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On the current debate about soil biodiversity

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Abstract

Extreme exploitation and maltreatment of land in a number of countries had devastating impacts on terrestrial ecosystems (i.e., loss of biodiversity of flora and fauna). Biodiversity became a political topic (UNEP, and Convention on Biological Diversity (CBD) of the United Nations) decades ago and was recently linked to agricultural practices in general (OECD, FAO). A survey of reports on "sustainable land use", "soil fertility", and "soil biodiversity" which are published by such organizations leave the impression that soil fertility is controlled by soil biodiversity. In essence this would mean that a low soil fertility occurs together with a decrease in soil biodiversity. Here is the point where assumptions and scientific evidence are far apart with respect to below-ground biodiversity. Because the current discussion propagates soil biodiversity as a soil quality indicator, it seems necessary to question this approach with respect to microbial biodiversity of soils. Biological soil functions such as the maintenance of soil fertility are based on the concerted action of soil organisms such as soil microflora and soil fauna. For both biological entities no specific soil functions can be assigned to species diversity per se. Since organic matter turnover and nutrient turnover are mainly dependent on the activity of the soil microbial biomass (bacteria and fungi), the present paper concentrates on this biological soil fraction.

An attempt will be made to give an overview of the scientific background of soil microbial biodiversity. Interdependencies between the abiotic and biotic components will be described, together with the relationship between above-ground and below-ground biodiversity.

Keywords: soil microbial biodiversity, eco-physiological quotients, fungal:bacterial ratio, C_{mic}/C_{org} ratio, qCO_2

Zusammenfassung

Zur gegenwärtigen Auseinandersetzung zum Thema Bodenbiodiversität

Da frühere Fälle extremen Raubbaus an Böden und schlechter Bewirtschaftung verheerende Auswirkungen auf terrestrische Ökosysteme in einer Anzahl von Ländern hatten (z. B. Verlust der Biodiversität von Flora und Fauna), entwickelte sich der Begriff Biodiversität zu einem politischen Thema und wurde auch erst vor kurzem in einen allgemeinen Zusammenhang mit landwirtschaftlicher Praxis gebracht (OECD, FAO). Eine Sichtung von Berichten über "nachhaltige Landnutzung", "Bodenfruchtbarkeit" und "Bodenbiodiversität", die durch diese Organisationen veröffentlicht wurden, vermittelt den Eindruck, dass Bodenfruchtbarkeit durch Bodenbiodiversität gesteuert bzw. von ihr abhängig sei. Dem Sinn nach würde dies bedeuten, dass eine geringe Bodenfruchtbarkeit die Folge verminderter Bodenbiodiversität sei. Diese Sichtweise stellt jedoch eher eine Annahme dar, die gegenwärtig durch wissenschaftliche Belege nicht gestützt werden kann. Da in der zur Zeit anhaltenden Diskussion über "Bodenbiodiversität" der Begriff schon als Bodenqualitäts-Indikator vorgeschlagen wird, erscheint es aus mikrobiologischer Sicht angebracht, diesen Ansatz zu hinterfragen.

Biologische Bodenfunktionen, wie der Erhalt der Bodenfruchtbarkeit, basieren auf der Wechselwirkung zwischen Bodenorganismen wie der Bodenmikroflora und der Bodenfauna. Für beide biologischen Einheiten kann keine bestimmte Bodenfunktion genannt werden, die in irgendeiner Weise mit Artenvielfalt per se in Zusammenhang zu bringen wäre. Da der Umsatz organischer Substanz und der Umsatz von Nährstoffen in der Hauptsache von der Aktivität der mikrobiellen Biomasse des Bodens (Bakterien und Pilze) abhängig ist, konzentrieren sich die Ausführungen auf diese biologische Bodenfraktion.

Es wird versucht, Hintergrundwissen zum Thema mikrobielle Biodiversität von Böden aus der einschlägigen Literatur zusammenzustellen. Wechselwirkungen zwischen abiotischen und biotischen Komponenten von Böden finden ebenso Berücksichtigung wie die Beziehung zwischen der oberirdischen und unterirdischen Biodiversität.

Schlüsselworte: mikrobielle Bodenbiodiversität, ökophysiologische Quotienten, Pilz:Bakterien-Verhältnis, C_{mic}/C_{org} -Verhältnis, qCO_2

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1 Introduction

Since intensification of agricultural production was identified as one of the major factors of soil destruction and loss of biodiversity per se, international organizations (United Nations Conference on the Human Environment (UNEP), 1972; Convention on Biological Diversity (CBD) 1992; OECD, 2001) have provided the necessary platform and have worked out strategies on how to proceed in order to introduce and keep "sustainable land use" a political issue. In discussing ways how to protect terrestrial ecosystems with their natural resources and biota against irreversible losses, they have called upon their members to contribute indicators which would be applicable to many countries and would be helpful to policy makers for law enforcement. The following are excerpts of a paper held at the OECD Expert Meeting on Soil Erosion and Soil Biodiversity Indicators, Rome, March 2003.

With respect to indicators for agriculture, "soil (microbial) biodiversity" is generally linked to "soil fertility" (FAO, 2001). Here assumptions and scientific evidence do not agree. It is difficult to trace the first appearance of this combination of "soil biodiversity - soil fertility". With respect to the impacts of agricultural management on soils, attention has focused since the outset on identifying possible bio-indicators, specifically also microbiological bio-indicators which are suitable for defining "soil quality" or "soil health" (Lynch and Elliott, 1997; Dighton, 1997; Doran and Safley, 1997; Elliott, 1997). The definitions given for these two terms are actually interchangeable, whereby "soil health" comprises more the biological components of soils, i.e. "*the ability of a soil to perform functions that are required for the biological components of an ecosystem...*" (Dick, 1997). Pankhurst (1997) in his review assessed the possible link between soil biodiversity, soil functional processes and soil health while Altieri (1999) takes a very isolated position in that he indeed sees a relationship between soil biodiversity and soil fertility with respect to crop production management. Since one functional process of the microbial community is the turnover of nutrients and therewith the maintenance of "soil fertility," the pressure to aggregate viewpoints may have produced this oversimplification: soil biodiversity predicts soil fertility.

Except for extreme soil conditions - such as deserts - soil harbors the most diverse biotic communities on earth. According to Hawksworth and Mound (1991), up until now only a total of 70.000 species of bacteria and fungi have been described, while an assumed 1.530.000 species remain undiscovered. This would mean that not more than 5 % of microbes could potentially be identified. But even this is impossible since classical cultural methods are time consuming and for statistical treatment of species number and dominance estimations replicate soil analyses should be done (Domsch, 1960). After all, experts are needed to

identify isolated organisms. This does not speak for a quick routine lab procedure.

The last decade has produced a great number of scientific papers, mainly reviews, reflections or assumptions on soil microbial biodiversity and ecosystem function (i.e. Turco et al., 1994; Beare et al., 1995; Kennedy and Smith, 1995; Bengtsson, 1996, 1998; Wolters, (ed.), 1997; Giller et al., 1997; Sparling, 1997; Bowman, 1998; Andr n and Balandreau, 1999; Wardle et al., 1999a,b). Taken together, the majority of information given here does not allow the conclusion to be drawn that soil biodiversity regulates soil fertility. On the contrary, the majority of authors advocate an opinion which was provocatively expressed by Bengtsson (1996) "*there is no (direct) mechanistic relationship between diversity and ecosystem function. To think that one single number - species richness or a diversity index - can capture the complex relationships between many species and the functional roles of these interactions is ..naive .. and negates most ecological research since the 1960s*".

