Microbial Community Structure and Diversity as Indicators for Evaluating Soil Quality

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Abstract The living soil system is of primary importance in sustainable agricultural production. Soil quality is considered as an integrative indicator of environmental quality, food security and economic viability. Therefore, soil itself serves as a potential indicator for monitoring sustainable land management. As part of the soil quality concept, a healthy soil supports high levels of biological diversity, activity, internal nutrient cycling and resilience to disturbance. The use of microbial community structure and diversity as an indicator to monitor soil quality is challenging due to little understanding of the relationship between community structure and soil function. This review addresses two critical questions regarding soil quality: (1) which soil microbial properties, particularly diversity and community structure, most effectively characterize soil quality and can be used as indicators, and (2) how can soil quality assessed by such indicators be improved or maintained?

We provide an overview of available techniques to characterize microbial community structure and diversity, and furnish information pertaining to strategies that can improve microbial diversity, including mycorrhizae, in relation to soil quality by adopting suitable agricultural practices to sustain soil and crop productivity. These techniques include those for structural profiling, i.e. fatty acid methyl ester analysis, genetic profiling, i.e. PCR-DGGE, SSCP, T-RFLP, functional profiling,

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i.e. catabolic profiling, diversity of enzyme activity, and to profile both structural and functional communities comprehensively, i.e. gene chip. We identify the importance of minimum data sets (MDS) of microbial indicators, such that they must be (i) compatible with basic ecosystem processes in soil as well as physical or chemical indicators of soil health, (ii) sensitive to management in acceptable time frames, (iii) easy to assess or measure, (iv) composed of robust methodology with standardized sampling techniques, (v) cost-effective, and (vi) relevant to human goals, food security, agricultural production, sustainability and economic efficiency. We focus on specific agricultural strategies such as tillage, crop rotations, organic amendments and microbial inoculation to improve soil quality by managing microbial communities and diversity. Overall, we provide techniques to assess microbial communities and diversity, and their management through agricultural practices to improve quality of soil.

Keywords Soil quality • Microbial community • Diversity • Gene chip • AMF • MDS • Tillage • Crop rotation • Inoculation

1 Introduction

Agriculture today is often characterized by a high degree of intensity, particularly in developed countries. Heavy machines for tillage, planting and harvesting are repeatedly used during the growing season and crops are often given high amounts of fertilizers and pesticides to maximize yields. One outcome of this intensification during the last century was the Green Revolution, which increased food production and reduced hunger for millions of people by increasing both biological input such as high yielding cultivars as well as non-biological inputs like agrochemicals, fertilizers and irrigation. This approach has encouraged many developing countries of Asian and African continents to grow crops using monoculture and irrigation to ensure a maximum economic status. However, many rural communities in the tropics and sub-tropics are still persistently affected by insufficient household food production (Dalgaard et al. 2003).

The Food and Agricultural Organisation (FAO) defines food security as “when all people, at all times, have physical and economic access to sufficient, safe nutritious food to meet their dietary needs and food preference for an active and healthy life”. Technologies such as irrigation, mechanization and improved crop varieties have changed the socio-economic status of some people, but food insecurity still persists amongst the poorest and most vulnerable people. Therefore, food security is a major concern around the globe, because more than a billion people are still undernourished and have no access to food (Stocking 2003; Reynolds and Borlaug 2006).

Sustainable food security is ultimately dependent on the availability and condition of natural resources including soils, which are gradually deteriorating and increasing the pressure on food availability to human beings. Some agricultural soils can endure intensive cultivation practices, but many gradually show a lower ability to support

high productivity due to impaired soil quality. In recent years, there has been an increasing awareness of soil quality to ensure a greater sustainability of agricultural soils. This review addresses two critical questions regarding soil quality: (1) which soil microbial properties, in particular diversity and community structure, most effectively characterize soil quality and should be used as indicators, and (2) how can soil quality assessed by such indicators be improved or maintained? In particular, we provide an overview of techniques available to characterize microbial community structure and diversity for evaluating soil quality, and furnish information pertaining to strategies that can improve microbial diversity in relation to soil quality by adopting suitable agricultural practices to sustain soil and crop productivity.

2 The Concept of Soil Quality

In 1971, Alexander proposed for the first time development of soil quality criteria in the context of agriculture's role in environmental improvement. The soil quality concept per se was introduced by Warkentin and Fletcher (1997) as an approach to facilitate better land use planning for multiple functions. Their concept of soil quality was based on four criteria, upon which future concepts of soil quality were developed. These criteria were that (1) soil resources were constantly being evaluated for an ever-increasing range of uses, (2) several different stakeholder groups were concerned about the state of soil resources, (3) priorities and demand of society were changing, and (4) soil-resource and land-use decisions were made in a human and institutional context. In a broad sense, the concept of soil quality was not introduced until the mid-1980s, wherein emphasis was mainly given to soil resource management, particularly in controlling soil erosion and minimizing its effects on crop productivity (Pierce et al. 1984). Later, soil management gradually shifted from minimizing soil erosion to broader issues like sustainable agriculture, environmental health and prevention of soil degradation (Karlen et al. 2003a). In the 1990s, the pace in soil quality research was further accelerated by the recommendation of the U.S. National Research Council's (NRC) Board on Agriculture that "we conserve and enhance soil quality as a fundamental step toward environmental improvement" and that the concept of soil quality be in principle a guide to agricultural policies and practices (NRC 1993). Thereafter, many researchers contributed to developing a soil quality concept in the publications entitled, "Defining Soil Quality for Sustainable Environment" (Doran et al. 1994) and "Methods for Assessing Soil Quality" (Doran and Jones 1996).

Soil quality has been defined in several ways including 'fitness for use' and dependent upon the extent to which a soil fulfills its destined role (Larson and Pierce 1994; Singer and Edwig 2000). In a broad ecological sense, soil quality has been defined as the capacity of a soil to function within ecosystem boundaries to sustain plant-animal productivity, maintain or enhance water and air quality, and support human health and habitation (Karlen et al. 1997). Doran and Safely (1997) further defined soil quality by considering the continuous and dynamic nature of the soil as "the continued capacity of soil to function as a vital living system, within

ecosystem and land-use-boundaries, to sustain biological productivity, promote the quality of air and water and maintain plant, animal and human health". More recently, a healthy soil as part of the soil quality concept is defined as a stable soil system with high levels of biological diversity and activity, internal nutrient cycling and resilience to disturbance (van Bruggen et al. 2006). Overall, soil quality is considered as an integrative indicator of environmental quality, food security and economic viability (Herrick 2000) and therefore, it would serve as a good indicator for monitoring sustainable land management.

The concept developed in this review differs from traditional technical approaches that focus solely on productivity. Instead, soil quality is examined as a holistic concept, recognizing soil as a part of a dynamic and diverse production system with biological, chemical and physical attributes that relate to the demands of human society (Swift 1999; Sanchez et al. 2003). Society, in turn, actively adapts soil to its needs, mining it of its nutrients on demand and replenishing these nutrients in times of excess.

3 Indicators of Soil Quality

Assessment of soil quality is a major challenge because it is highly dependent on management of soil through resources available in a given agroecosystem and the agroclimatic conditions (Karlen et al. 2003b). Common approaches used for assessing the soil quality are either qualitative or quantitative. Qualitative indicators are often sensory descriptors e.g. appearance, smell, feel and taste recorded through direct observations usually made by the growers' (Garlynd et al. 1994; Dang 2007). Other observations include soil colour, yield response, frequency of ploughing or hoeing, and visual documentation of plant growth, selected weed species, and earthworm casts. The use of indigenous local knowledge and experience of growers provides a simple approach to characterize the status of and to diagnose any change in soil quality (Roming et al. 1995; Barrios et al. 2006).

Quantitative assessments of soil quality involve more sophisticated analytical approaches (Harris and Bezdicek 1994). Generally, soil quality is assessed by the combination of the physical, chemical and biological properties acting as indicators (He et al. 2003), and a large number of different physical, chemical and biological properties of soil are being employed as quantitative indicators to define soil quality (Roming et al. 1995; Dang 2007). Typical soil physical indicators include texture, bulk density and infiltration, water holding capacity and retention characteristics, porosity, aggregate stability and soil depth. Organic carbon, pH, electrical conductivity, cation exchange capacity, extractable N, P, K, S are important chemical indicators, and biological indicators include quantity, activity, and diversity of soil fauna and flora and soil enzymes. Several bio-indicators of soil quality have been developed (Trasar-Cepeda et al. 2000; Nielsen and Winding 2002; Anderson 2003). A number of soil biological properties respond to changes in agricultural practices, showing potential use as indicators of soil quality. Other biological

indicators include organic matter content; soil macrofauna like earthworms, springtails, collembulas and nematodes; and the overall litter decomposition ability of living organisms (Pfiffner and Mäder 1997; Wardle et al. 1999). Among biological parameters, soil microorganisms and their functions (i.e. enzyme activities such as FDA, phosphatase, amidohydrolase, nitrogen mineralization, nitrification, etc.) are also widely recognized as integral component of soil quality because of their crucial involvement in ecosystem functioning and their capability to respond quickly to environmental changes (Aseri and Tarafdar 2006; Sharma et al. 2005).

