops and crop varieties, rotations, crop sequences and the botanical composition of field margins and non-productive elements in agricultural landscapes, in most cases soil biodiversity can only be managed indirectly and the options for such management are less evident.
4. Valuing soil biodiversity. The intrinsic value of soil biodiversity is less obvious than for aboveground biodiversity. Therefore, making a case for increasing and maintaining soil biodiversity will need to be substantiated even more in economic terms than is aboveground biodiversity.

The evidence for soil biodiversity as an asset for farmers ''working with nature'' to achieve sustained production in a way which is valued by society at large, is still scant. The objectives of this paper are to critically highlight some such evidence and address challenges for future research.

2. Understanding the "importance" of soil biodiversity for the resistance and resilience against stress and disturbance

2.1. Abiotic stress and disturbance

Disturbances such as fires, storms and insect outbreaks are natural phenomena in ecosystems, interrupting the development to a climax state and resulting in a mosaic of habitats at the landscape level. Following a disturbance, an ecosystem may re-start succession from the stage to which it was set back or transcend into a new stability domain. Re-establishment or reorganization after release from disturbance or stress may take a long time and is influenced by spatial heterogeneity of source areas for re-colonization, as dispersal abilities of organisms have come to differ widely as a result of habitat selection in the past. Dispersal rates are low for soil organisms relative to aboveground biota.

A plethora of biodiversity studies have focussed on one trophic level, such as research on the effects of plant diversity on photosynthesis and biomass production (e.g. Naeem et al., 1994; Tilman, 1999). Studies on soil organisms often focus on only one trophic interaction, e.g. on microbes decomposing organic matter, fauna grazing microbes and indirectly affecting nutrient cycling, earthworms affecting soil structure and comminuting organic matter, thereby stimulating decomposition and mineralization. With respect to soil biodiversity we deal with multi-trophic level communities for which the biodiversity-ecosystem functioning relationship is much more complex (Thébault and Loreau, 2003). One of the hypotheses is that in multi-trophic level communities biodiversity enhances process stability. This hypothesis was explored in several experimental studies (Griffiths et al., 2000; Griffiths et al., 2001a,b; Tobor-Kapłon et al., 2005, 2006). In these experiments processes like CO_2 production were studied in soils in which biodiversity was high or low. Before discussing the results of these experiments, we will define some terms and aspects linked to the experimental treatments and variables.

First, low diversity is in most cases the result of a manipulation and therefore accompanies 'stress'; in this way the experiments mimic reality where decreased diversity is in many cases the result of human-induced stress or disturbance. So low versus high diversity may coincide with stressed versus non-stressed conditions. There are two, more or less, conflicting hypotheses regarding the effect of stress on ecosystem stability (Tobor-Kapłon et al., 2005). The first predicts that stressed communities are less stable, as the organisms have to spend energy to deal with the adverse effects of stress and are then less capable to handle a next stress event. The second is that stress enhances stability, as the first stress has selected for relative 'stable' species and populations. When talking about stress we can distinguish a short term, transient stress event, like a dry/wet or a heat shock. If the populations recover, an equilibrium state can be reached similar to the one before the stress event. In accordance with Tobor-Kapłon et al. (2006) we refer to a short-term, transient event as ‘disturbance’. There are also more persistent stress factors, such as heavy metal contamination. If populations are capable to handle this kind of stress, the equilibrium reached might be different from the original one, because of the presence of the stress factor, continuously affecting the energy budget of the organisms. We refer to this kind of stress as ‘stress’ (Tobor-Kapłon et al., 2006). Finally, also stability can be defined differently, as related to resistance, which is the ability to recover from a stress or disturbance, or to resilience, which refers to the rate with which populations recover from stress or disturbance (Griffiths et al., 2000; Tobor-Kapłon et al., 2005).

The basic set-up of the experiments on the relationship between stress/disturbance – biodiversity – ecosystem functioning in soils was that of a stress (disturbance)-on-stress (disturbance) experiment (Fig. 1). In the experiments of Griffiths et al. (2000) the first stress was applied by exposing the soil to chloroform vapour (fumigation) for 0 h (unfumigated control), 0.5, 2, or 24 h. This first stress reduced the diversity of the soil community progressively as fumigation time increased, leading to the disappearance of many functional groups, species and genetic variation, especially in the soils fumigated for 2 and 24 h (Griffiths et al., 2000). Overall there was a 60% reduction in biodiversity. The fumigation also affected soil ecosystem processes, but to a more limited degree: many species disappeared but no ecosystem process was eliminated. The results of the first stress therefore indicated a level of functional redundancy: although many groups of organisms disappeared, ecosystem processes still continued (Griffiths et al., 2000). The second stress was applied as either a persistent stress by adding a heavy metal (copper as $CuSO_4$), which reduced growth rates, or a transient disturbance (brief heating to 40 °C) reducing population sizes. The effects of the second stress/disturbance were measured as changes in the respiration from the decomposition of freshly added organic matter. Respiration in the most diverse soils (0 and 0.5 h of fumigation) was hardly affected by the Cu addition, whereas respiration in the reduced-diversity soils (2 and 24 h of fumigation) decreased by up to 70% (Fig. 2). Soils given the transient heat stress showed a trend in resilience, with the least diverse soils regaining the pre-temperature stress level of function after 57 days, whereas in the most diverse soils processes recovered completely within 15 days. Hence, whereas the effects of the first stress indicated functional redundancy for soil organic matter decomposition, measured as respiration, the effects of the second stress showed that the stability of this process was reduced.