The objective of this paper is to give a short overview of the scientific information on soil microbial diversity. The intention is to point out the weakness of "soil biodiversity" as an indicator of soil functions, particularly whenever a link between soil fertility and microbial biodiversity is attempted. Since nutrient turnover for plant growth is a key function of the soil microbial decomposer community, the present paper concentrates on this biological fraction. Alternative microbial indicators for soil monitoring purposes are proposed.

2 Species richness of soil microorganisms and ecosystem development

Not every natural soil ecosystem contains the same number of taxonomic entities. Traditionally ecologists determine the degree of species richness or diversity by simply counting all species in an area (or sample) of interest. By weighting the relative abundance of one species to the total number of species, a qualitative index can be obtained which can differentiate between rare and dominant species (Krebs, 1985). This information can be of ecological significance. Microbial ecologists have adopted this procedure when trying to quantify below-ground biodiversity. It is an accepted ecological concept that the set of environmental conditions shapes the degree of species richness which an ecosystem can sustain. The development from a simple to a diverse system is dynamic. According to Odum (1969), there is an increase in species diversity, concurrent to the succession of an ecosystem from developmental stages to maturity, which can, as the system ages, decrease again.

With respect to soil microorganisms, the organic extracellular metabolites become important. Since the microflora is dependent on products from the primary pro-

ducer, it is a logical consequence to ask if a possible link exists between above-ground and below-ground biodiversity. As could be expected, this has opened a new discussion (Wardle and Giller, 1996; Bardgett et al., 1998; Wall and Moore, 1999; Hooper et al., 2000; Adams and Wall, 2000; Wolters et al., 2000) on an old topic. Early publications trace the appearance of microorganisms to specific plant residues (Domsch and Gams, 1968; Martyniuk and Wagner, 1978) and an increase in taxonomic fungal diversity with increasing resource heterogeneity (Zak and Visser, 1996 (sensu Gochenaur, 1975)). New experimental reports are scarce.

In an experiment where soil was primed with different C-sources, an increase in *in situ* catabolic potential of the microflora was found (Degens, 1998a), while Stephan et al. (2000) determined the catabolic diversity of culturable soil bacteria (BIOLOG method) which increased with the number of plant species in a grassland ecosystem. However, in both of these studies indirect methods are applied and it remains unclear whether the observed increased catabolic potential or diversity was due to the appearance of new organisms or if the old community stayed unchanged but reactivated catabolic potentials. Brodie et al. (2002), studying a grassland transect (from 25 to 6 plant species), did not see a relationship between plant species diversity and bacterial diversity when using a molecular approach, a bacterial community fingerprinting technique (TRFLP analysis). The highest plant diversity had the lowest bacterial diversity, bacterial numbers, microbial biomass-C and catabolic potentials (BIOLOG). Unfortunately, the soil pH was lowest (3.9) in the plot with the highest plant diversity and highest (6.3) in the plot with the lowest plant diversity. Here a pH effect was measured and not the effect of the number of plant species on the microbial community since it has been shown that soil pH controls the microbial community and that bacteria will decrease at low pH (Anderson, 1998; Blagodatskaya and Anderson, 1998, 1999). This indicates that soil physico-chemical factors are the primary determinants in establishing microbial communities, and that further diversification may then be controlled by the degree of available heterogeneous extracellular metabolites or organic substrates, respectively. However, it still remains open whether such a diversification must be understood as an increase in the number of species or if heterogeneous plant products induce diversification of catabolic functions or both. These two alternatives were highlighted in the work of Broughton and Gross (2000). The authors did not find a relationship between plant species richness and microbial species richness as indicated by fatty acid methyl ester (FAME) profiles, however, they found an increase in catabolic potentials (BIOLOG). This aspect of plant species richness and microbial species richness needs further exploration since it is a fundamental ecological question and experimental evidence is still too scarce

to draw a final judgement (see also recent review by Wardle and van der Putten, 2002).

Spatial heterogeneity (number of habitats or niches per unit area) is another physical factor for diversity gradients (Risser, 1995). In a recent review, Ettema and Wardle (2002) delivered theoretical arguments for the causes of subsequent spatial variability of organism distribution and how this may influence the plant community. A system is structured by species interactions with their habitat and by species to species interactions which leads to higher species diversity. Waid (1999) cites two main modes of organismal interactions: *direct* interactions, such as trophic, symbiotic, parasitic, or predatory types of interaction, and the *indirect* interactions, where organisms change the environment enabling others to emerge. He revived the old term *metabiosis* to describe such indirect interactions. Soil ecology of the past has contributed a great wealth of knowledge on *direct* interactions. Particularly early studies on pioneer organisms and successional stages of organismal appearance during organic matter degradation (Swift, et al., 1979), in addition to the studies on the significance of food webs in structuring soil communities (Lavelle, 1995, Lavelle et al. 1997; Duffy, 2002; Dunne et al., 2002), have given some insight on how communities evolve. On the other hand, the concept of *indirect* interactions has not extended over the borders of theoretical ecology with only little experimental work so far. It must be assumed, however, that metabiosis interrelationships "*whereby organisms must modify their environment before others are able to live and evolve*" (Waid, 1999) must first occur before *direct* interactions can take place. Further, under conditions of environmental (i.e., climatic) stability, the highest degree of diversity can be expected.

The question of ecological organization of communities has engaged the ecological literature for a long time. The majority of authors agree that it is not each individual species in a community that has the same impact on its habitat, but that a community can be differentiated into "drivers and passengers" (Peterson et al., 1998, Risser, 1995). A "driver" would have a strong ecological function, which in microbiological studies is similar to the term "keystone" species (Beare et al., 1995). This is independent of species richness. The general ecological notion until now has been that of an undirected development of community differentiation into species richness. This development is rather stochastic. Given the possibility of two similar habitats, will the same microbial spectra evolve in both? No prediction can be made here (Swift, 1984). Ecosystem theory discusses, however, an underlying principle of development of a system to higher efficiency in conserving energy (Odum, 1969; Reynolds, 2002). All this shows how difficult and inexact the term (microbial) diversity can be. We do not know what kind of species richness can be expected in a habitat. A summary