In comparison to the rapid shifts in biochemical and biological properties that occur after soil disturbance (Le Roux et al. 2008), changes in physical properties may occur relatively less quickly. Among the biological properties, soil microorganisms are very sensitive to external perturbations and can act as a sensor for monitoring soil response, and more generally soil quality. Soil microbial biomass, soil enzymes and basal soil respiration are among the most important biological parameters and have proven to be powerful tools in monitoring soil quality (Karlen et al. 2006; Nogueira et al. 2006), although some authors have reported that soils experiencing different treatments can have similar microbial biomass whereas their functioning can markedly differ (Patra et al. 2005). Other microbial indicators of soil status encompass the diversity and structure of microbial communities. Many methods for analyzing microbial diversity have been developed in recent years and utilized as indicators for assessing soil quality in congruence with established indicators. Numerous studies have reported the beneficial impacts of conservation tillage management, organic amendments, crop rotation and application of microbial inoculants on enzyme activities (Naseby and Lynch 1997; Acosta-Martinez et al. 2003; Melero et al. 2006), microbial biomass (Liebeg et al. 2004; Monokrousos et al. 2006; Franchini et al. 2007; Saini et al. 2004) and microbial community structure and diversity (Sun et al. 2004; Roesti et al. 2006; Mathimaran et al. 2007; Acosta-Martinez et al. 2007; Govaerts et al. 2008).

4 Rationales for Using Microorganisms as Soil Quality Indicators

Microorganisms are a component of the 'biological engine of the earth' and provide an integrated measure of soil quality, an aspect that cannot always be obtained with physical and chemical measures and/or analysis of higher organisms. Microorganisms are driving many fundamental nutrient cycling processes, soil structural dynamics, degradation of pollutants, various other services (Bloem et al. 1994) and respond quickly to natural perturbations and environmental stress due to their short generation time and their intimate relation with their surroundings, attributed to their higher surface to volume ratio. This allows microbial analyses to discriminate soil quality status, and shifts in microbial population and activity could be used as an indicator of changes in soil quality (Kennedy and Smith 1995; Pankhurst et al. 1995).

Microbial indicators have been defined as "properties of the environment or impacts that can be interpreted beyond the information that the measured or observed [indicator] represents itself" (Nielsen and Winding 2002). Stenberg (1999) listed five different levels at which microorganisms can be studied. These are: (1) as individuals; (2) at population levels (Hill et al. 2000); (3) at the functional group level, including autotrophic nitrification (Stenberg et al. 1998), arbuscular mycorrhiza (Kahiluoto et al. 2001) and specific soil enzymes; (4) as the whole microbial community studied using genetic or physiological diversity or quantitative methods to enumerate the total community including microbial biomass, basal respiration rate, nitrogen mineralization, denitrification and general soil enzymes (Griffiths et al. 2001) and (5) at the ecosystem level which can describe data from all the other levels. It is not possible to use all ecosystems or soil attributes as indicators of soil quality (Karlen and Andrews 2000) and thus, there is a need to select specific indicators having high discriminating potential and high value to account for actual soil quality status of agricultural systems: an indicator would not be so useful if it is very sensitive to disturbances. In particular, the search for indicator organisms associated with healthy or deteriorated soil requires a unified concept of soil quality. In this context, microbial indicators can be divided into general, or universal, and specific indicators (Nielsen and Winding 2002). Universal indicators may include biodiversity, stability and self-recovery from stress (Parr et al. 2003). *Rhizobium*, mycorrhizae and nitrifying bacteria could be used as specific indicators because of their high sensitivity to agrochemicals (Domsch et al. 1983) or management regimes (Le Roux et al. 2008), and clearly defined roles among soil functions. Specific indicators are dependent on the geographic zone, climate, soil type and land use history.

Although the relationship between soil quality and microbial diversity is not completely understood, a medium to high diversity in agricultural soil is generally considered to indicate a 'good' soil quality (Winding 2004). This statement is based on the assumption that there is a functional redundancy in a healthy soil, so that soil ecosystem will recover from a stress factor that eliminates part of the microbial community (Yin et al. 2000) (Fig. 1) In addition, the active microbial pool is a reserve pool of quiescent microorganisms, which can respond to foreign substances in the soil (Zvyaginstsev et al. 1984). This diverse microbial pool maintains soil homeostasis. The larger the microbial diversity and functional redundancy, the quicker the ecosystem can return to stable initial conditions after exposure to stress or disturbance. This concept is highly debated. Indeed, several removal experiments (in which microbial taxa are successively removed from an innate community through a stressing agent or dilution of the original community) have shown that the functioning and stability of soil microbial communities can be maintained following strong erosion of microbial diversity (Griffiths 2000; Wertz et al. 2006; 2007). Furthermore, although some observational studies show some links between soil microbial community structure and functioning (Patra et al. 2006), the shifts in functioning often appear to be linked to key species rather than due to richness.

Besides these controversies, many authors argue that measurements of the structure and activities of specific microbial communities contributing to soil processes has the potential to provide rapid and sensitive means of characterizing changes to

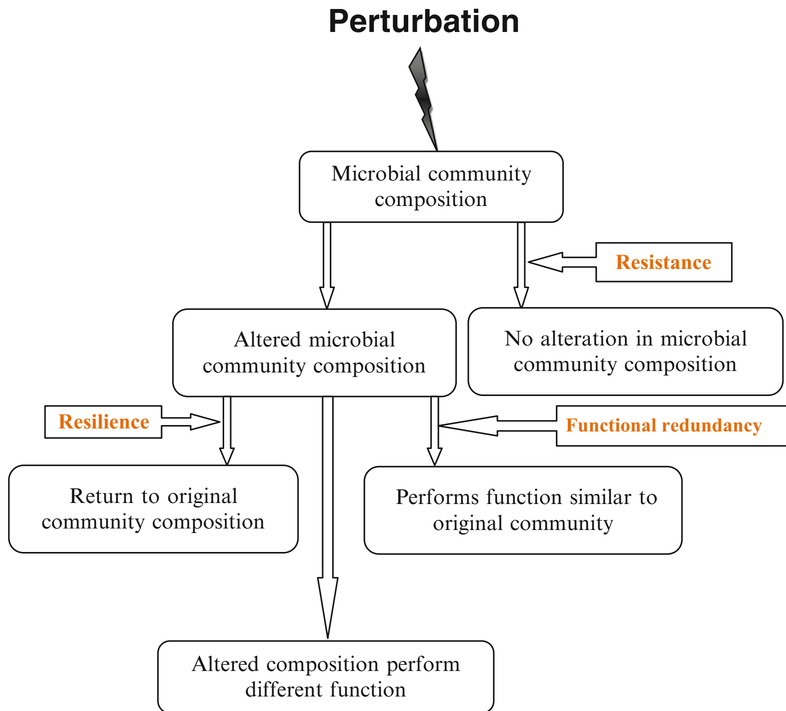

Fig. 1 Schematic representation of impact of perturbation on changes in microbial community composition and function (Modified from Allison and Martiny 2008)

soil quality (Waldrop et al. 2000; Bending et al. 2004; Enwall et al. 2005; Bressan et al. 2008). In particular, the size and diversity of specific functional microbial groups such as AM fungi and nitrifying bacterial communities have the potential to characterize the effects of management on the sustainability of soil (Chang et al. 2001). Additionally, a number of features viz. fast growth rate, high degree of physiological flexibility and rapid evolution (mutation) of microorganisms could make microbial communities more resilient to the new environment (Fig. 1) (Allison and Martiny 2008).

5 Evaluation of Microbial Community Structure and Diversity: Tools, Their Use and Misuse

Microbial diversity viz. structural and functional diversity in soil is increasingly assessed for measurement of soil health (Visser and Parkinson 1992). In the following sections, different methods for evaluating microbial community structure and diversity will be described in detail (Fig. 2).