Under hypothesis 1 (see above) these experimental results cannot be interpreted as direct effects of reduced biodiversity on process stability. A second experiment was carried out to separate disturbance effects from biodiversity effects (Griffiths et al., 2001b). Basically, the experimental set-up was the same as in the first experiment, but the first stress was now applied by inoculating sterile soils with serially diluted soil suspensions prepared from the parent soil. The results of this experiment showed that the first stress led to similar effects as in the first experiment, with progressively decreasing biodiversity (bacterial, fungal and protozoan) with increasing dilution factor, whereas process rates were less affected (Griffiths et al., 2001b). The second stress/disturbance, which was the same as in the first experiment, showed similar responses in all dilution treatments, with the strengths of the responses comparable to those in the least diverse soils (2 and 24 h of fumigation) in the first experiment. These results indicate that in the first experiment it might have been the stress itself (the initial fumigation) that reduced process stability, not necessarily changes in biodiversity.

In agriculture though, reduced soil biodiversity can be due to stress and, therefore, a third experiment was carried out to analyse soil ecosystem stability depending on

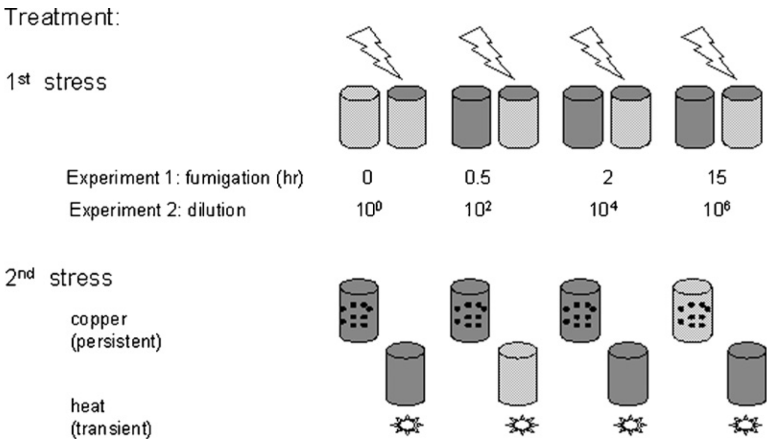

Fig. 1. Design of two stress-on-stress experiments (Griffiths et al., 2000; Griffiths et al., 2001b). In the first experiment, the first stressor is soil fumigation of various duration and in the second experiment it is inoculating sterile soils with serially diluted soil suspensions from the parent soil. In both experiments, the second stressors are a persistent stress (Cu-addition) or a transient (heat-shock) disturbance.

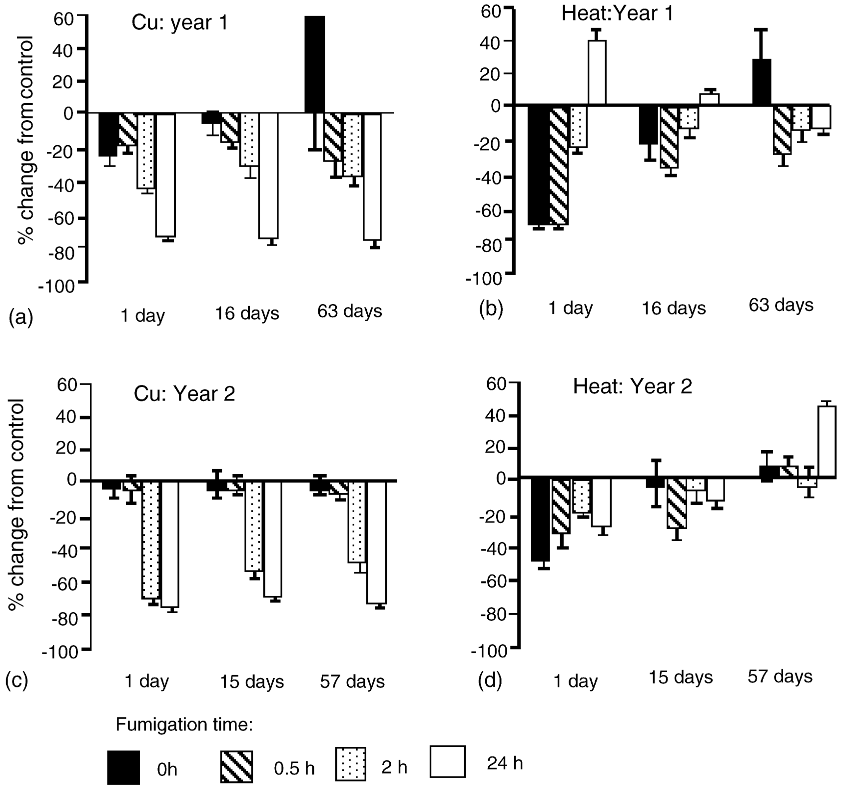

Fig. 2. Effect of Cu addition or heat treatment on the ability of soils fumigated for different lengths of time to decompose grass residues, at increasing time intervals following the application of the perturbation. Values are the mean ($n = 3$; bars show S.E.) percentage change in decomposition relative to unperturbed soil that had originally been fumigated for the same time span. From: Griffiths et al. (2000).

agricultural management regimes, *in casu* intensive or organic horticulture (Griffiths et al., 2001a). Stability was analysed by applying combinations of copper and heat stress. The results of this experiment showed that stability depended on management regime: the organically managed soil was more stable than the intensively managed soil (Griffiths et al., 2001a).

The mechanism behind these stability effects of stress and diversity is not yet fully understood. It seems to depend on type of stress or disturbance, and on the combination of stress and disturbance effects (Tobor-Kapłon et al., 2005, 2006). For example, when the system is stressed through heavy metal contamination, the community might become more stable to another heavy metal pollution, because of selection and adaptation (hypothesis 2), but less stable to a second treatment like heat or salt. Another explanation might be at the level of community structure. A stress or disturbance might alter the basic set-up of communities in terms of population sizes, trophic pyramids and food chain length These structural effects might be that food chain length has become too short given the level of resource availability (de Ruiter et al., 2005) or that the shape of the trophic biomass pyramid is disturbed, leading to potentially unstable configurations in the patterns of interaction strength among the trophic groups constituting the food webs (Neutel, 2001; Neutel et al., 2002).