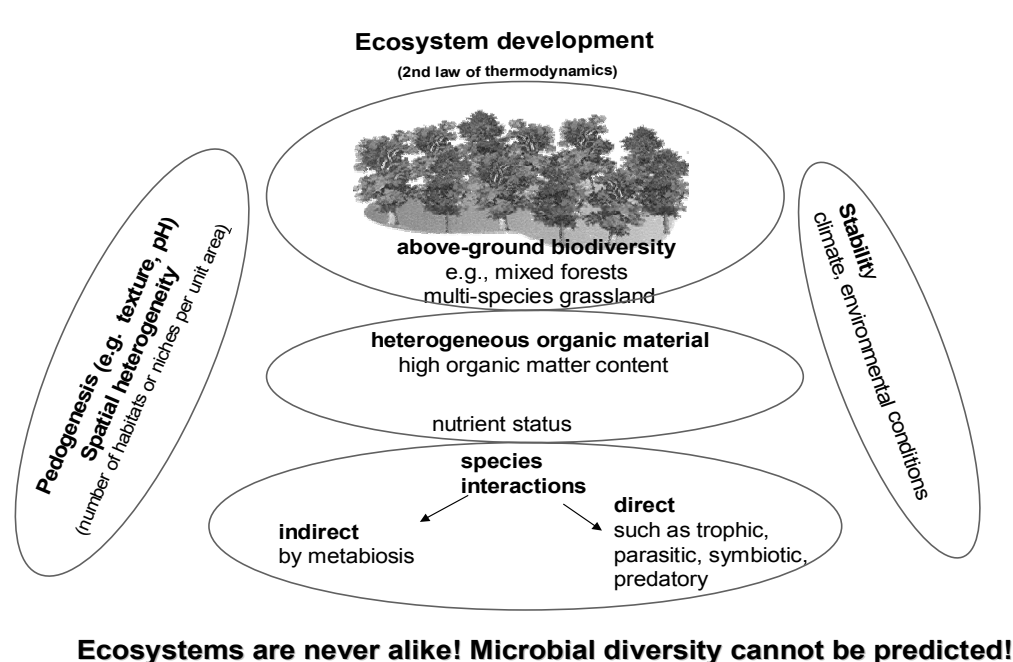


Fig. 1: Main factors which determine natural microbial diversity. These principles apply as well to man-manipulated soil systems. A threshold value of soil microbial diversity at the species level cannot be established.

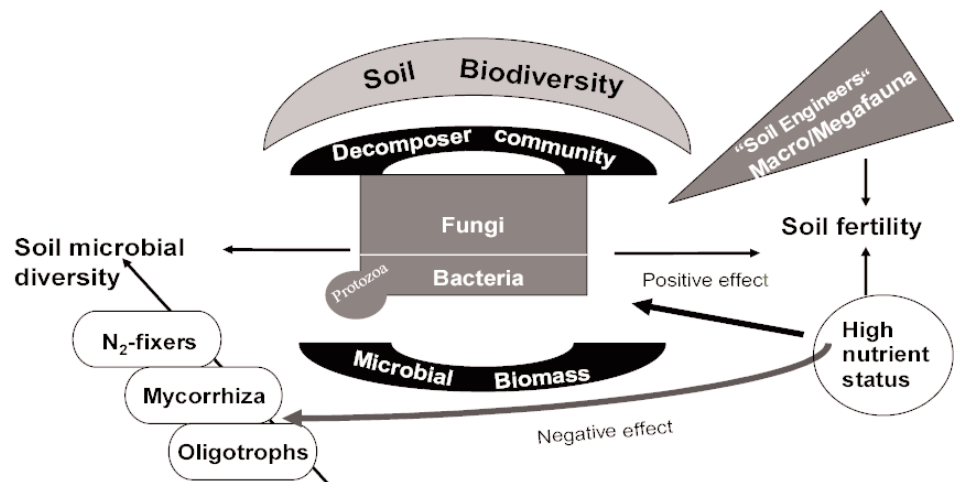
of the points made here is given with a schematic overview in Figure 1.

3 Natural versus man-made soil fertility - links to microbial soil biodiversity

Because of the unpredictability of species richness development and the current belief that species richness is not linked to **known** functions of ecosystems, but rather that single organisms or groups of organisms occupy functions, the majority of papers propagate the necessity to identify “keystone processes”, “keystone species” or “keystone groups” of organisms (e.g. Domsch, 1968; Hawksworth and Mound, 1991; Walker, 1992; Beare et al., 1995; Risser, 1995; Giller et al., 1997; Jones and Bradford, 2001; Tebbe et al., 2002) which drive ecosystems. One prominent keystone process is the development or maintenance of “soil fertility”. The topic of protecting soils against loss of soil fertility caused by agricultural intensification has engaged the international policy advisory boards for many years (FAO, CBD). Since plant (crop) production is dependent on soil fertility, the main concern is that losses of organisms which are controlling agents of soil fertility could lead to losses in crop yield. The natural intrinsic soil fertility and knowledge about the natural soil (microbial) biota and its reaction to degrees of fertility or environmental stress is appropriate to be used as a baseline (Domsch, 1977; Domsch et al., 1983). It is obvious that natural soil fertility differs due to pedogenesis (soil-building processes), which lead to the origin of

soil texture, soil pH and as well to the capacity to retain nutrients and moisture. These are key properties of soils for the development of above-ground vegetation and main properties which are - among others - connected with soil fertility. These properties are not equally distributed in nature, and from the practical viewpoint of an agronomist with respect to field-crop production and potential crop yield, gradients of low to extremely high soil fertility would be identified as seen with chernozems. The most intriguing fact from an ecological point of view is, however, that the most naturally “fertile” soils carry the least species richness of plants, animals and most probably of microflora and fauna as well (Marrs, 1993; Risser, 1995). That means, the assumptions commonly expressed that soil biodiversity would be an indicator of agricultural soil fertility or *vice versa* is diametrically opposed to observations made in natural environments.

More recent investigations on semi-natural plant production show an increase in net primary productivity (NPP) with increasing plant species richness in grassland ecosystems (Tilman et al., 1996, 1997, 2002; Hector et al., 1999, 2002; Bullock, et al., 2001; Knops et al., 2001). Particularly from the work of Hector et al., (1999) where eight European countries were involved in the study, it can be assumed that this observed increase in phytomass with increasing plant species richness was independent of the underlying natural soil fertility of those sites. Two very important aspects emerged from these studies: the increased productivity lead to a higher uptake by the plants of available soil nitrogen but did not lead to a faster



- Applies to natural and man manipulated soils
- Not all groups of microorganisms can be active at the same time
- Specification of key organisms or groups is needed to stimulate their activity
- The microbial decomposer community is the key group for sustaining soil fertility

Fig. 2:

Schematic view of the biotic components which are assembled under the term "soil biodiversity". **The need to differentiate!** Dark grey sections show the decomposer (called microbial biomass of fungi and bacteria) which are the main actors of organic matter degradation and nutrient turnover together with the soil fauna which physically transform litter to smaller pieces for better attacks by microbes. Both activities are contributions for a higher soil fertility. A high nutrient status (high soil fertility) will positively affect the decomposer community (the bacteria and fungi) while other groups of organisms (white fields) will be suppressed.

rate of litter degradation (Tilman et al., 1996; Knops et al., 2001; Catovsky et al., 2002). Since the heterotrophic microflora competes for the same mineral nutrients as plants do, the inorganic form of N, such as nitrate, may be less available for this group of microbes under such conditions. Low nitrate availability and low soil fertility, however, promotes microbial specialists, the free-living nitrogen fixing organisms (bacteria), and rhizosphere organisms of leguminous plants such as rhizobia (see review by Brockwell et al., 1995) and a special form of rhizosphere organisms, the arbuscular mycorrhizal fungi (AMF) (van der Heijden, et al., 1998a,b).

The bulk soil harbors the main important heterotrophic microbial community responsible for organic matter decomposition, nutrient cycling and soil building processes (structuring soil by extra-polysaccharide production). These functions of a microbial community are related to soil fertility by the soil biologist, while the agronomist often includes the other plant promoting "services" as well which are lumped under the label soil fertility (e.g., rhizosphere effects, control of pathogens, etc.). As pointed out above, heterotrophic organisms need nutrients (N, P, K) for growth and decomposition activity while nutrient poor environments will promote the specialist. This is illustrated in Figure 2. In other words, normal agricultural practices counteract processes of species diversity development which happen in natural ecosystems.