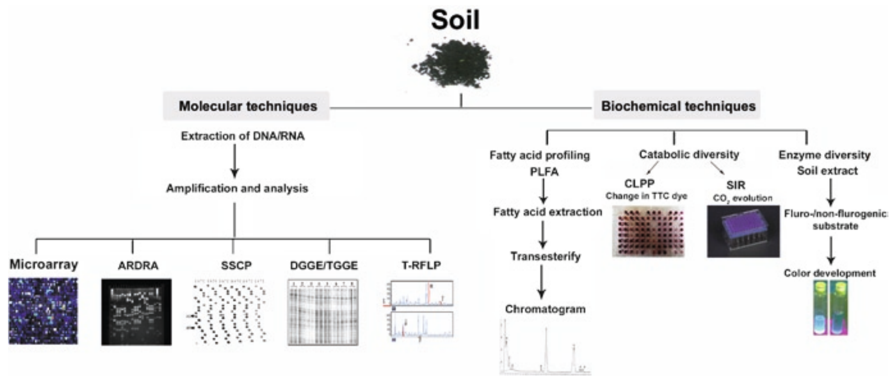

Fig. 2 An overview of techniques used for soil microbial community structure and diversity

5.1 Structural Profiling Technique

Structural diversity is defined as the number of parts or elements within a system, indicated by such measures as the number of species, genes, communities or ecosystems (Avidano et al. 2005). Several indices such as species richness and evenness are used to describe the structural diversity of a community (Ovreas 2000). However, these indices cannot be used for soil microbes as easily as for macroorganisms. Indeed, with the rise of molecular tools in microbial ecology, it became evident that we have described only a very small portion of the diversity in the microbial world. Most of this unexplored microbial diversity seems to be hiding in the high amount of yet uncultured bacteria. New direct methods independent of culturing and based on the genotype and phenotype of microbes allow a deeper understanding of the composition of microbial communities in a soil ecosystem (Amann et al. 1995). Based on molecular studies, it could be estimated that 1 g of soil consists of more than 10^9 bacteria belonging to about 10,000 different microbial species (Ovreas and Torsvik 1998) or even much more (Gans et al. 2005). This huge level of diversity makes it difficult to employ the microbial community structure as an indicator of soil quality. A widely observed result is that the structural diversity of a bacterial community is often sensitive to environmental changes and exhibits a shift in its composition (Kandeler et al. 1999; Saison et al. 2006). Ovreas and Torsvik (1998) compared the influence of crop rotation and organic farming on microbial diversity and community structure and found higher values for proxies of diversity in soils under organic farming management as compared to conventional practices. In addition to shifts in community structure, there have been reports that indices of bacterial diversity suggested a reduced diversity in soils contaminated with phenyl-urea herbicides, fumigants etc. (El Fantroussi et al. 1999; Yang et al. 2000; Ibekwe et al. 2001) Although, these management practices certainly induce change in microbial community, the extent of soil function loss in relation to reduction in microbial diversity is not known. With regard to soil quality assessment, it is also important to note that in addition to examining microbiological effects of

various management practices (e.g. herbicides, fungicides, tillage) these changes must also be weighted against chemical- and physical-indicators changes that may also occur in response to these practices.

5.1.1 Fatty Acid Methyl Ester (FAME) Analysis

Phospholipid fatty acids (PLFAs) are a potentially useful biomarker molecule that is being used to elucidate structure of microbial community in soil because of their presence in all living cells and rapid degradation upon cell death (White et al. 1979; Pinkart et al. 2002). In microorganisms, PLFAs are found exclusively in cell membranes and not in other parts of the cell such as storage products. Fatty acid methyl ester (FAME) analysis, which directly extracts PLFAs from soil, is a biochemical method that does not rely on culturing of microorganisms and provides information on the microbial community composition based on groupings of the fatty acids (Ibekwe and Kennedy 1998; Drenovsky et al. 2004; Drenovsky et al. 2008). PLFAs compose a relatively constant proportion of the cell biomass and signature fatty acids exist that can differentiate major taxonomic groups within a community. Individual PLFAs or signature fatty acids are specific for subgroups of microorganisms, e.g. gram-negative or gram-positive bacteria, methanotrophic bacteria, fungi, mycorrhiza, and actinomycetes (Zelles 1999). It is possible to quantify different groups of microorganisms by this method, and PLFA profiles can be related to microbial community structure using multivariate analysis (e.g., canonical correspondence analysis, principal components analysis). Therefore, a change in the fatty acid profile would represent a change in the microbial populations. It has been used in the study of microbial community composition and population changes due to chemical contaminants (Siciliano and Germida 1998; Kelly et al. 1999), land use history (Myers et al. 2001; Steenwerth et al. 2003), agricultural practices (Bossio et al. 1998), and rhizosphere effects (Ibekwe and Kennedy 1998). Based on phospholipid fatty acid profiles, Bossio et al. (1998) detected changes in microbial communities consistent with different farming practices. When these researchers calculated the Shannon diversity index based on PLFA relative abundance, no difference could be detected. This could be because of a difference in the community structure but not in diversity (Bossio et al. 1998). These studies clearly demonstrated the utility of this method in determining gross community changes associated with soil management practices. This method has been recommended for soil quality monitoring programme in Scotland and Northern Ireland (Chapman et al. 2000).

5.2 Genetic Profiling Techniques

The genetic diversity of soil microorganisms is an indicator that provides the basis for all actual and potential functions. Techniques for determining genetic diversity include several molecular methods, a few of which have been suggested to be

implemented for Dutch soil monitoring programme (Bloem and Breure 2003). Taxonomic diversity of microorganisms at the genetic level is most commonly studied by determining the DNA gene coding for ribosomal RNA. The 16S rRNA genes are used for phylogenetic affiliation of Eubacteria and Archaea, while 18S rRNA genes are used for fungi. The conserved regions within the rRNA genes have facilitated the design of primers targeting the majority of members of defined groups of bacteria or fungi. Several comparable molecular methods based on DNA analyses using polymerase chain reaction (PCR) followed by an analysis of the diversity of PCR products through denaturing gradient gel electrophoresis (PCR-DGGE), temperature gradient gel electrophoresis (PCR-TGGE), terminal restriction fragment length polymorphism (T-RFLP), single strand conformation polymorphism (SSCP), restriction fragment length polymorphism (RFPL) and amplified ribosomal DNA restriction analysis (ARDRA) targeting 16S rDNA gene have been employed for community analysis.

5.2.1 Polymerase Chain Reaction-Denaturing Gradient Gel Electrophoresis (PCR-DGGE) and PCR-Temperature Gradient Gel Electrophoresis (PCR-TGGE)

The PCR-DGGE (Muyzer et al. 1993) and PCR-TGGE (Heuer and Smalla 1997) are widely used methods for estimation of microbial community fingerprining. They are based on variation in base composition and secondary structure of fragments of the 16S rDNA molecule. A fragment of 16S rDNA gene of known size can be amplified by PCR, with primers mainly targeting all eubacteria or selected subgroups (Table 1). Following PCR, denaturing gradient gel electrophoresis separates the products. In DGGE, the gel itself contains a chemical-denaturing gradient, making

Table 1 Gene specific primers used in DGGE for the amplification of 16S rRNA gene of bacteria or archaea

Primer name	Sequence (5′–3′)	16S rDNA target (base number)[a]
PRBA338F	59[b]AC TCC TAC GGG AGG CAG CAG 39	Bacteria V3 region (338–358)
PRUN518R	59ATT ACC GCG GCT GCT GG 39	Universal V3 region (534–518)
PRBA968F	59[b]AA CGC GAA GAA CCT TAC 39	Bacteria V6 region (968–983)
PRBA1406R	59ACG GGC GGT GTG TAC 39	Bacteria V9 region (1406–1392)
PRA46F	59C/TTA AGC CAT GCG/A AGT 39	Archaea (46–60)
PREA1100R	59T/CGG GTC TCG CTC GTT G/ACC 39	Archaea (1117–1100)
PARCH340F	59[b]CC TAC GGG GC/TG CAG/C CAG 39	Archaea V3 region (340–358)
PARCH519R	59TTA CCG CGG CG/TG CTG 39	Archaea V3 region (534–519)

[a]Bases numbered relative to *E. coli* 16S rRNA sequence
[b]GC clamp added to the 59 end of the primer, 59CGC CCG CCG CGC GCG GCG GGC GGG GCG GGG GCA CGG GGG G 39
Nakatsu et al. (2000)

the fragments denature along the gradient according to their base composition. In PCR-TGGE, a temperature gradient is created across the gel, resulting in the same type of denaturation. The number and position of the fragments reflect the dominant genus in the community. Similar to other profiling methods, PCR-DGGE/TGGE detects only a limited part of the microbial diversity in a community, due to generally high diversity. Soil communities may easily contain more than 10,000 different species per 100 g of soil (Torsvik et al. 1998), while the resolution of more than 20–50 bands on a gel is difficult. To show up as a visible band on the gel, a species has to constitute approximately 1% of the entire population (Casamayor et al. 2000). Sequencing and identification of visible bands on the gel following PCR-DGGE may further improve the resolution (Casamayor et al. 2000). DGGE/TGGE has been used to assess the diversity of bacteria and fungi communities in rhizosphere (Smalla et al. 2001) caused by changes in nutrient applications (Iwamoto et al. 2000). It has also been used for forest soils (Marschner and Timonen 2005), grasslands (Ritz et al. 2004), and to evaluate agricultural management effects of manure and fertilizers (Sun et al. 2004), and anthropogenic chemicals (MacNaughton et al. 1999; Whiteley and Bailey 2000). Continuous cereal crops had similar rhizoplane communities while communities from cereal-legumes rotation showed greater variability in West African soils (Alvey et al. 2003). PCR-DGGE of bacterial 16S rRNA genes has recently been implemented in the Dutch Soil Monitoring Programme (Bloem and Breure 2003). Results from the first round visit of 60 farms showed that the number of DNA bands was dependent on soil type and also, to a lesser extent, land use. Such changes in PCR and all other indicators of microbial diversity confirm the responsiveness of the soil microbial community to soil and crop management practices, but a critical unknown is what constitutes a "good community" and specifically how does or doesn't this affect soil quality. This is a critical question which can only be answered with investment in basic soil science research not only in India but throughout the world.