2.2. Biotic stress and disturbance

Many soil organisms are detrimental to plant production and human societies. For example some animals (such as moles, rodents, snails, slugs, termites, ants, beetles and nematodes) may seriously damage crops or become a nuisance in both rural and urban homes. Many species of bacteria and actinomycetes can cause plant diseases, but most damage is caused by fungi, which account for most soil-borne crop diseases, such as wilts, root rot, clubrot, and blight.

Therefore, resistance against outbreaks or stress of pests and diseases and resilience from disturbance is of particular importance in agriculture. General suppressiveness of soils is the inhibition of pathogens as a result of a high total microbial biomass combined with a very intense competition for carbon and/or nutrients. This leads to a permanent state of starvation inhibiting the growth of pathogens. Specific suppression, i.e. the suppression of specific pathogens by specific antagonists, always operates against a background of general suppression (Cook and Baker, 1983). Various organic amendments are known to have effects on disease incidence. Effects may be positive or negative and various mechanisms may be involved: toxic substances, enhancement of disease-suppressing or promoting organisms (Litterick et al., 2004). However, the importance of soil biodiversity, if any, in exerting such effects is still largely unknown.

A case in point is a study in a long-term experiment, where fields were subjected to different treatments: species-rich permanent grassland, grassland turned 2 years previously to arable land under rotation or monoculture of maize, and long-term arable land under rotation or monoculture of maize (Garbeva, 2005). The highest suppression of the soil-borne pathogen *Rhizoctonia solani* AG3 on potatoes, planted in small subplots, was measured in grassland turned into monoculture of maize (Table 1). Using *in vitro* screening for antagonistic isolates against *R. solani* AG3, higher numbers of such isolates were found in soil under permanent grassland and under grassland turned into arable land than in soil under arable land (data not shown). Using the Shannon–Weaver index for DGGE bands of the soil microbial community, highest disease suppression was found in plots with highest soil microbial diversity. These plots were all found in grassland or grassland-derived arable land, suggesting that part of the disease suppression was retained in the grassland-derived plots. The pattern held for bacteria and fungi in general and also for *Bacillus* bacteria, but less clearly so for actinomycetes (Table 1). By applying a quantitative real-time PCR assay to study the abundance of the *prn*D gene (the gene encoding the biosynthesis of the antibiotic pyrrolnitrin) in the different treatments, highest densities of these genes were detected in the permanent grassland and in grassland turned into arable land, whereas in the original arable land the *prn*D genes were present at low densities or absent (Garbeva et al., 2004a). Because both grassland-derived and arable-derived plots had highest disease suppression in the maize monoculture, it follows that the crop also exerted a considerable influence on disease incidence.

van Bruggen and Semenov (2000) propose that changes in microbial community structure (indicated by copiotrophic to oligotrophic ratio, microbial succession stage, metabolic profiles, PLFA analyses or various DNA fingerprinting techniques) and the time required to return to the initial state after application of various disturbances or stresses could be characteristic for disease-suppressive soils. Because microbial diversity and community structure are influenced by plant (crop), soil type and management (Garbeva et al., 2004a,b), relationships between soil biodiversity and soil suppressiveness will have to be studied and interpreted in such a wider context. In addition, in the wider context of soil biodiversity studies not only single- and two-level trophic interactions, i.e. competition among the microflora and between microflora and plant, respectively, should be addressed, but also multi-trophic interactions have to be included.

3. Understanding the “importance” of soil biodiversity for the sustainable use of resources

The sustainable use of water and nutrients are of utmost importance in agriculture. Increasing agricultural sustainability under resource-limited conditions means increasing water use efficiency (WUE, ‘‘more crop per drop’’) and nutrient use efficiency (NUE, ‘‘more cropping per dropping’’). In industrialized countries, increasing nutrient use efficiency contributes to the reduction of contamination of surface and ground water with nutrients. In developing countries, increasing nutrient use efficiency means lower demands for often scarcely available or affordable artificial fertilizers. Water use efficiency is important worldwide so as to minimize water losses during and after rainfall or irrigation in periods with natural drought.

3.1. Nutrient use efficiency

Ecosystem nutrient use efficiency equals net primary productivity (NPP) over soil nutrient supply. This can be divided in:

Ecosystem NUE = NPP/nutrient uptake (=plant nutrient *utilization* efficiency) *x* nutrient uptake/soil nutrient supply (=plant nutrient *uptake* efficiency).

In a study using model tropical ecosystems comprised of three tree species, and polycultures in which each of the tree species was co-planted with species of two additional life forms, Hiremath and Ewel (2001) investigated ecosystem nutrient use efficiency. In 2 out of the 3 tree systems and in 2 out of 4 years of study, the polycultures significantly

Table 1
Percentage of healthy[a] plants[b], as related to the microbial diversity in soil. After: Garbeva, 2005

Rotation	Healthy plants (%)	Shannon–Weaver diversity index of DGGE bands			
		Bacteria total	Fungi total	Bacillus	Actinomycetes
G → AM	100	3.51	3.26	2.85	2.75
G → AR	60	3.55	3.24	2.85	2.55
G	60	3.24	3.35	2.85	2.34
A → M	30	3.10	2.90	2.25	2.45
A → R	17	3.10	3.02	2.13	2.40

G: permanent grassland; G → AM: grassland turned into arable monoculture of maize; G → AR: grassland turned into 4-year arable rotation; A → M: arable rotation turned into monoculture of maize; A → R: 3 year arable turned into 4 year arable rotation.