In natural soil systems the heterotrophic microbial community is not evenly distributed. A linear relationship was

determined between soil microbial biomass and soil organic carbon (Anderson and Domsch, 1980) in agricultural and forest soils (Anderson and Domsch, 1989, 1992). Since the microbial biomass is a potential source for plant nutrients (Anderson and Domsch, 1980; Marumoto et al., 1982a,b; Brookes et al., 1984) a high level of microbial biomass is an indicator of a highly fertile soil. As pointed out above, increasing plant species diversity resulted in higher litter production. With time such systems should also produce a higher level of soil organic matter. Recent reports seem to verify this relationship between plant species richness and increases of microbial biomass (Broughton and Gross, 2000; Bardgett and Shine, 1999; Spehn, et al., 2000). Based on recent experimental evidence one can assume, however that soils with higher microbial biomass levels will also carry a greater species diversity. Yan et al., (2000) described an increase in possible species diversity (indirectly measured by CLPP method using BIOLOG) up to a soil organic carbon content of 1.76 %. Beyond this value catabolic potentials remained constant. Also Øvreås and Torsvik (1998) showed for all test parameters applied (BIOLOG and molecular methods, e.g., amplified rDNA restriction analysis (ARDRA)) a higher bacterial species richness in an organic soil with 25 % C_{org} as compared to a soil with 4.5 % C_{org} . Also, Degens et al. (2000) found a relationship between catabolic potential of the microbial communities to different % of organic C by studying 22 soils of different texture. There was a decline in catabolic diversity in

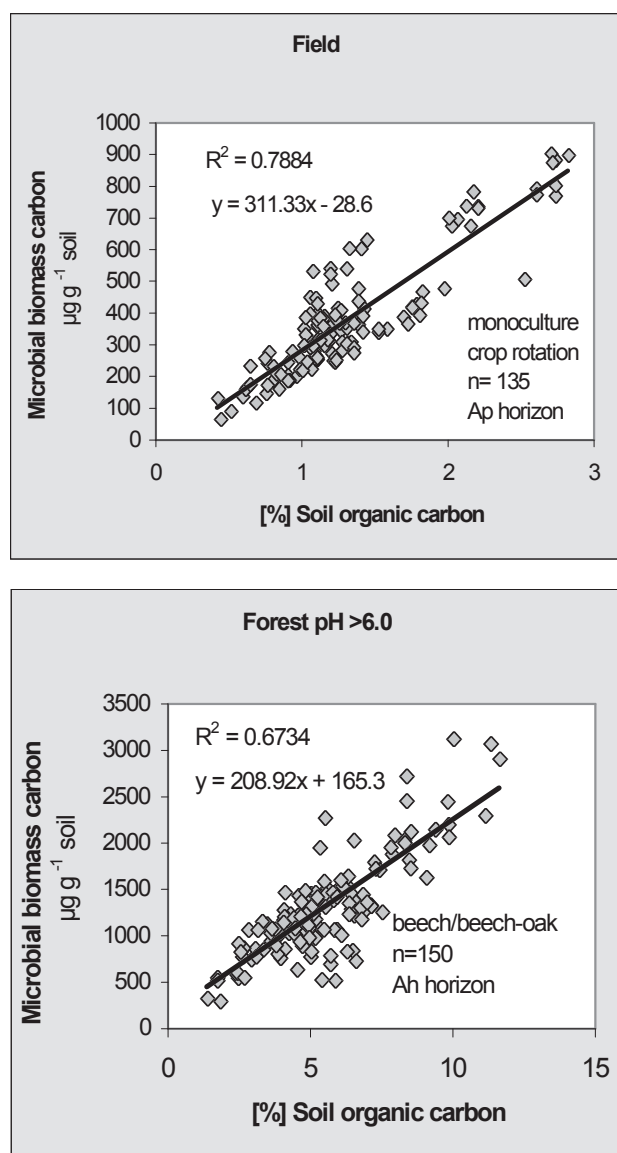


Fig. 3: Relationship between soil organic carbon and microbial biomass carbon in agricultural and forest soils. The plots show data points from either long-term (>15 yrs) monocultures or crop rotations or pure beech stands and mixed beech/oak stands. Data points above the regression lines are from crop rotations or mixed forest stands while data points below the regression lines are from monocultures or pure beech stands. This indicates that diversity of the above-ground phytomass will positively affect the level of microbial biomass (data extracted from Anderson and Domsch, 1989; Anderson, 2003).

soils where carbon is lost by management. Figure 3 and Table 1 give examples of the relationship between soil organic carbon and microbial carbon. The aspect, however, of the relationship between soil carbon content, level of microbial biomass together with studies of species richness has found little attention so far, but seems vital in identifying indicators of species richness.

If impacts on the microflora by agricultural management should be assessed, it is necessary to take a look

Table 1: Comparison of calculated C_{mic} -to- C_{org} * values taken from Fig. 3 of different agricultural managed plots and forest sites.

| Type of land use | soil conditions | C_{mic} in C_{org} (%) |
|------------------|-----------------|----------------------------|
| <i>Field</i> | | |
| Monoculture | NPK | 2.36 |
| | FYM | 2.60 |
| | GM+S | 4.00 |
| Crop Rotation | NPK | 2.90 |
| | FYM | 2.50 |
| | GM+S | 2.71 |
| <i>Forest</i> | | |
| MonoBeech | pH > 6.0 | 2.30 |
| MonoSpruce | pH > 6.0 | 2.00 |
| Mixed-Beech-Oak | pH > 7.0 | 2.70 |

* Calculated % C_{mic} in C_{org} (Field) are from a great number of long-term European field plots. They could be used as threshold values for a particular soil management (Anderson and Domsch, 1989). FYM = farmyard manure; GM+S= green manure + straw.

what natural stressors can produce. Early thorough investigations of **naturally** occurring stresses and their impact on soil microorganisms (e.g., temperature, pH, O_2 tensions, desiccation, physical disturbance, nutrient supply) demonstrate that more than 50 % of organisms or metabolic activity can be lost, which can be considered as a normal natural phenomenon (Table 2). Depending on the mean doubling time of a community, time must elapse until a community has reached the initial level of organisms again. In the majority of stress cases explored, the microorganisms recovered within less than 30 days. Similar observations were made in pesticide-side effect studies where 89 % of all cases (60 pesticides) showed a recovery time of less than 30 days (Domsch, 1977; Domsch et al., 1983). The monitoring of time is an impor-

Table 2: Natural stress impacts on populations and metabolic processes of soil microbial communities (Data extracted from Domsch et al., 1983).

| Cause | Organisms/ Process | Depression (%) |
|---------------|--------------------|----------------|
| Compaction | Nitrification | 50 - 75 |
| Drainage | Denitrification | 66 - 93 |
| Flooding | Ammonification | 98 |
| Flooding | (aerobic) bacteria | 48 - 91 |
| Flooding | Actinomycetes | 76 - 98 |
| Reduced O_2 | Fungi (growth) | up to 80 |
| Reduced O_2 | Bacteria | 90 - 100 |
| Reduced O_2 | Nitrification | 28 - 70 |
| Protozoa | Bacteria | 66 |
| Collembola | Fungi | 70 - 95 |

tant criterion for assessment of the resilience of a community and its ability to recover. The resilience in response to a natural impact could serve as a yardstick when assessing negative anthropogenic impacts (Domsch, 1977; Domsch et al., 1983) (Figure 4).