5.2.2 Single Strand Conformation Polymorphism (SSCP)

Like DGGE/TGGE, the SSCP technique was originally developed to detect point mutations in DNA (Orita et al. 1989). When DNA is denatured into single strands, each strand folds up into a configuration based not only on size but also on sequence. This feature can separate single stranded DNA on an agarose gel according to folding and secondary structure (Lee et al. 1996). Reannealing of the DNA during electrophoresis remains a potential problem of the method. Schwieger and Tebbe (1998) further refined the method by removing one of the two DNA strands before electrophoresis. Each band in the agarose gel should then represent a single species; however, multiple sequences within a single band have been reported (Schmalenberger and Tebbe 2003). SSCP has been used to measure succession of bacterial communities (Peters et al. 2000), rhizosphere communities (Schwieger and Tebbe 1998; Schmalenberger et al. 2001), bacterial population changes in an anaerobic bioreactor (Zumstein et al. 2000) and AMF species in roots (Simon et al. 1993; Kjoller and

Rosendahl 2000). To date, SSCP alone has been applied in soil quality assessment but it may be optimized and then integrated with other well established tools and techniques of soil quality assessment.

5.2.3 Restriction Fragment Length Polymorphism (RFLP)

RFLP, also known as amplified ribosomal DNA restriction analysis (ARDRA) is another tool used to study microbial diversity that relies on DNA polymorphism. In a study by Liu et al. (1997), PCR amplified rDNA is digested with a 4-base pair cutting restriction enzyme. Different fragment lengths are detected using agarose or non-denaturing polyacrylamide gel electrophoresis in the case of community analysis (Liu et al. 1997; Tiedje et al. 1999). RFLP banding patterns can be used to screen clones (Pace 1996) or to measure bacterial community structure (Massol-Deya et al. 1995). This method is useful for detecting structural changes in bacterial communities in soil inoculated with biocontrol agents (Bakker et al. 2002).

5.2.4 Terminal Restriction Fragment Length Polymorphism (T-RFLP)

The T-RFLP, a polymerase-chain reaction-fingerprinting method, is an improved alternative method for examining comparative microbial community analysis (Liu et al. 1997; Marsh 1999). T-RFLP is a technique that addresses some of the limitations of RFLP (Tiedje et al. 1999). The method can be used to analyse communities of bacteria, archaea, fungi, other phylogenetic groups or subgroups, as well as functional genes (Thies 2007). For 16S rRNA genes, a number of primer sequences have been published that are complementary to highly conserved sequences of the bacteria or the archaea or are conserved among specific subgroups within these domains such as alpha- or beta-proteobacteria (Table 2). It follows the same principle

Table 2 Primers used commonly to amplify short-subunit rRNA genes from microbial community DNA extracts

Primer name	Sequence (5′–3′)	Specificity
1511R	YGCAGGTTCACCTAC	Universal
1492R	ACCTTGTTACGACTT	Universal
27F	AGAGTTTGATCMTGGCTCAG	Bacteria 16S
63F	CAGGCCTAAYACATGCAAGTC	Bacteria 16S
1387R	GGGCGGWGTGTACAAGGC	Bacteria 16S
21F	TTCCGGTTGATCCYGCCGGA	Archaea 16S
25F	CTGGTTGATCCTGCCAG	Eukarya 18S
BLS342F	CAGCAGTAGGGAATCTTC	Bacilli
BETA680F	CRCGTGTAGCAGTGA	Beta-proteobacteria
Pln930R	CTCCACCGCTTGTGTGA	Planctomycetes
Act1159R	TCCGAGTTRACCCCGGC	Actinomycetes
Bas1105F	CCGTTGTAGTCTTAACAG	Basidiomycota

Theis (2007)

as RFLP except that one PCR primer is labeled with a fluorescent dye, such as TET (4,7,2′,7′-tetrachloro-6-carboxyfluorescein) or 6-FAM (phosphoramidite fluorochrome 5-carboxyfluorescein). This allows detection of only the labeled terminal restriction fragment (Liu et al. 1997). The primers are labeled with a fluorescent tag at the terminus resulting in labeled PCR-products. The products are cut with several restriction enzymes, one at a time, which result in labeled fragments that can be separated according to their size on agarose gels. As the PCR products are labeled at the terminus, only restriction enzyme fragments containing either of the terminal ends of the PCR product will be detected. The digested PCR products are subsequently loaded on a sequencer. The output includes fragment size and quantity. Marsh (2005) provided detailed protocols for performing T-RFLP analysis.

T-RFLP has been used for bacterial community analysis in response to spatial and temporal changes (Acinas et al. 1997; Lukow et al. 2000; Mummey and Stahl 2003), organic amendments (Wang et al. 2006), microbial inoculants (Conn and Franco 2004), tillage (Buckley and Schmidt 2001), inorganic fertilization (Mohanty et al. 2006), changes in farming systems (Hartmann et al. 2006), in different soil types (Singh et al. 2006) and cultivation practices (Buckley and Schmidt 2001). Lasting changes in the composition of soil bacterial population due to soil solarization (Culman et al. 2006), herbicides (Moran et al. 2006), pesticide use (Rousseaux et al. 2003) and soil pollutants (Jung et al. 2005) were readily detected by T-RFLP analysis. Recently in Switzerland, Hartmann and Widmer (2006) emphasized that changes in microbial community structure but not soil bacterial diversity analyzed through T-RFLP offer a better understanding of the impact on soil quality in agriculturally managed systems (biodynamic, bioorganic, conventional and conventional with inorganic fertilizers) thus making it highly useful tool for soil monitoring after its optimization.

5.3 Functional Profiling Techniques

The functional diversity of microbial communities includes the range and relative expression of activities involved in functions namely decomposition of organic carbon, nutrient transformation, plant growth promotion/suppression and soil physical processes as influenced by microorganisms (Giller et al. 1997). The functional diversity of microbial communities has been found to be very sensitive to environmental changes (Kandeler et al. 1999). Among the functional diversity indicators, the carbon utilization pattern and the measurement of enzymatic activity profiles expressed by the whole bacterial community have been suggested as useful tools to evaluate the soils (Nielsen and Winding 2002). The metabolic profile, obtained by a Biolog assay and MicroResp, provides a physiological fingerprinting of the potential functions of the microbial community (Garland and Mills 1991; Campbell et al. 2003). Since enzymatic activities in the soil are mainly of bacterial and fungal origin, the characterization of soil enzyme patterns can improve our knowledge on microflora activity, soil productivity and the impact of pollutants (Pankhurst et al. 1995).

5.3.1 Catabolic Profiling-Based on Substrate Utilization

The diversity in decomposition functions performed by heterotrophic microorganisms represents one of the important components of microbial functional diversity. A simple approach to measure functional diversity is to examine the number of different C-substrates utilized by the microbial community. The two most common methods of measuring substrate utilization patterns are the community-level physiological profiling by Biolog plates methods (Garland and Mills 1991) and in situ substrate-induced respiration (SIR) (Degens and Harris 1997; Campbell et al. 2003).

Community-Level Physiological Profiling (CLPP)

Garland and Mills (1991) developed a technique using a 96-well Biolog microtitre plate utilizing sole carbon source to assess physiological profiles of bacterial communities to reflect their functional diversity. This culture-dependent technique is widely used for analyzing soil microbial communities. Gram-negative (GN) and gram-positive (GP) plates containing 95 different carbon sources and one control well per plate without a substrate, growth medium and redox dye tetrazolium salt are available from the Biolog (Hayward, CA, USA, www.biolog.com). Subsequently, Biolog introduced an Eco-plate (Insam 1997; Choi and Dobbs 1999) containing three replicates of 31 different environmentally relevant carbon sources and one control well per replicate. The tetrazolium salt changes colour as bacteria metabolize the substrate. Since many fungal species are not capable of reducing the tetrazolium salt (Praveen-Kumar and Tarafdar 2003), Biolog developed fungal specific plates SFN2 and SFP2, having the same substrates as GN and GP plates but without tetrazolium salt (Classen et al. 2003). The important considerations in the use of this method for community analysis are: (1) density of initial inoculum must be standardized, (2) functional diversity is based on the assumption that color development in each well is solely a function of the proportion of organisms present in the sample able to utilize a particular substrate, and (3) substrates found in commercially available Biolog plates are not necessarily ecologically relevant and most likely do not reflect the diversity of substrates found in the environment (Hill et al. 2000).

The CLPP is used extensively in analyzing microbial communities because it is sensitive, reproducible and has the power to distinguish between tillage systems (Govaerts et al. 2007a), contaminated soil sites (Boivin et al. 2002), rhizosphere (Grayston et al. 1998, 2004; Soderberg et al. 2004), inoculation of microorganisms (Bej et al. 1991) and, soil management practices (Schouten et al. 2000; Mäder et al. 2002). This method is currently implemented in the Dutch Soil Monitoring Programme where the CLPP of microbial communities is determined in the Biolog ECO plate to discriminate between different types of soil and management practices (Schouten et al. 2000, 2002). The assay is also recommended in the soil-monitoring programme of Scotland and Northern Ireland (Chapman et al. 2000). For the monitoring of soils, commercial plates must contain a uniform composition and concentration, and they should be available in the market.