[a] With respect to *Rhizoctonia solani* AG3.

[b] Potato plants, planted in small sub-plots of plots with different land use histories and cropping systems.

increased N and P uptake and uptake efficiency relative to the monocultures (Fig. 3). Causes of these differences between years are unknown. This may indicate that not in all systems and not in all years nutrients were limiting. But in the cases where they were, both ecosystem N and P use efficiency reflected patterns of NPP, the plant-related term in the equation (data not shown). This result is consistent with the finding of van Ruijven and Berendse (2005), that under nitrogen-limited conditions, 5 out 8 species (grasses and non-leguminous dicots) showed significant increases in N *utilization* efficiency at increasing species richness from 1 to 8, probably as a result of changes in allocation patterns to aboveground biomass. More interesting in the framework of our paper, in the study of Hiremath and Ewel (2001) ecosystem N and P use efficiencies more strongly reflected patterns of nutrient *uptake* efficiency (Fig. 3), which includes soil nutrient supply in the denominator of the ecosystem NUE equation. This raises the question whether soil nutrient supply is related to the soil biota and to soil biodiversity. There is evidence that this is indeed the case. van der Heijden et al. (1998) showed that with increasing arbuscular mycorrhizal diversity hyphal length, plant P at the vegetation level increased, while soil P decreased, which they attributed to more efficient exploitation of soil P.

For non-mutualistic soil organisms that potentially influence plant nutrient uptake efficiency, the evidence is indirect. For example, in an experiment in central Burkina Faso, we compared different mulch-amended treatments with or without soil fauna (mostly termites) in terms of *apparent* N use efficiency, which is expressed in terms of the amount of N taken up per unit of N applied. Under N limitation, treatments with soil fauna showed significantly higher apparent N use efficiency than those without, except in the cases with low quality amendments (*Andropogon*

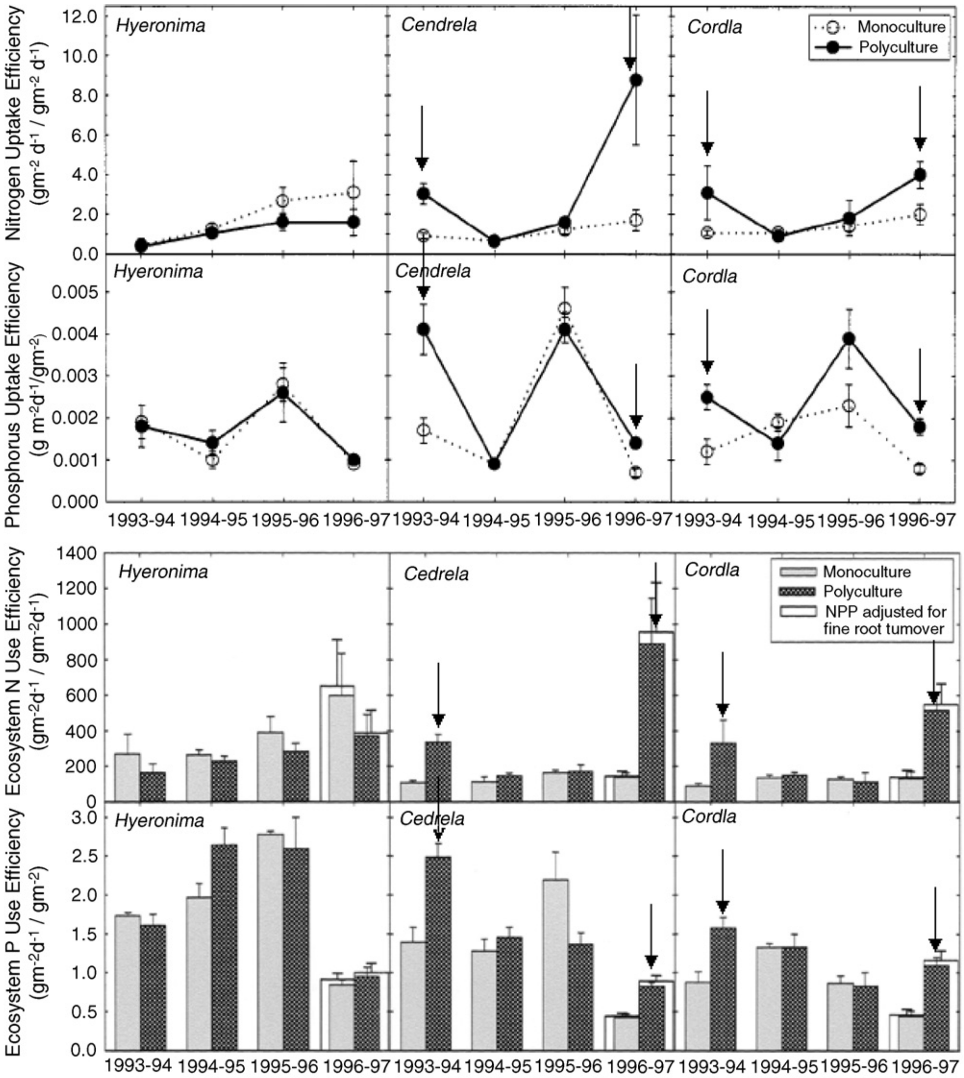

Fig. 3. N and P uptake efficiencies (upper two panels) and ecosystem nutrient use efficiencies estimated as the ratio of net primary productivity to rate of nitrification or to soil P (lower two panels) in monocultures and polycultures dominated by *Hyeronima alchorneoides*, *Cedrela odorata*, and *Cordia alliodora*. Values are means with standard errors of three blocks. Arrows point to cases where monocultures and polycultures were significantly different. From: Hiremath and Ewel (2001).