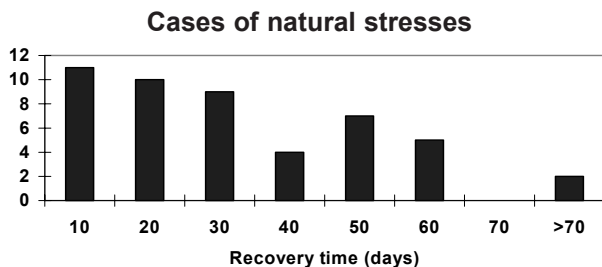


Fig. 4: Example of recovery time of soil microorganisms after impacts of different types of natural stress. Compare Table 2 (according to Domsch et al., 1983).

Agricultural land should yield enough crops for the world's food demand and yield is the source of income for the farmer. Even if all the propositions would be met which are cited in the agro-ecological test KUL (VDLUFA, 1998) for sustainable land use, agricultural soils will still be overloaded with nutrients which are necessary for obtaining an optimal crop yield. Since plants (crops) are harvested and not returned to the soil, it is necessary to supply the soil with available nutrients. Still soil C loss can be substantial in the long run (Saggar et al., 2001). Even under the most careful mechanical soil treatment, there will be disturbances of microbial communities (Domsch, 1986). The otherwise self-regulating soil system is continuously interrupted by these activities. This again means, **below-ground soil biodiversity in agricultural soils can never be attained to such an extent as under natural conditions.** Using an indirect test by determining the functional diversity of microbial communities of uncultivated and cultivated soils, community level physiological profiles (CLPP) were greater in uncultivated soils (BIOLOG test, Yan et al. 2000). The high load of nutrients raises a problem, for instance, when measures of agricultural extensification are to be carried out by turning agricultural land into floristically rich natural sites; the removal of surplus nutrients can take many decades (Gough and Marrs, 1990). It can be stated, however, that in conventionally managed soils, microbial species richness also is great. A seven-year study by Wardle et al., (1999b) did not indicate loss of microbial activity due to agricultural intensification. Also, experimental approaches in which soil biodiversity was diminished or changed did not show a decrease in decomposition rate or heterotrophic activity (Andrén et al., 1995; Degens, 1998b; Griffiths et al., 2001). Andrén et al. (1995) discuss the role of functional redundancy (functionally equivalent species) particular with respect to degradation. The abili-

ty to degrade litter is a vital property of the heterotrophic soil microbial community.

4 Soil microbial indicators which are sensible for monitoring sustainable land use

The examined literature does not allow the conclusion to be drawn that under conventional agricultural practices in the temperate regions (except for heavy metal contaminations or soil erosion cases) soil fertility is lost. Changes observed in the microbial community under necessary agricultural practices (tillage, plowing, pesticide treatment, fertilizing) were transient and could not be related to decreased activities of the heterotrophic soil community to degrade organic matter, the key function for nutrient cycling. Agriculturally managed land cannot evolve into a species-rich habitat compared to natural systems; its function to produce crop yield counteracts a development to higher species richness in a system. Vandermeer et al., (1998) demonstrated this by comparing different types of land use, from unmanaged systems to low or middle intensity managed systems up to degrees of high intensity such as plantations and orchards, intensive cereal or vegetable production. Along with land use intensification, a decrease in the overall species diversity was observed. However, because of the functional redundancy of heterotrophic abilities of the microflora nutrient turnover will be secured in every type of land use.

This may be a very narrow and utilitarian view to focus only on the function "soil fertility" or other functions which "serve" man. Although organisms are complementary - if one species is lost, another species takes over (Griffiths et al., 2001) -, it cannot be ruled out that lost species had genetically fixed traits for functions which we have not yet identified. Sustainable land use should be propagated for protecting the intrinsic soil biodiversity in the light of a possible changing world (global change) (Weigel, 1997) and as stated in the CBD "to meet the needs and aspirations of present and future generations".

Microbiological indicators of biodiversity should meet the following criteria according to the OECD Joint Working Party on Agriculture and Environment (JWP). They should be: policy-relevant, analytically sound, measurable, and easy to interpret. This would exclude for the time being descriptive methods (non-quantitative) such as new molecular methods (White and Mcnaughton (1997). Here, more experience is needed to understand limitations of the methods employed, and quantification is a must for comparative purposes and statistical treatments. The same would apply for the biochemical phospholipid fatty acid (PLFA) method which discriminates between bacteria and fungi (White, 1983). Both approaches are alluring since they will ultimately eventually give a direct insight into species diversity (community structure). In addition to the obstacle mentioned above, the results obtained cannot be

related to a function per se, since we do not know if the molecular or fatty acid signals obtained belong to organisms which are engaged in activities under study or if they include dormant organisms as well. Organisms can survive over decades in a resting stage!

Ecophysiological indicators are an alternative to overcome these current limitations. The advantage is that these indicators integrate abiotic and biotic components. One such indicator is the metabolic quotient, qCO_2 , (CO_2 production per unit cell mass and time) which was extrapolated from *in vitro* studies on the microbial biomass in soil (Anderson and Domsch, 1985a,b; Anderson 1994) and which links respiratory activity (basal respiration) to the size of the biomass. Negative environmental changes will be reflected in this quotient (Anderson and Domsch, 1993). It also satisfies the concept of comparing a measured effect with the reaction under “normal,” undisturbed conditions. The CO_2 release from basal respiration also reflects to a certain degree the maintenance carbon requirement of the cells. To adapt to adverse changes the microbial community will have a higher maintenance requirement, expressed as qCO_2 . This quotient has been accepted by the scientific community and a large body of experimental results is available. The same applies to the C_{mic}/C_{org} ratio. It relates microbial biomass (C_{mic}) to total soil organic carbon (C_{org}). As pointed out above, this relationship between microbial biomass and soil carbon is not sporadic but very stable. It reflects the availability of the soil carbon for the microbes. In the temperate zone the C_{mic}/C_{org} ratio is about 2.5 % of total organic carbon (Table 1). For instance, changes in the organic matter quality will be reflected in this ratio. If a community is stressed a high qCO_2 is expected which must, should the stress remain, lead to a lower C_{mic}/C_{org} ratio (Anderson, 1998, Anderson and Domsch, 1989). These two ratios together are useful for monitoring soil systems (Turco et al, 1994; Sparling, 1997; Dilly and Blume, 1998; Staddon et al., 1999; Anderson, 2003). The fungal/bacterial respiratory ratio (Anderson and Domsch, 1975) is an additional physiological parameter. It can differentiate between the respiratory activity of bacteria and fungi by selectively inhibiting the respiration with antibiotics. Normally agricultural soils have a respiratory ratio where fungal respiration is 80 % and bacterial respiration is 20 % of total respiration. This ratio changes if one microbial fraction is impaired or lost. In this respect this quotient also reflects changes in diversity. For instance, a decrease in bacterial respiratory activity with decreasing soil pH (Anderson, 1998; Blagodatskaya and Anderson, 1998, 1999) was identified (Figure 5).