Substrate-Induced Respiration

Catabolic conversion can be used to assess catabolic diversity in soil microbial communities utilizing many simple organic substances through the Substrate-Induced Respiration (SIR) test. Degens and Harris (1997) developed this concept using multiple SIR tests for the measurement of patterns of in situ catabolic potential of microbial communities and does not require extraction and culturing of microorganism while in Biolog system this problem exists. They tested 83 simple sugars, carboxylic acids, amino acids, polymers, amines and amides, and subsequently identified 36 substrates providing the greatest difference in SIR responses among five different soils of ecological importance. It is expected that only a limited number of species will contribute to the SIR response in a specific test. Using this catabolic response profile to estimate heterotrophic evenness and diversity, Degens and co-workers found that a decrease in microbial diversity does not consistently result in declines in soil functions (Degens 1998), consistent with Wertz et al. (2006). Furthermore, reduction in the catabolic diversity due to changed land use could reduce the resistance of microbial communities to stress or disturbance (Degens et al. 2001). This resistance might be coupled to organic matter content in soil, as depletion of organic C may cause a decline in catabolic diversity (Degens et al. 2000).

Since Degens's method is more laborious and time consuming, a comprehensive micro-respiratory system (MicroResp) containing 96- deep- wells-microtitre plate has been developed by Campbell et al. (2003) based on CO_2 evolution within a short period of time (4–6 h). Incubation of a substrate for a short period allows microorganisms to grow to some extent and allows active microorganism groups to act directly on the substrate applied. This whole-soil method discriminates vegetation types and soil treated with wastewater sludge (Campbell et al. 2003). Hence, both methods, although not yet applied in any routine soil assessment programs, do offer promising opportunities for community profiling and subsequent application in soil quality monitoring programmes.

5.3.2 Diversity of Enzyme Activity

Kandeler and Böhm (1996) suggested that the enzyme diversity of a soil provides an effective approach to examine its functional diversity. The responsiveness of enzymes to environmental disturbance makes them a potential indicator of the soil biological quality (Dick 1994). Only extracellular enzymatic activity is used to determine the diversity of enzyme patterns in soil extracts. Activity of ecto- and free- enzymes can be quantified by incubation of the soil extract with commercial fluorogenic enzyme substrates like 4-methylumbelliferin (MUF or MUB) and 4-methylcoumarinyl-7- amide or 7-amino-4-methyl coumarin (MC or AMC) (Kemp et al. 1993; Marx et al. 2001). The use of a microplate fluorometric assay using MUB and AMC to study the enzyme diversity in soils has recently been reported (Marx et al. 2001). Colorimetric substrates like remazol brilliant blue,

p-nitrophenol, or tetrazolium salt-coupled specific compounds of interest (e.g., cellulose or phosphate) also can be used to assay functional diversity of microbial communities (Wirth and Wolf 1992). For example, Verchot and Borelli (2005) have reported application of para-nitrophenol (pNP) conjugated with β-glucopyranoside, N-acetyl-β-D-glucosaminide, β-D-cellobioside and phosphate for measuring respective enzyme activity in degraded tropical soils. Measurement of only released pNP derived from all the pNP-linked substrates is the advantage of this method because only one method is employed for all enzyme analysis. The advantages of these assays include the independence of cellular growth and new enzyme synthesis due to a shorter incubation time and thus closer approximation of the in situ function. However, a few dominating organisms expressing high enzyme activity may give a biased result while measuring a diverse set of enzyme activities (Miller et al. 1998).

5.4 The Gene-Chip for Profiling of Structural and Functional Communities of Microorganisms

The development and application of a microarray-based genomic technology for microbial detection and community analysis has received a great deal of attention. Because of its increasingly high-density and high-throughput capacity, it is expected that microarray-based genomic technologies will revolutionize the analysis of microbial community structure, function and dynamics. The basic principle of DNA microarray technology is the identification of an unknown nucleic acid mixture (targets) by hybridization to numerous known diagnostic nucleic acids (probes), which are immobilized in an arrayed order on a miniaturized solid surface (Loy et al. 2006). They are originally developed for the analysis of gene expression in a variety of model organisms, but have great potential in community analysis and in detection of different functional characteristic (Sessitsch et al. 2006). For the first time in 1997, the microarray approach was introduced to environmental microbiology for microbial community composition analysis using a prototype array consisting of nine 16S rRNA-targeted probes for the identification of selected nitrifying bacteria (Guschin et al. 1997). Since then, this field has grown rapidly and today many different microarray systems consisting of more than 30,000 probes (Wilson et al. 2002) are available for detection of target nucleic acids (Taylor et al. 2007; Zhou 2003). Microarrays for microbial community analysis have been classified into two main categories: Phylochips and Functional Gene Arrays (FGAs).

Phylochips contain short nucleotide probes, targeting a phylogenetic marker gene (rRNA genes), and they are usually applied in order to detect specific bacteria such as pathogens (Franke-Whittle et al. 2005) in an ecosystem or to study diversity and structure of microbial communities (Loy et al. 2004; Günther et al. 2005). A functional group of microorganisms with considerable ecological and economic importance in the terrestrial ecosystem is the nitrifying bacteria. Nitrifying bacteria convert ammonium to nitrate by the process of nitrification.

Nitrification measurements are included in the soil-monitoring programme of Austria, Czeck Republic and Germany. A microarray for the nitrifying bacteria (Nitrifier-Phylochip) group (Loy et al. 2006) containing about 200 probes of 18-mer oligonucleotides has enabled extensive monitoring of this functional group. The majority of DNA microarray applications in microbial ecology have focused on determination of community structure based upon phylogenetic markers such as the 16S rRNA gene (Gentry et al. 2006). Although this approach provides powerful and detailed pictures of microbial community structure in complex environmental samples, it generally provides little insight into microbial function.

Functional gene arrays contain DNA probes targeting genes that encode key enzymes conferring a specific functional capability to the respective microorganisms. Some examples of functional enzymes catalyzing different steps in the global nitrogen, sulphur and carbon cycles are nitrite reductase (*nir*S) for denitrification, ammonium monooxygenase (*amo*A) for ammonia oxidation, nitrogenase (*nif*A) for nitrogen fixation (Taroncher-Oldenburg et al. 2003; Wu et al. 2001), dissimilatory bisulphate reductase (*dsr*AB) for sulphate reduction (Wagner et al. 2005) and methane monooxygenase (*pmo*A) for methane oxidation (Bodrossy et al. 2003). The FGAs composed of the formerly cited genes have been mainly developed to understand microbial ecology and biogeochemical cycle of aquatic systems. Functions linked to these identified genes are highly important for soils. These arrays used in aquatic systems may lay the foundation for developing further specific arrays that target soil microorganisms. However, additional probes with increased specificity for soil microorganisms may be required. For example, a 70-mer long oligonucleotide FGA containing *nir*S, *nir*K, *nif*H and *amo*A probes has been used to study change in the community involved in nitrogen cycle in aquatic environment (Taroncher-Oldenburg et al. 2003).

The greatest advantage of FGAs is that microorganism identification is directly linked to potential physiological traits. One of the greatest challenges in using FGAs for detecting functional genes and/or microorganisms in the environment is to design oligonucleotide probes specific to the target genes/microorganisms of interest because sequences of a particular functional gene are highly homologous and/or incomplete, especially in sequences derived from laboratory cloning of environmental samples. Another challenge for using FGAs to study the microbial communities in natural systems is the lack of arrays containing comprehensive probe sets. To tackle these challenges, recently, He et al. (2007a) developed a comprehensive FGA, termed *GeoChip 2.0* version, which contains more than 24,000 oligonucleotide (50-mer) probes covering more than 150 functional groups of 10,000 gene sequences involved in biogeochemical cycling of carbon, nitrogen, phosphorus and sulphur along with metal resistance, metal reduction and organic contaminant degradation (Table 3). Almost all (approximately 98.2%) of the gene sequences were from bacteria whereas the rest (approximately 1.8%) were from fungi. Two major types of applications of the developed *GeoChip* can be visualized. One is to track microbial community dynamics under different environmental/treatment conditions. The developed *GeoChip* has been successfully used to track the changes of the responsible microbial populations during the bioremediation processes of groundwater

Table 3 *Geochip* 2.0 containing number of probes of the functional genes

Gene category	Total gene probes	Percentage (%) of probe target the genes
Nitrogen fixation	1,225	5.0
Denitrification	2,306	9.5
Nitrification	347	1.4
Nitrogen mineralization	1,432	5.9
Carbon fixation	1,018	4.2
Cellulose, lignin and chitin degradation	2,542	11.6
Sulphate reduction	1,615	6.7
Metal reduction and resistance	4,546	18.8
Contaminant degradation	8,028	33.1

Modified from He et al. (2007a)

contaminated with uranium (He et al. 2007a). The other is to use it as a genetic tool for profiling the differences between microbial communities. For this purpose, the *GeoChips* have been used to analyze microbial communities from a variety of habitats, including bioreactors, soils, marine sediments and animal guts. *GeoChip 2.0* also has been employed in ecological applications to detect carbon- and nitrogen-cycle genes that were significantly different across different sample locations and vegetation types of an Antarctic latitudinal transect (Yergeau et al. 2007).