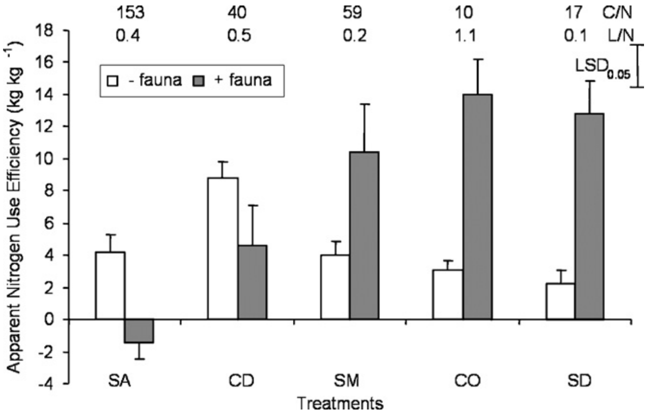

Fig. 4. Sorghum apparent N use efficiency in fauna and no-fauna plots at Kaibo, Burkina Faso, after application of organic resources of different qualities. SA: *Andropogon* straw, CD: cattle dung, SM: maize straw, CO: compost, SD: sheep dung. Bars represent standard deviations. LSD: Least Significant difference at $P = 0.05$. C/N: carbon–nitrogen ratio, L/N: lignin–nitrogen ratio. From: Ouédraogo et al. (2006).

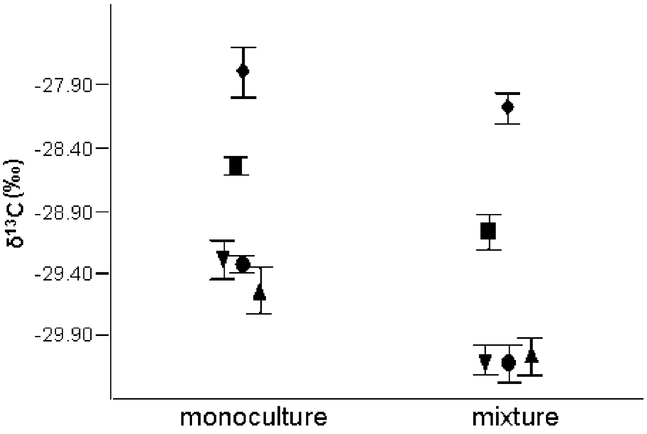

Fig. 5. Leaf carbon isotope ratios ($\delta^{13}C$) of 5 plant species in monocultures and in species-rich mixtures (8 and 14 sown species). Mean of measurements in 2 years. Bars represent one standard error. (◆): *Dactylis glomerata*; (■): *Holcus lanatus*; (▼): *Plantago lanceolata*; (●): *Trifolium subterraneum*; (▲): *Ornithopus compressus*. After: Caldeira et al. (2001).

straw and cattle dung in Fig. 4; Ouédraogo et al., 2006), which probably resulted in N immobilization. Although the soil fauna clearly affected the N use efficiency in this study, it is as yet unclear to what extent it is related to increased soil faunal *diversity*.

Species belonging to the same trophic group, but different ecological or life-history groups may markedly differ in effects on N mineralization at the same level of diversity in taxa as different as nematodes (Postma-Blaauw et al., 2005) and earthworms (Postma-Blaauw et al., 2006). In a microcosm study Heemsbergen et al. (2004) showed that not soil biodiversity *per se*, but the mean functional dissimilarity within a species assemblage was positively related with soil nutrient supply, measured as gross nitrate productivity.

3.2. Water use efficiency

In a study on soil water availability and water use, Caldeira et al. (2001) used stable carbon isotope analysis as an indicator of long-term plant water use in experimental plant communities of different species richness. The leaf carbon isotope ratio served as an index of intercellular to ambient CO_2 concentrations when carbon in the leaf is assimilated, which can be related to stomatal behaviour and, hence, to water use by plants. Caldeira et al. (op. cit.) studied the response of monocultures and species-rich communities during a brief rainy period in a Mediterranean grassland in 2 years. In both years, the total biomass in species-rich mixtures was significantly higher than, and the absolute value of leaf $\delta^{13}C$ lower than in monocultures (Fig. 5). Above-ground biomass was significantly related to differences in leaf $\delta^{13}C$. Measurements of leaf N concentration and soil water were consistent with the conclusion that the species-rich communities had more water available in the upper soil where roots were concentrated. Here again, mycorrhizas may well have contributed considerably to the observed effects. As reviewed by Augé (2004), even when AM plants and non-AM controls have similar size and P concentrations, mycorrhizal plants often show higher stomatal conductance and transpiration. This suggests that AM root systems scavenge water of low activity more effectively. Although in the study referred to earlier, van der Heijden et al. (1998) did not study water relationships, their finding of higher vegetation biomass with increasing mycorrhizal diversity is consistent with the hypothesis that this result is associated with increased water uptake efficiency. Part of such results may be indirect, i.e. due to mycorrhiza-mediated effects on soil structure. The moisture characteristics of a soil depend on the size and distribution of its pores. Because mycorrhizal fungi are effective in stabilizing soil structure, it seems logical that AM colonization of a soil might affect its moisture retention characteristics and, hence, the behaviour of plants, growing in the soil, particularly when it is dry. Indeed, Augé (2004) showed that the effect of mycorrhizal fungi on stomatal conductance was approximately equally due to root and soil colonization. This means that even non-mycorrhizal plants may benefit from mycorrhizal fungi for water uptake.

For non-mutualistic soil organisms that potentially influence plant water uptake efficiency the evidence is again indirect. We investigated the importance of the soil fauna in increasing water use efficiency in Burkina Faso. Crusted soils in the north were colonized by termites, which broke the crust after the introduction of mulches. As a result the water infiltration rate increased (Mando et al., 1996), as did water use efficiency (Table 2; Mando et al., 1999). Increased water use efficiency coincided with increased plant diversity (Mando et al., 1999). Although in this case it was evident that the soil fauna contributed significantly to the observed effects, it is as yet unclear to what extent the increased WUE is related to increased soil faunal *diversity*.