These three microbial quotients are relatively easy to measure, are reproducible, understandable, and, with exception of the initial costs for the necessary equipment are relatively inexpensive. They are applicable across all countries. An additional advantage is that there exists a

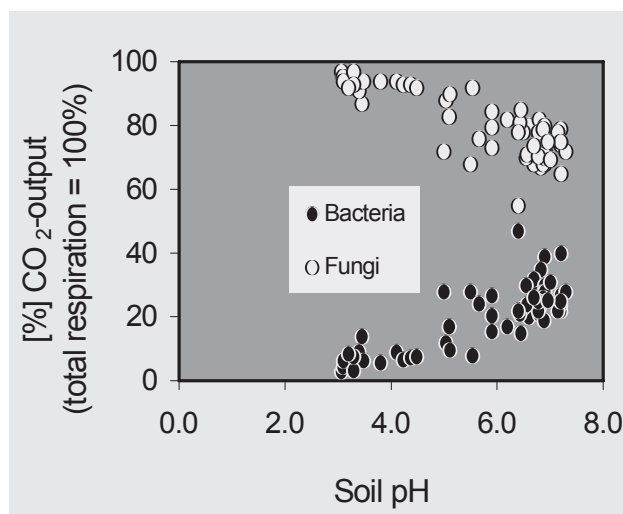


Fig. 5: The respiratory response of fungi and bacteria in relation to soil pH. Percent of respiratory contributions by bacteria decreases with decreasing soil pH. Forest soils (A_h) of Lower Saxony, Germany, $n=60$ (Anderson, 2005, in print).

large body of scientific background information on these quotients.

5 Concluding remarks

Possible driving forces of soil microbial diversity which could be considered for sustainable land use or land conservation were sought in the body of scientific literature. In addition, an attempt was made to place the term “soil fertility” into the correct perspective at the level of soil microbial biomass and not at the intrinsically existing biodiversity of a microbial community.

The following inter-relationships were identified:

1. With respect to a higher diversity of plant species (long-term)
 - a. by production of more phytomass
 - b. a higher level of organic matter is attained with time
 - c. which will contribute to a more heterogenous supply of organic matter below-ground, and thus may influence diversification of the microbial community (Figure 1) (here research is still needed).
2. The level of organic carbon will be a driving force for microbial biomass development (Figure 3).
3. A high microbial biomass level under agricultural conditions would be an indicator of high soil fertility and
4. first results indicate a relationship between species or functional diversity to high biomass levels (here research is still needed).
5. Soil pH is one of the main abiotic factors controlling diversification. Under neutral pH the highest fungal and bacterial diversity can be expected, with decreasing pH bacterial activity will decrease (Figure 5).

Literature

- Adams GA, Wall DH (2000) Biodiversity above and below the surface of soils and sediments : linkages and implications for global change. *BioScience* 50:1043-1048
- Altieri MA (1999) The ecological role of biodiversity in agroecosystems. *Agric Ecosyst Environ* 74:19-31
- Anderson JPE, Domsch KH (1975) Measurement of bacterial and fungal contributions to respiration of selected agricultural and forest soils. *Can J Microbiol* 21:314-322
- Anderson JPE, Domsch KH (1980) Quantities of plant nutrients in the microbial biomass of selected soils. *Soil Sci* 130:211-216
- Anderson T-H (1994) Physiological analysis of microbial communities in soil : Applications and limitations. In: Ritz K, Dighton J, Giller KE (eds) *Beyond the biomass : compositional and functional analysis of soil microbial communities*. Chichester : Wiley, pp 67-76
- Anderson T-H (1998) Einfluss des Standortes auf die Gesellschaftsstruktur von Mikroorganismen und deren Leistungen unter besonderer Berücksichtigung der C-Nutzung. In: Verbundprojekt "Veränderungsdynamik in Waldökosystemen" : Abschlußbericht 1998 ; Teil 2. Göttingen : Forschungszentrum Waldökosysteme, pp 385-394
- Anderson T-H (2003) Microbial eco-physiological indicators to assess soil quality. *Agric Ecosyst Environ* 98:285-293
- Anderson T-H (2005) Soil impacts on microbial biomass carbon in Lower Saxony of Germany. In: Brumme R (ed) *Functioning and Management of European Beech Ecosystems*. Ecological Studies. Heidelberg : Springer. In print
- Anderson T-H, Domsch KH (1985a) Maintenance requirements of actively metabolizing microbial populations under in situ conditions. *Soil Biol Biochem* 17:197-203
- Anderson T-H, Domsch KH (1985b) Determination of ecophysiological maintenance carbon requirements of soil microorganisms in a dormant state. *Biol Fertil Soils* 1:81-89
- Anderson T-H, Domsch KH (1989) Ratios of microbial biomass carbon to total organic-C in arable soils. *Soil Biol Biochem* 21:471-479
- Anderson T-H, Domsch KH (1992) Stoffwechselfkoeffizienten mikrobieller Sekundärproduzenten. *Ber Forschungszentrums Waldökosysteme / B* 31:154-164
- Anderson T-H, Domsch KH (1993) The metabolic quotient for CO₂ (qCO₂) as a specific activity parameter to assess the effects of environmental conditions such as pH, on the microbial biomass of forest soils. *Soil Biol Biochem* 25:393-395
- Andr n O, Balandreau J (1999) Biodiversity and soil function - from a black box to a can of worms? *Appl Soil Ecol* 13:105-108
- Andr n O, Bengtsson J, Clarholm M (1995) Biodiversity and species redundancy among litter decomposers. In: Collins HP, Robertson GP, Klug MJ (eds) *The significance and regulation of soil biodiversity*. Dordrecht : Kluwer Academic Publ, pp 141-151
- Bardgett RD, Shine A (1999) Linkages between plant litter diversity, soil microbial biomass and ecosystem function in temperate grassland. *Soil Biol Biochem* 31:317-321
- Bardgett RD, Wardle DA, Yeates GW (1998) Linking above-ground and below-ground interactions : how plant responses to foliar herbivory influence soil organisms. *Soil Biol Biochem* 30:1867-1998
- Beare MH, Coleman, DC, Crossley DA, Hendrix PF, Odum EP (1995) A hierarchical approach to evaluating the significance of soil biodiversity to biogeochemical cycling. *Plant Soil* 170:5-22
- Bengtsson J (1996) What kind of diversity? Species richness, keystone species or functional groups? In: Wolters V (ed) *Functional implications of biodiversity in soil*. *Ecosystem Res Rep* 24, EUR 17659 EN, pp 59-85
- Bengtsson J (1998) Which species? What kind of diversity? Which ecosystem function? Some problems in studies of relations between biodiversity and ecosystem function. *Appl Soil Ecol* 10:191-199
- Blagodatskaya EV, Anderson T-H (1998) Interactive effects of pH and substrate quality on the fungal-to-bacterial ratio and QCO₂ of microbial communities in forest soils. *Soil Biol Biochem* 30:1269-1274
- Blagodatskaya EV, Anderson T-H (1999) Adaptive responses of soil microbial communities under experimental acid stress in controlled laboratory studies. *Appl Soil Ecol* 11:207-216
- Bowman DMJS (1998) Death of biodiversity - the urgent need for global ecology. *Global Ecol Biogeogr* 7:237-240
- Brockwell J, Bottomley PJ, Thies JE (1995) Manipulation of rhizobia microflora for improving legume productivity and soil fertility : a critical assessment. *Plant Soil* 174:143-180
- Brodie E, Edwards S, Clipson N (2002) Bacterial community dynamics across a floristic gradient in a temperate upland grassland ecosystem. *Microbial Ecol* 44:260-270
- Brookes PC, Powlson DS, Jenkinson DS (1984) Phosphorus in the soil microbial biomass. *Soil Biol Biochem* 16:169-175
- Broughton LC, Gross KL (2000) Patterns of diversity in plant and soil microbial communities along a productivity gradient in a Michigan old-field. *Oecologia* 125:420-427
- Bullock JM, Pywell RF, Burke JW, Walker KJ (2001) Restoration of biodiversity enhances agricultural production. *Ecol Lett* 4:185-189
- Catovsky S, Bradford MA, Hector A (2002) Biodiversity and ecosystem productivity: implications for carbon storage. *Oikos* 97:443-447
- CBD, Convention on biological diversity (1992) [online], zu finden in: <www.biodiv.org> [zitiert am 14.8.2003]
- Degens BP (1998a) Microbial functional diversity can be influenced by the addition of simple organic substrates to soil. *Soil Biol Biochem* 30:1988-1998
- Degens BP (1998b) Decreases in microbial functional diversity do not result in corresponding changes in decomposition under different moisture conditions. *Soil Biol Biochem* 30:1989-2000
- Degens BP, Schipper LA, Sparling GP, Vojvodic-Vukovic M (2000) Decreases in organic C reserves in soils can reduce the catabolic diversity of soil microbial communities. *Soil Biol Biochem* 32:189-196
- Dick RP (1997) Soil enzyme activities as integrative indicators of soil health. In: Pankhurst CE, Doube BM, Gupta VVS (eds) *Biological indicators of soil health*. New York : CAB International, pp 121-156
- Dighton J (1997) Is it possible to develop microbial test systems to evaluate pollution effects on soil nutrient cycling? In: van Strahlen NM, L kke H (eds) *Ecological risk assessment of contamination in soil*. London : Chapman & Hall, pp 51-69
- Dilly O, Blume H-P (1998) Indicators to assess sustainable land use with reference to soil microbiology. *Adv Geoccol* 31:29-36
- Domsch KH (1960) Das Pilzspektrum einer Bodenprobe. I. Nachweis der Homogenit t. *Arch Mikrobiologie* 35:181-195
- Domsch KH (1968) Mikrobiologische Pr senz- und Aktivit tsanalysen von fungizidbehandelten B den. *Arb Univ Hohenheim* 44:1-79
- Domsch KH (1977) Biological aspects of soil fertility. In: *Proceedings of the International Seminar on Soil Environment and Fertility Management in Intensive Agriculture (SEFMIA)*. Tokyo, Japan : Society of the Science of Soil and Manure, pp 737-743
- Domsch KH (1986) Influence of management on microbial communities in soil. In: Jensen V, Kj ller A, S rensen LH (eds) *Microbial communities in soil*. Barking : Elsevier Applied Science, pp 355-367
- Domsch KH, Gams W (1968) Die Bedeutung vorfruchtabh ngiger Verschiebungen in der Bodenmikroflora. *Phytopathol Z* 63:64-74
- Domsch KH, Jagnow G, Anderson T-H (1983) An ecological concept for the assessment of side-effects of agrochemicals on soil microorganisms. *Residue Rev* 86:65-105
- Doran JW, Safley M (1997) Defining and assessing soil health and sustainable productivity. In: Pankhurst CE, Doube BM, Gupta VVSR (eds) *Biological indicators of soil health*. New York : CAB International, pp 1-28
- Duffy JE (2002) Biodiversity and ecosystem function : the consumer connection. *Oikos* 99:201-219