A new generation of the *GeoChip* (v. 3.0) is being developed with several new features compared to *GeoChip* 2.0. *GeoChip* 3.0 is expected to cover >37,000 gene sequences of 290 gene families, allowing access to more information about microbial communities across more diverse environmental samples. It also includes phylogenic markers, such as *gyrB* (the structural gene for the DNA gyrase *b* subunit) and verifies the homology of automatically retrieved sequences by key words using seed sequences so that unrelated sequences are removed. Additionally, a software package (including databases) has been developed for sequence retrieval, probe and array design, probe verification, array construction, array data analysis, information storage, and automatic updates, which greatly facilitate the management of such a complicated array, especially for future updates. Finally, *GeoChip 3.0* also includes *GeoChip 2.0* probes, and those *GeoChip 2.0* probes are checked against new databases for changes in ecosystem management, and environmental cleanup and restoration (He et al. 2007b). In particular, it provides direct linkages of microbial genes/populations to ecosystem processes and functions. All of these results suggest that the developed *GeoChip* is useful for studying various biogeochemical, ecological and environmental processes and associated microbial communities in natural settings in a rapid, high throughput and potentially quantitative fashion. With the developed *GeoChips*, it is possible to address many fundamental and applied research questions in microbial ecology important to human health, agriculture, energy, global climate changes, ecosystem management and environmental cleanup and restoration. Hence, FGAs contain probes from the genes with known biological functions, and they will be useful in linking microbial diversity to ecosystem processes and functions. Due to their ability to connect microbial

community analysis to the structural and functional levels, these chips are expected to be a future tool in soil quality monitoring programme for agricultural systems.

5.5 Arbuscular Mycorrhizae Fungi (AMF) Community Structure and Diversity

Arbuscular mycorrhizal (AM) fungi are ubiquitous in nature and constitute an integral component of terrestrial ecosystems, forming symbiotic associations with plant root systems of over 80% of all terrestrial plant species, including many agronomically important species (Smith and Read 1997; Harrier and Watson 2003). Mycorrhizae exist alone or in association with helper rhizospheric bacteria that maintain soil health, and hence, AMF can serve as key species for monitoring soil quality (Jeffries et al. 2003). AMF efficiently deliver soil minerals particularly phosphorus (P) (Sharma and Adholeya 2004) and nitrogen (N) to the plant (Govindarajulu et al. 2005), and in turn the fungi are energized by sugar from the plant (Pennisi 2004). Sharma and Adholeya (2004) reported that mycorrhization of strawberry can save 35 kg^{-1} ha^{-1} of phosphorus fertilizer when compared to non-mycorrhizal strawberry plants grown at a particular P applied level. They play an important role in P uptake and growth of many cereals, legumes and other crop plants (George et al. 1995; Sharma and Sharma 2006). This process of enhancing P absorption by plants appears to be particularly important in highly weathered, fine textured, and acid tropical soils, where great proportions of applied P fertilizer are not available to plants due to strong fixation of P on iron and aluminum oxides (Jama et al. 1997; Bunemann et al. 2004; Sharma et al. 1996). Mycorrhizal associations can also exert a positive influence on plant diversity, stress, disease tolerance, and soil aggregation (Gosling et al. 2006).

Colonization by AMF has been shown to be highly dependent on the presence of host plants, land use and management practices (Kling and Jakobson 1998). Spore abundance and diversity can be distinct between extensively and intensively managed soils (Oehl et al. 2003). AMF diversity has been reported to be sensitive to heavy metal contamination, organic pollutant and atmospheric deposition. (Egeston-Warburton and Allen 2000; Egli and Mozafar 2001). Furthermore, nitrogen enrichment induces a shift in AM community composition. In particular, an increasing input of nitrogen was associated with the displacement of the larger-spore species of *Scutellospora* and *Gigaspora* (due to a failure to sporulate) with a concomitant proliferation of small-spore *Glomus* species (e.g., *G. aggregatum, G. leptotichum*). Such changes also indicated that AMF species are sensitive indicators of nitrogen enrichment (Egeston-Warburton and Allen 2000). Abundance and diversity of AMF is determined by extraction of spores from soil samples and subsequent counting in a microscope (Oehl et al. 2003). Thus, spores build up in soil and plant root colonization by AMF has been proposed as an important indicator of plant and soil ecosystem

health (van der Heijden et al. 1998; Stenberg 1999; Oehl et al. 2003). More than 150 species have been described within the phylum Glomeromycota on the basis of their spore development and morphology, although recent molecular analyses indicate that the number of AMF taxa may be much higher (Daniell et al. 2001; Vandenkoornhuyse et al. 2002). Finally, methods for direct detection and quantification of AMF in soil samples or roots include 18S rRNA gene PCR (Chelius and Triplett 1999), and nested PCR at the species level (Jacquot et al. 2000). Quantitative analysis of the density of a particular AMF based on spore morphology has been implemented as a microbial indicator in the Swiss soil quality-monitoring network for ascertaining the heavy metal contamination (Egli and Mozafar 2001).

6 Minimum Data Set (MDS) of Microbial Indicators

Given the large number of soil microbial characteristics that can be measured as indices of the soil quality, the question is: what is the 'minimum data set', i.e. a set of specific soil measurements considered as the basic requirement for assessing the soil quality (Doran and Parkins 1996). Microbial indicators of MDS must be (i) compatible with basic ecosystem processes in soil as well as physical or chemical indicators of soil health, (ii) sensitive to management in acceptable time frames, (iii) easy to assess or measure, (iv) composed of robust methodology with standardized sampling techniques, (v) cost-effective, and (vi) relevant to human goals, food security, agricultural production, sustainability and economic efficiency (Bunning and Jimenez 2003)

Many countries have developed their own MDS of microbiological indicators for monitoring of soil quality (Table 4) where microbial biomass and soil respiration are the most commonly used indicators. However, some of the recent tools such as Biolog, PLFA, DGGE/TGGE etc have been recommended for microbial diversity assessment to monitor soil quality in certain countries (Chapman et al. 2000, Winding et al. 2005). In India, no 'minimum data set' for monitoring soil quality has been recommended but soil enzyme activities, respiration and microbial biomass are being used widely (Ramesh et al. 2004a, b; Rao et al. 1995; Sharma et al. 2005). Therefore, to help improve soil management and retain or remediate soil quality throughout India, a MDS to assess quality of agricultural soils within the country should be developed. This would provide a structured approach that could be followed to determine if the soils have deteriorated or are deteriorating in terms of soil productivity or other critical soil functions. Then, based on the magnitude of soil deterioration, stakeholders can develop better practices to manage their soils and increase the sustainability of their agricultural practices. Assuming that soil microbial diversity and function are linked, the progress of soil rehabilitation could later be evaluated by the resultant microbial diversity and various functional attributes.

Table 4 Minimum data set (MDS) of microbial indicators for soil quality monitoring as defined in different countries

	Country	Microbial indicators
1.	United Kingdom[a]	Microbial biomass; soil respiration; microbial diversity by Biolog; *Rhizobium* population; biosensor bacteria
2.	United States of America[a]	Microbial biomass; potential N-mineralization; soil respiration; soil enzymes
3.	Germany[a]	Soil respiration; microbial biomass; potential N-mineralization; soil enzymes; metabolic quotients
4.	The Netherlands[a]	Microbial biomass; potential C-mineralization; potential N-mineralization; microbial diversity by Biolog and DGGE
5.	Switzerland[b]	Microbial biomass; soil respiration; potential N-mineralization; arbuscular mycorrhizae
6.	Czech Republic[a]	Microbial biomass; soil respiration; nitrification; N-mineralization; soil enzymes
7.	Russia, Sweden[a], Finland	Soil respiration, soil enzymes; potential N-mineralization
8.	Austria[a]	Microbial biomass; soil enzyme; nitrification; mycorrhizae
9.	India[c]	Soil enzymes; soil respiration; microbial biomass

Modified from [a]Winding et al. 2005; [b]Mader et al. (2002); [c]Ramesh et al. (2004a, b); [c]Rao et al. (1995); [c]Sharma et al. (2005)

7 Agricultural Strategies to Improve Soil Quality by Managing Microbial Communities and Diversity

In recent years, agricultural practices that improve soil quality and agricultural sustainability have received increased attention from researchers and growers. An understanding of soil processes is key to estimate the influence of farming practices on the fertility and quality status of the soil, and thus, on the environment. Species diversity can give rise to ecosystem stability through the ability of the species or functional groups it contains to respond differentially and in compensatory fashion to perturbations in the soil environment (Sturz and Christie 2003). Shifts in bacterial community structure or diversity and associated physiological responses can be used as indicators of these perturbations or disturbances in agroecosystems (Calderón et al. 2001), although some results cast some doubts on the strength of biodiversity-ecosytem functioning relationships as observed for macroorganisms when extrapolated to bacteria (Griffiths 2000; Wertz et al. 2006; 2007). Changes in the community structure have been caused by changes in agronomic practices such as types of amendment (Kennedy et al. 2004; Marschner et al. 2004), reduced or no-tillage (Drijber et al. 2000), crop rotations (Lupwayi et al. 1998) and microbial inoculation (Roesti et al 2006; Srivastava et al. 2007). Some even suggest that it is appropriate to adopt agricultural practices that preserve and restore microbial diversity than practices that destroy it (Lupwayi et al. 1998). In addition, the soil microbial