Table 2
Effects of termites and mulch on water use efficiency on originally crusted soil in northern Burkina Faso, 1 year after plot establishment. After: Mando et al. (1999)

Treatment	RUE ($kg\ ha^{-1}\ mm^{-1}$)	IUE ($kg\ ha^{-1}\ mm^{-1}$)
Straw + termites	6.08 a	7.09 a
Wood + termites	6.31 a	8.69 a
Straw + wood + termites	8.03 a	10.63 a
Straw − termites	2.69 b	3.51 b
Wood − termites	1.15 b	2.73 b
Straw + wood − termites	2.40 b	2.79 b
Bare soil	0 b	0 b
Block	ns	ns
Termites	***	*
Mulch	ns	**
Termites × mulch	***	***

RUE: rainfall use efficiency; IUE: infiltrated rainfall use efficiency. Figures in a column followed by the same letter are not significantly different at $P = 0.05$. ns: not significant.

[*] $P \leq 0.05$.

[**] $0.05 < P \leq 0.01$.

[***] $0.01 < P < 0.001$.

As different species or functional groups may affect soil structure differently (Lavelle, 2002), the diversity of soil structural components may be more closely related to water use efficiency than with the diversity of species (groups) themselves.

Taking these studies together, it would seem that further joint investigation of relationships between soil biodiversity and soil nutrient and water supply with plant biodiversity and nutrient and water uptake and utilization efficiencies holds promise for raising ecosystem nutrient and water use efficiencies. A conceptual framework as given in Fig. 6 may be helpful in designing such studies.

4. Managing soil biodiversity

Soil animal and microbial diversity is part of the biological resources of agroecosystems, and must be considered in the management decisions. As indicated in Fig. 6, the main management options comprise tillage, crop rotation (and sequence) and organic matter management. The available literature indicates that high-input agriculture, particularly tilled agroecosystems with narrow crop rotation/short fallow management, leads to a decrease in species richness and dominance of some species. In contrast, management characterized by rotations, no-tillage, organic amendments and maintenance of non-productive (‘‘natural’’) elements leads to an increase in species richness and overall density. Drainage and irrigation can work out positively, depending on agro-ecological conditions, whereas soil cultivation and the amount and type (especially its quality) of organic matter applied can have either positive or negative effects on species richness in soil (Fig. 7; Brown et al., in press).

Management of agroecosystems can be performed at various levels, and Swift (1999) proposed a series of potential ‘‘entry points’’ or management practices that can affect soil biological processes, biodiversity and the contribution of soil biota to agricultural sustainability (Fig. 8):

- The choice of plants and their spatio-temporal organization in the system, and the inclusion or not of livestock (and their management);
- Alteration of the plant’s resistance to disease, or the quality of residues (roots and shoots) produced, through genetic plant improvement;
- Change in the amount and/or quality of the organic residues entering the soil (external or internal to the

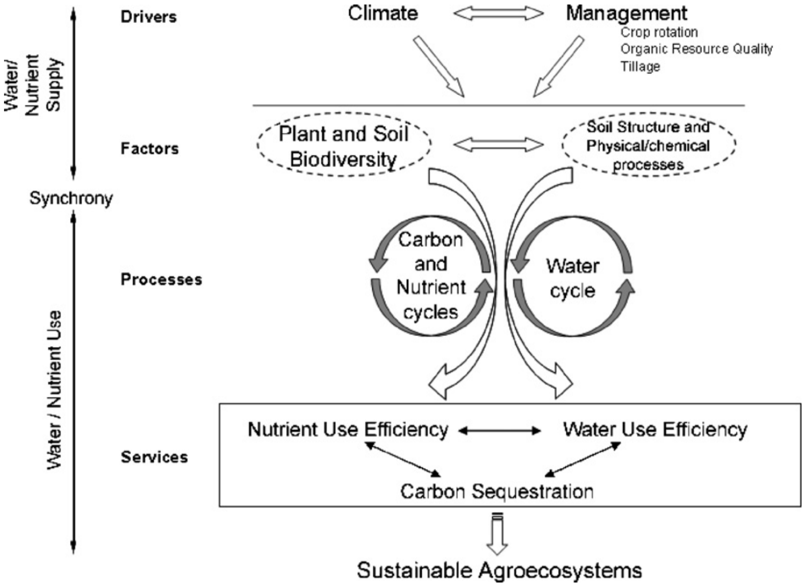

Fig. 6. Conceptual diagram on the relationships between management, plant and soil biodiversity, soil structure and nutrient and water use efficiencies in agroecosystems. Modified from original drawing by J. Six.