- Dunne JA, Williams RJ, Martinez ND (2002) Network structure and biodiversity loss in food webs : robustness increases with connectance. *Ecol Lett* 5:558-567
- Elliott ET (1997) Rationale for developing bioindicators of soil health. In: Pankhurst CE, Doube BM, Gupta VVSR (eds) *Biological indicators of soil health*. New York : CAB International, pp 49-78
- Ettema C, Wardle DA (2002) Spatial soil ecology. *TREE* 17:177-183
- FAO (2001) Soil biodiversity portal : conservation and management of soil biodiversity and its role in sustainable agriculture. [online], zu finden in: <www.fao.org/ag/AGL/agll/soilbiol/default.htm> [zitiert am: 14.8.2003]
- Giller KE, Beare MH, Lavelle P, Izac AMN, Swift, M (1997) Agricultural intensification, soil biodiversity and agroecosystem function. *App Soil Ecol* 6:3-16
- Gochena SE (1975) Distributional patterns of mesophilous and thermophilous microfungi in two Bahamian soils. *Mycopathol Mycol Appl* 57:155-164
- Gough MW, Marrs RH (1990) A comparison of soil fertility between semi-natural and agricultural plant communities : implications for the creation of species-rich grassland on abandoned agricultural land. *Biol Conserv* 51:83-96
- Griffiths BS, Wheatley KR, Kuan HL, Boag B, Christensen S, Ekelund F, Sørensen SJ, Muller S, Bloem J (2001). An examination of the biodiversity - ecosystem function relationship in arable soil microbial communities. *Soil Biol Biochem* 33:1713-1722
- Hawksworth DL, Mound LA (1991) Biodiversity databases : the crucial significance of collections. In: Hawksworth DL (ed) *The biodiversity of microorganisms and invertebrates : its role in sustainable agriculture*. Wallingford : CAB International, pp 17-29
- Hector A et al (1999) Plant diversity and productivity experiments in European grasslands. *Science* 286:1123-1127
- Hector A, Loreau M, Schmid B, BIODEPTH project (2002) Biodiversity manipulation experiments : studies replicated at multiple sites. In: Loreau M, Naeem Sh, Inchausti P (eds) *Biodiversity and ecosystem functioning : synthesis and perspectives*. Oxford : Oxford University Press, pp 36-46
- Hooper DU, Bignell DE, Brown VK, Brussard L, Dangerfield JM, Wall DH, Wardle DA, Coleman DC, Giller KE, Lavelle P, Van der Putten WH, De Ruiter PC, Rusek J, Silver WL, Tiedje JM, Wolters V (2000) Interactions between aboveground and belowground biodiversity in terrestrial ecosystems: patterns, mechanisms, and feedbacks. *BioScience* 50:1049-61
- Jones TJ, Bradford MA (2001) Assessing the functional implications of soil biodiversity in ecosystems. *Ecol Res* 16:845-858
- Kennedy AC, Smith KL (1995) Soil microbial diversity and sustainability of agricultural soils. *Plant Soil* 170:75-86
- Knops JMH, Wedin D, Tilman D (2001) Biodiversity and decomposition in experimental grassland ecosystems. *Oecologia* 126:429-433
- Krebs CJ (1985) *Ecology : the experimental analysis of distribution and abundance*. New York : Harper & Row
- Lavelle P, Lattaud C, Trigo D, Barois I (1995) Mutualism and biodiversity. *Plant Soil* 170:23-33
- Lavelle P, Bignell D, Lepage M, Wolters V, Roger P, Ineson P, Heal OW, Dhillion S (1997) Soil function in a changing world : the role of invertebrate ecosystem engineers. *Eur J Soil Biol* 33:159-193
- Lynch JM, Elliott LF (1997) Bioindicators : perspectives and potential value for land users, researchers and policy makers. In: Pankhurst CE, Doube BM, Gupta VVSR (eds) *Biological indicators of soil health*. New York : CAB International, pp 79-96
- Marrs RH (1993) Soil fertility and nature conservation in Europe : theoretical considerations and practical management solutions. *Adv Ecol Res* 24:241-300
- Martyniuk S, Wagner GH (1978) Quantitative and qualitative examination of soil microflora associated with different management systems. *Soil Sci* 125:343-350
- Marumoto T, Anderson JPE, Domsch KH (1982a) Decomposition of ¹⁴C- and ¹⁵N-labelled microbial cells in soil. *Soil Biol Biochem* 14:461-467
- Marumoto T, Anderson JPE, Domsch KH (1982b) Mineralization of nutrients from soil microbial biomass. *Soil Biol Biochem* 14:469-475
- Odum EP (1969) The strategy of ecosystem development. *Science* 164:262-270
- OECD, Organisation for Economic Cooperation and Development, Switzerland (2001) OECD Expert Meeting on Agri-Biodiversity Indicators : 5-8 November, 2001 in Zürich, Switzerland [online], zu finden in: <www1.oecd.org/agr/biodiversity/index.htm> [zitiert am 14.8.2003]
- Øvreås L, Torsvik V (1998) Microbial diversity and community structure in two different agricultural soil communities. *Microb Ecol* 36:303-315
- Pankhurst CE (1997) Biological Indicators of soil health : synthesis. In: Pankhurst CE, Doube BM, Gupta VVSR (eds) *Biological indicators of soil health*. New York : CAB International, pp 419-435
- Peterson G, Allen CR, Holling CS (1998) Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6-18
- Reynolds CS (2002) Ecological pattern and ecosystem theory. *Ecol Model* 158:181-200
- Risser PG (1995) Biodiversity and Ecosystem function. *Conserv Biol* 9:742-746
- Saggat S, Yeates GW, Shepherd TG (2001) Cultivation effects on soil biological properties, microfauna and organic matter dynamics in Eutric Gleysols and Gleyic Luvisol soils in New Zealand. *Soil & Tillage Res* 58:55-68
- Sparling GP (1997) Soil microbial biomass, activity and nutrient cycling as indicators of soil health. In: Pankhurst CE, Doube BM, Gupta VVSR (eds) *Biological indicators of soil health*. New York : CAB International, pp 97-119
- Spehn EM, Joshi J, Schmid B, Alpehi J, Körner C (2000) Plant diversity effects on soil heterotrophic activity in experimental grassland ecosystems. *Plant Soil* 224:217-230
- Staddon WJ, Duchesne LC, Trevors JT (1999) The role of microbial indicators of soil quality in ecological forest management. *Forestry Chronicle* 75:81-86
- Stephan A, Meyer AH, Schmid B (2000) Plant diversity affects culturable soil bacteria in experimental grassland communities. *J Ecol* 88:988-998
- Swift MJ, Heal OW, Anderson JM (1979). *Decomposition in terrestrial ecosystems*. Oxford : Blackwell
- Swift MJ (1984) Microbial diversity and decomposer niches. In: Klug MJ, Reddy CA (eds) *Current perspectives in microbial ecology*. Washington : American Society for Microbiology, pp 540-545
- Tebbe C, Anderson T-H, Larink O, Schrader S (2002) Biologische Wechselwirkungen : wie wichtig ist Vielfalt für die Funktion von Böden? *SchrR Bundesminist Ernähr Landwirtsch Forsten R A Angew Wiss* 494:160-165
- Tilman D, Wedin D, Knops J (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379:718
- Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E (1997) The influence of functional diversity and composition on ecosystem processes. *Science* 277:1300-1302
- Tilman D, Knops J, Wedin D, Reich P (2002) Plant diversity composition : effects on productivity and nutrient dynamics of experimental grasslands. In: Loreau M, Naeem S, Inchausti P (eds) *Biodiversity and ecosystem functioning : synthesis and perspectives*. Oxford : Oxford University Press, pp 21-35
- Turco RF, Kennedy AC, Jawson MD (1994). Microbial indicators of soil quality : defining soil quality for a sustainable environment. *Soil Sci Soc Am Spec Publ* 35:73-90
- UNEP, United Nations Conference on the Human Environment (1972) Stockholm