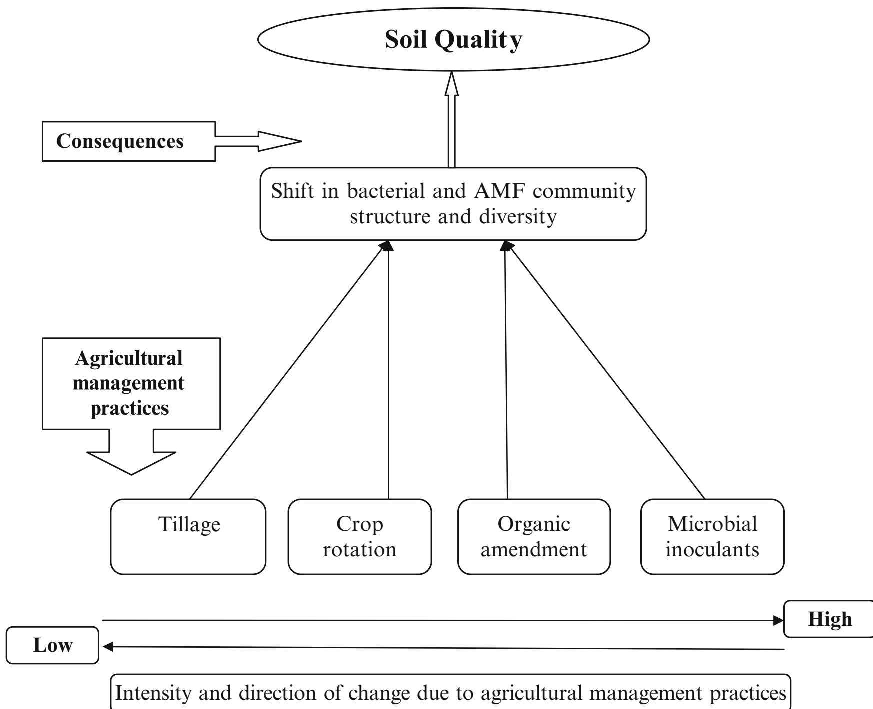

Fig. 3 An overview of agricultural management practices on soil microbial community structure and diversity and their possible influence on soil quality

community may serve as a fingerprint associated with certain land use practices, soil conditions, and associated function, suggesting that achievement of such a fingerprint and its associated soil characteristics may be gained through adoption of a suitable site-specific suite of agricultural practices (Steenwerth et al. 2003, 2005). In this section, we address impacts of agricultural practices on soil microbial communities, with a primary focus on arbuscular mycorrhizal fungi due to their readily defined functions in agricultural systems (Fig. 3).

7.1 Tillage

Studies on tillage indicate that many critical soil quality indicators and functions can be improved by decreasing tillage intensity (Jackson et al. 2003; Karlen 2004; Govaerts et al. 2006; Govaerts et al. 2007b). Recent approaches aim to reduce excessive cultivation in favor of limited or more strategic tillage practices. Such practices are grouped under the term conservation or reduced tillage as opposed to conventional tillage (Carter 1994). Compared to conventional tillage, reduced tillage practices offer not only long term benefits to soil stability, reduce erosion, but

also enhance soil microbial diversity (Davis et al. 2002; Phatak et al. 2002; Welbaum et al. 2004; Govaerts et al. 2008). Conventional tillage promotes a vicious cycle of soil aggregate disruption and reconsolidation that result in denser soils with the loss of organic matter (Six et al. 1999). Soils in humid thermic regimes are more sensitive to degradation from repeated tillage due to loss of soil organic matter and erosion (Lowrance and Williams 1988; Langdale et al. 1992). Thus, they are better candidates for adoption of no-tillage systems. It is also well-known that no-till practices combined with crop residue retention increase soil organic matter content in the surface layer, improve soil aggregation, and preserve the soil resources better than conventional till practices (Govaerts et al. 2006, 2007c). Increased soil organic matter content associated with no-till practices not only improves soil structure and water retention, but also serves as a nutrient reservoir for plant growth and a substrate for soil microorganisms.

In terms of functional diversity, tillage influences microbial communities in many different ways. It causes a physical disruption of AMF fungal mycelia and may change physico-chemical properties of the soil (Evans and Miller 1990, Kabir, 2005). Soil disturbances reduce the density of AMF spores, species richness and the length of extraradical mycelium of AMF relative to undisturbed soil (Kabir 2005; Boddington and Dodd 2000). Conversely, no-tillage often stimulates mycorrhizal activity in soil, thereby influencing nutrient uptake by plants (Dodd 2000). Glomalin, an exudation product of AMF hyphae having a role in soil aggregation, was 1.5 times higher in no-till than tilled soils (Wright et al. 1999). Based on spore morphology and sequencing of ITS rDNA, at least 17 AMF species were identified including five genera (*Glomus*, *Gigaspora*, *Scutellospora*, *Aculospora* and *Entrophospora*) from soils exposed to different tillage practices (Jansa et al. 2002). Under reduced tillage, the incidence of certain AMF in agricultural soils increased, excluding *Glomus* spp. In contrast, *Glomus* species (G. *mosseae, G. claroideum, G. caledonium, G. constrictum, G. clarum*-like) were predominant under conventional tillage.

Giller (1996) and Lupwayi et al. (1998) suggested that the diversity in microbial communities provoked by tillage resulted from a reduction in substrate richness and microbial uniformity under conventional tillage (CT). In terms of functional diversity, as measured with the Biolog method, soils under reduced tillage (RT) had a higher average well color development (AWCD) and a higher Shannon's Diversity index (H) compared to those under CT. This confirmed the adverse effect of intense tillage on microbial diversity (Diosma et al. 2006). Giller (1996) suggested that soil microbial diversity could be reduced by such disturbances as desiccation, mechanical destruction, soil compaction, reduced pore volume and food resources and/or access to them. For example, in semi-arid highland of Mexico, soil microbes under zero tillage and crop residue addition resulted in higher AWCD than those under zero tillage without residue addition. This suggested that zero tillage, in the absence of crop residue retention, is an unsustainable practice that may lead to poor soil health (Govaerts et al. 2007a). Different tillage intensities can also select for specific dominant microbial populations within the soil bacterial community, as depicted by 16S rRNA and *rpoB* genes using DGGE (Peixoto et al. 2006).

7.2 Crop Rotation

Crop rotation is a very ancient cultural practice (Howard 1996) that has a strong influence on soil structure, organic matter, and microbial communities (Janvier et al. 2007). Traditionally, it has been used primarily to disrupt disease cycles (Curl 1963) and fix atmospheric nitrogen by legumes for subsequent non-leguminous crops (Pierce and Rice 1998). Crop rotation can cause changes in substrate utilization patterns, suggesting that soil bacterial communities under crop rotation have greater species diversity than under continuous wheat (*Triticum aestivum* L.) or summer fallow (Lupwayi et al. 1998). For instance, functional diversity measured by the Biolog method increased in soil under wheat/maize rotation with crop residue addition as compared to that exposed to a monoculture of maize alone (Govaerts et al. 2007a).

Relatively limited work has been executed to characterize mycorrhizal community composition and diversity, which is crucial in furthering our understanding of mycorrhizal functions in agro-ecosystems (Johnson and Pfleger 1992). Traditionally, AMF communities in field soil employ spore surveying, which is sometimes complemented by trap culturing (Douds et al. 1993; Jansa et al. 2002; Oehl et al. 2004). These spore-based surveys are considered as a baseline to assess the impact of agricultural practices on AMF communities (Douds and Millner1999). However, it has become clear that morphological characterization of the AMF spore community and its diversity might not reflect the actual functional symbiosis that refers to active fungal structures within and outside roots (Clapp et al. 1995; Jansa et al. 2003).