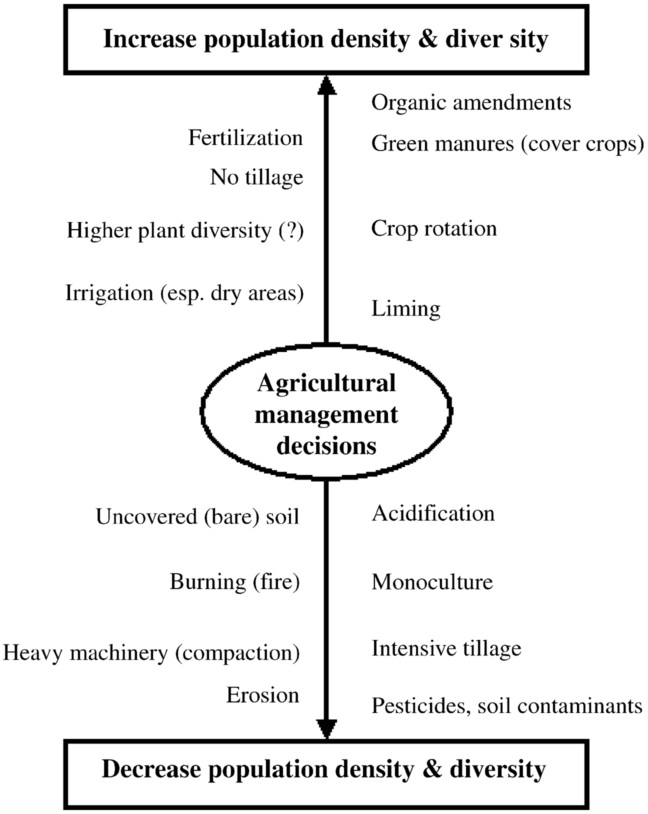

Fig. 7. The effect of different agricultural management practices on soil animal populations (density and diversity) (Brown et al., in press; after Hendrix et al., 1990). The position of the various practices on the *y*-axis represents their hypothetical relative contribution (importance) to increasing or decreasing soil animal populations.

system) to help control pests and feed beneficial soil biota;
- Minimum soil disturbance and use of pesticides, irrigation, and fertilizers (when and if necessary);
- Use of biological control (pests and diseases) practices;
- Inoculation of beneficial soil organisms (disease antagonists, microsymbionts, rhizobacteria, and earthworms) for disease control and soil fertility improvement.

These entry points (management decisions) can influence positively and/or negatively soil animal populations directly and/or indirectly. Greatest benefits to soil biota (activity and diversity), particularly over the long term, are likely to come from the proper choice of crops and trees and their distribution in space and time in the agroecosystem, the enhancement of natural pest and disease resistance of the chosen plants, improvement in the quality of residues produced, and management of organic matter and other external inputs (e.g. fertilizers) into the system. Minimum tillage and maintenance of crop residue cover on the soil surface also benefit belowground food webs and processes compared with conventionally cultivated soils (House and Parmelee, 1985; Brown et al., 2002). The adoption of all these practices should help increase food quality and quantity for the soil community and create a more suitable environment for their activities. However, further research is needed, particularly to optimize the supply of organic resources (and in particular, their quality, including mixtures of different litter types) in different agroecosystems under various soil and climate conditions.

Some of the above interventions, particularly direct ones like the selection of N fixing plant species and varieties, rhizobia inoculation in grain legumes, mycorrhiza inoculation for tree establishment and bio-control agents for disease and pest control are already well developed techniques, widely used by farmers in many developed and some developing countries. Nevertheless, they continue to be underutilized in many less developed countries, particularly by resource-poor farmers.

Agroecology and farming systems approaches have greatly contributed to the design of more sustainable and productive agro-ecosystems (Pimbert, 1999). Spatial statistics have been used to predict soils and regions within landscapes or fields that are more or less productive, helping farmers to decide where they should plant their crops, in what densities, at what times of the year, and where fertilizer side-dressing should be performed (Mausbach and Wilding, 1991). Genetic manipulation of crops can also provide immense opportunities to improve their abilities to resist adverse environmental conditions (climatic, edaphic, biological), as well as improve the quality of the residues (above- and below-ground), but possible adverse effects like gene transfer and other effects on beneficial soil biota still have to be adequately addressed, in the case of transgenic plants. These latter indirect techniques will be particularly important in determining decomposition and mineralization rates.

However, the key to successful soil biological management is its development in an integrated manner (TSBF, 1999). The management of each of the potential entry points must not be conducted independently, but in a holistic fashion, especially because of the recurrent interactions between different management strategies, different hierarchical levels of management, and between different soil organisms (Swift, 1999). Manipulation of the system at the highest level (e.g. the cropping system, see entry point 1 in Fig. 8) will influence all the other levels of management, and will generally lead to more rapid system responses than manipulations at lower levels (e.g. organic matter management, tillage, soil fauna or microbial inoculation). Therefore, interventions at highest levels are likely to be more successful than those at lower levels that affect soil fertility and plant production mostly indirectly. The goal is to establish the most direct link possible between the management intervention and the target; the more specific the intervention, the more likely it is to be successful (Swift, 1999).

The assessment, management and conservation of soil biodiversity is more than just technology development and intervention. Integrated management of soil biota, biodiversity and agricultural ecosystems is a holistic process that