- Van der Heijden MGA, Boller T, Wiemken A, Sanders IR (1998a) Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. *Ecology* 79:2082-2091
- Van der Heijden MGA, Klironomos JN, Ursic M, Moutoglou P, Streitwolf-Engel R, Boller T, Wiemken A, Sanders IR (1998b) Mycorrhizal fungal diversity determines plant biodiversity and productivity. *Nature* 396:69-72
- Vandermeer J, van Noordwijk M, Anderson J, Chin Ong, Perfecto I (1998) Global change and multi-species agroecosystems : concepts and issues. *Agric Ecosyst Environ* 67:1-22
- VDLUFA (1998) Kriterien umweltverträglicher Landbewirtschaftung. Darmstadt: VDLUFA
- Waid JS (1999) Does soil biodiversity depend upon metabiotic activity and influences? *App Soil Ecol* 13:151-158
- Walker BH (1992) Biodiversity and ecological redundancy. *Conserv Biol* 6:18-23
- Wall DH, Moore JC (1999) Interactions underground : soil biodiversity, mutualism, and ecosystem processes. *Bioscience* 49:109-118
- Wardle DA, Giller KE (1996) The quest for a contemporary ecological dimension to soil biology. *Soil Biol Biochem* 28:1549-1554
- Wardle DA, Giller KE, Barker GM (1999a) The regulation and functional significance of soil biodiversity in agroecosystems. In: Wood D, Lenné JM (eds) *Agrobiodiversity : characterization, utilization and management*. New York : CAB International, pp 87-121
- Wardle DA, van der Putten WH (2002) Biodiversity, ecosystem functioning and above-ground-below-ground linkages. In: Loreau M, Naeem S, Inchausti P (eds) *Biodiversity and ecosystem functioning : synthesis and perspectives*. Oxford : Oxford University Press, pp 155-168
- Wardle DA, Yeates GW, Nicholson KS, Bonner KI, Watson RN (1999b) Response of soil microbial biomass dynamics, activity and plant litter decomposition to agricultural intensification over a seven-year period. *Soil Biol Biochem* 31:1707-1720
- Weigel HJ (1997) Globale Umweltänderungen und biologische Vielfalt. SchrR Bundesminist Ernähr Landwirtsch Forsten R A *Angew Wiss* 465:185-202
- White DC (1983) Analysis of microorganisms in terms of quantity and activity in natural environments. In: Slater JH, Whittenbury R, Wimpenny, JWT (eds) *Microbes and their natural environments : thirty-fourth symposium of the Society for General Microbiology held at the University of Warwick, April 1983*. Cambridge : Cambridge Univ. Press, pp 37-66
- White DC, Macnaughton SJ (1997) Chemical and molecular approaches for rapid assessment of the biological status of soils. In: Pankhurst CE, Doube BM, Gupta VVSR (eds) *Biological indicators of soil health*. New York : CAB International, pp 371-396
- Wolters V (ed) (1997) Functional implications of biodiversity in soil. *Ecosystem Res Rep* 24, EUR 17659 EN
- Wolters V, Silver WL, Bignell DE, Coleman DC, Lavelle P, van Der Putten WH, De Ruiter P, Rusek J, Wall DH, Wardle DA, Brussard L, Dangerfield JM, Brown VK, Giller KE, Hopper DU, Sala O, Tiedje J, Van Veen JA (2000) Effects of global changes on above- and below-ground biodiversity in terrestrial ecosystems : implications for ecosystem functioning. *Bioscience* 50:1089-1098
- Yan F, McBratney AB, Copeland L (2000) Functional substrate biodiversity of cultivated and uncultivated A horizons of vertisols in NW New South Wales. *Geoderma* 96:321-343
- Zak JC, Visser S (1996) An appraisal of soil fungal biodiversity : the crossroads between taxonomic and functional biodiversity. *Biodiversity Conservation* 5:169-183