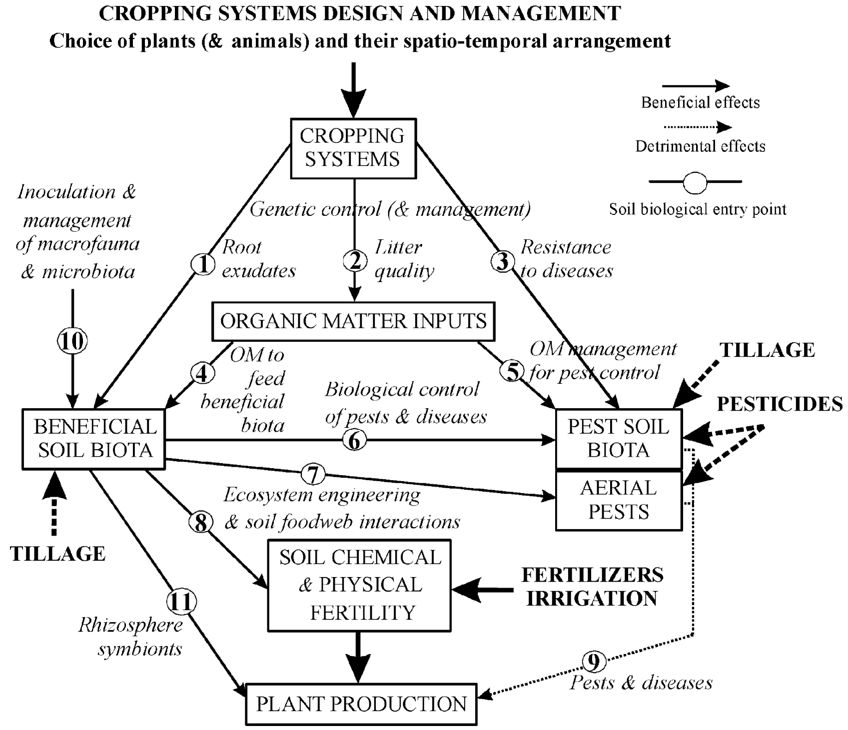

Fig. 8. The potential entry points for biological management of beneficial and pest soil organisms, cropping systems, OM inputs and soil fertility, affecting plant production (adapted from Swift, 1999; modified from Susilo et al., 2004). OM: organic matter.

relies largely on locally available resources, climate, socioeconomic conditions and, above all, direct involvement of farmers and other stakeholders in identifying and adapting management practices to their specific context.

For the whole process to work, support services are necessary at various levels and from various sources (government agencies, NGO's, research institutions, local farmer cooperatives or groups). Furthermore, basic resources or aid may also be necessary, depending on their availability to farmers (for instance in resource-poor regions), such as the provision of seeds of selected crop species/varieties, the supply of fertilizers at affordable prices, training of artisans for manufacture of adapted tools, and further farmer training in livestock management for organic matter and fertilizer applications.

Overall, an understanding of how limitations to agricultural production at various levels (social, cultural, economic, political, agronomic, biological, environmental, edaphic, genetic) can be overcome is essential, using local or imported resources, knowledge and capacity, as well as how agricultural practices affect soil biota and their activity, to predict possible management options and solutions to sustainable use of soils and conservation of its biodiversity in agroecosystems.

5. Valuing soil biodiversity

Much more than a factory for plant production, soil is an extremely biodiverse entity, the place of endless reactions that control a host of services of use to humanity and to the natural environment. We acknowledge that the relationships between soil biodiversity and ecosystem functioning are still a field of rapid scientific development. Yet, we feel that now is the time to use the available knowledge to express ecosystem functioning in terms of ecosystem services to society and to relate these to soil biodiversity to the best of our knowledge. Although we recognize the controversial nature and difficulty in determining these values, some estimates are already available in the literature. These reveal the potential immense value of the services provided each year by the soil biota worldwide, possibly exceeding 1.5 trillion US dollars (Pimentel et al., 1997; van der Putten et al., 2004).

The economic benefits of soil biodiversity clearly shift the debate from theoretical grounds for conservation and sustainable use, to the practical grounds of making concrete improvements in current land management practices to adequately promote soil biodiversity conservation. Nevertheless, the benefits of soil biodiversity and other environmental goods are not commonly priced on the market. Therefore, a major and important step to make towards effective conservation includes adequately pricing and charging for the ecosystem services derived from soil biodiversity.

On an economic basis, soil biodiversity has both direct (the organisms themselves and/or their metabolic products) and indirect (the long-term outcome of their activities) uses. Of these, the most important is the recycling of organic wastes, representing approximately 50% of the total benefits of soil biotic activity worldwide (>US$ 760 billion). Humans produce annually more than 38 billion metric tons of organic waste worldwide. Were it not for the decomposing/recycling activity of soil organisms, much of the world's land surface would be literally covered with organic debris. Biological N fixation is another important service provided by the soil biota, particularly in agricultural ecosystems, where leguminous plants may fix more than 100 kg N ha^{-1} $year^{-1}$. Total annual contribution of N fixation by microorganisms in both agricultural and natural ecosystems has been estimated at ca. 140 to 170 million tons of N, valued at about US$ 90 billion $year^{-1}$. Four other important services mediated by soil organisms and influenced by their biodiversity include the bio-remediation of polluted soils and water (US$ 121 billion $year^{-1}$), the control of pests, particularly in agricultural systems (US$ 160 billion $year^{-1}$), the usefulness of various wild insects, plant roots and mushrooms as food for human societies (US$ 180 billion), and the pollination of plants, performed by many insects that often spend a critical stage of their life-cycles within the soil (US$ 200 billion $year^{-1}$).

6. Conclusions

The available evidence suggests that soil biodiversity confers disease suppressiveness. The extent to which this is the case under a range of conditions in the field warrants further research, especially in view of disease-suppressing properties of crops. Soil biodiversity also confers resistance and resilience against disturbance and stress. The extent to which this is the case under a range of conditions in the field also warrants further research. As the stability of the soil community appears to be related to the biomass distribution of trophic levels, the possible correlation between this distribution and soil biodiversity should be further investigated.

Under resource limitation both water and nutrient use efficiencies are increased in the presence of (burrowing and mulch-processing) soil fauna and associated with increased plant and mycorrhizal diversities and aboveground production. With higher functional dissimilarity of the soil fauna, the net diversity effect on ecosystem processes is higher. This will be an important finding in explaining the contribution of soil biodiversity to the efficiency of resource use, which is still to be substantiated.

Although the functional aspects of agro-ecosystems which are important to farmers are much more numerous than those treated in this paper, it is clear that soil biodiversity will only be meaningful, when integrated with above-ground biodiversity to sustain ecosystem functioning. We feel that the knowledge gained and to be developed will be useful only, if inspired by, and combined with farmers' knowledge, perceived problems and opportunities for application. The value of soil biodiversity is also to be recognized by society at large. We suggest that identifying the value of soil biodiversity in terms of economic benefits is a meaningful step in a research programme aimed at sustaining soil biodiversity and its use and as part of a wider strategy of conserving and using agrobiodiversity (cf. Perrings et al., 2006).

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