It has also been shown that introduction of leguminous crops for a season into a conventional system of continuous cultivation of maize (*Zea mays* L.) increased microbial diversity (Bunemann et al. 2004; Bossio et al. 2005). In a Kenyan ferrasol, the species diversity of AMF spores was neither affected by crop rotation nor by P fertilization. However, the composition of AMF spore communities was significantly affected by crop rotation (Mathimaran et al. 2007). Johnson et al. (1992) found that maize had higher yield and nutrient uptake on soils that had previously cultivated continuously with soybean (*Glycine max* (L.) Merrill) for 5 years than on soil that had grown continuously with maize for the 5 years. Conversely, soybean had both lower yields and nutrient uptake on soil supporting 5 years of continuous soybean as compared to its increased growth on soils exposed to 5 years of continuous maize. The most abundant AMF species in the continuous maize soil was negatively correlated with maize yield, but positively correlated with soybean yield; there was a similar effect with soybean soil. This yield decline after continuous cropping of soybean and maize is attributed to selection of AMF species which grow and sporulate most rapidly and these AMF species offer the least benefit to the respective monocrop because they divert more resources to their own growth and reproduction and the mycorrhizal group acts as 'resource cheater'. The non-specific association of mycorrhizae with monocropping was further confirmed by Bever (2002) who demonstrated a negative feedback between AMF and plants. A substantial part of soil microbial communities belongs to the AMF (Leake et al. 2004). Agricultural management practices affect AMF communities both qualitatively and quantitatively (Sieverding 1990; Miller et al. 1995). This has been

documented in many studies showing that crop rotation, fertilization, and tillage affect the composition and diversity of AMF communities as well as spore and mycelium densities in temperate and tropical agro-ecosystems (Sieverding 1990; Jansa et al. 2002; Oehl et al. 2003). However, active structures such as fungal hyphae and arbuscules in the roots and the soil can only be properly identified by means of molecular or immunological approaches (Treseder and Allen 2002; Redecker et al. 2003; Sanders 2004), which may require calibration for each specific field site (Jansa et al. 2003).

7.3 Organic Amendments

Organic amendments cover a wide range of inputs, including animal manure, solid waste, and various composts, and often improve soil quality and productivity. Girvan et al. (2004) and Melero et al. (2006) showed that these amendments, as well as crop residues, resulted in significant increases in total organic carbon (TOC), Kjeldahl-N, available-P, soil respiration, microbial biomass, and enzyme activities (e.g., protease, urease, and alkaline phosphatase). Microbial diversity and crop yields also increased as compared to conventional management. Applying cattle manure increased the amount of readily available organic C and mineral nutrients. This improved soil structure and promoted growth of both r-strategists (fast growing microorganisms having high reproductive capacity and successful only in resource-rich environment) and K-strategists (slow growing microorganisms having slow reproductive capacity and successful in resource-limited situations) while chemical fertilizers enriched the K-strategists bacterial community. As a result, the richness, evenness and diversity of the microbial community in manure-treated soil were enhanced and were positively correlated with soil productivity (Parham et al. 2003). In the Netherlands, organically managed soils had also shown higher biological diversity in both nematodes and eubacteria (van Diepeningen et al. 2006). In another long-term experiment comparing organic and synthetic soil fertility amendments, cotton (*Gossypium hiristium* L.) gin trash application was found to maintain significantly higher bacterial community diversity as assessed by CLPP and DGGE analyses compared to synthetic fertilizer (Liu et al. 2007).

Organic amendments do not always elicit a shift in bacterial diversity. Srivastava et al. (2007) reported that the incorporation of okra (*Hibiscus esculetus* L.), pea (*Pisum sativum* L.) and cowpea (*Vigna unguiculata (L.) Walp.*) residues significantly increased fungal activity but bacterial community composition as revealed by DGGE analysis remained the same. Furthermore, in semiarid conditions of southern Italy, the composition of diversity of total bacteria as well as ammonium oxidizers exhibited no significant change after incorporation of crop residues in soil under monoculture of durum wheat. However, a change was detected after applying nitrogenous fertilizer (Crecchio et al. 2004, 2007). In both cases, despite a lack of change in microbial community, soil fertility was found to be high. In contrast, Saison et al. (2006) detected clear changes in the bacterial community structure after amendment of rape compost in sandy soil.

Oehl et al. (2004), using a soil from Switzerland, found that *Glomus* spp. were similarly abundant whether fertilized with mineral or organic fertilizers, but spores of *Acaulospora* and *Scutellospora* spp. were more abundant in soil that only received organic fertilizers. Spore dominance of two genera viz., *Gigaspora* sp. and *Glomus* sp. was recorded in a rehabilitated site where *Gigaspora* genera showed a strong positive correlation with organic carbon content (Gaur et al. 1998). Different forms of organic fertilizers also differentially affected AMF communities in other studies. For example, addition of leaf compost combined with either chicken litter (poultry) or cow (*Bovine* spp.) manure, enhanced spore populations of some AMF species (*Glomus etunicatum* and *G. mosseae*) relative to those found in soils fertilized with raw dairy-cow manure or with mineral fertilizer (Douds et al. 1997). Supplementation of organic amendments continuously for 10 years in corn, soybean and citrus did not show any AMF diversity and richness (Franke-Snyder et al. 2001). Nevertheless, the organic apple orchard had the highest AMF richness, even though sporulation and the Shannon diversity index were higher for the conventional orchard (Purin et al. 2006). Broadly, organic amendments application in soil either increased or do not affect microbial diversity but improve soil quality and crop productivity.

7.4 Microbial Inoculation

Inoculation of microbial inoculants is generally being done to improve soil fertility and crop productivity through various microbe-mediated mechnaisms. The introduction of microbial inoculant to soils either through seed bacterization or direct application results in a disturbance of the rhizosphere's biological equilibrium. Significant increases in soil enzymes such as α-galactosidase, β-galactosidase, α-glucosidase and β-glucosidase, chitibiosidase and urease and a decrease in alkaline phospahatese activity has been observed upon soil perturbation through separate inoculation of *Flavobacter* spp and *Pseudomonas fluorescens* (Mawdsley and Burns 1994; Naseby and Lynch 1997). De Leij et al. (1995) reported only transient perturbations in the indigenous microbiota in the rhizosphere with the introduction of wild and genetically modified- *P. fluorescens* in rhizosphere of wheat. A minor impact on the composition of the microbial rhizosphere community of *Medicago sativa* and *Chenopodium album* was reported after inoculation with *Sinorhizobium meliloti* L33 (Meithling et al. 2000; Schwieger and Tebbe 2000). The inoculation of plant growth promoting rhizobacteria (PGPR) alone through seed bacterization or soil application near seeds may cause negligible to extreme shifts in microbial community composition (Nacamulli et al. 1997; Lottmann et al. 2000; Marschner et al. 2001a,b; Kozdroj et al. 2004). Furthermore, inoculation of PGPR and AMF alone or in combination in soils supporting wheat and vegetable crops modified the bacterial community (Roesti et al. 2006; Srivastava et al. 2007).They also showed that an increase in crop yield occurred, further suggesting that inoculations with selected beneficial microorganisms can enhance crop yield.

AM symbiosis influences the structure and function of surrounding bacterial communities (Marschner and Timonen 2005). In canola, which is considered to be a non-mycorrhizal species, inoculation with *Glomus intraradices* increased the shoot dry weight compared to *G. versiforme* and the non-mycorrhizal control plants and also induced changes in the bacterial community composition in the rhizosphere, as analyzed by DGGE. Surprisingly, less than 8% of the canola's root length was colonized. In contrast, although 50% of the clover's root length was colonized and inoculation with *G. versiforme* resulted in a higher shoot dry weight compared to *G. intraradices* or the control plants, no change in the rhizosphere bacterial community composition was recorded (Marschner and Timonen 2005). In another study, inoculation of *G. intraradices* induced greater plant growth in autoclaved soil than in non-autoclaved soil, an effect that was positively related to inoculum density (Dabire et al. 2007). Catabolic evenness and richness were positively correlated with the number of inoculated AM propagules in the autoclaved soil, but negatively correlated in the non-autoclaved soil. In non-autoclaved soil, application of G. *intraradices* inoculum induced disequilibria in microbial functionalities. Hence, it was suggested that AM inoculation of the non-autoclaved soil increased the susceptibility of soil microflora to stress and disturbance (Degens et al. 2001). Although *G. intraradices* inoculation had stimulated plant growth, this fungal inoculant had not improved soil microbial diversity. In addition, after soil autoclaving and AM inoculation, catabolic evenness and richness were significantly higher than in the control (non-inoculated soil) and in the non-disinfected (non-autoclaved) soil without AM inoculation (Dabire et al. 2007).

It has also been reported that rhizosphere soils contain a higher proportion of culturable bacteria that were r-strategists and were, therefore able to respond and multiply quickly in presence of available nutrients (Sarathchandra et al. 1997). An increase in the number of AM propagules in autoclaved soil enhanced catabolic diversity by stimulating the growth of contaminant r-strategist microorganisms (*e.g. Bacillus* spp., *Pseudomonas)* that were probably received from water used during irrigation. However, *G. intraradices* inoculation in non-autoclaved soil resulted in decreased soil microbial catabolic diversity by inhibiting the growth of r-strategist microorganisms. It has also been reported that populations of total culturable bacteria decreased in mycorrhizal-inoculated rhizospheres (Vazquez et al. 2000). Hence, it seems that AMF inoculation not only favors plant growth but also microbiological activities contributing to soil quality.

8 Future Perspectives

The importance of microorganisms in soil functions by mediating various processes for nutrient cycling has long been acknowledged, underscoring the importance of understanding microbial diversity and associated functions for sustainable agriculture. The indices accounting for microbial diversity or community structure in soil are considered to be of immense significance to manage soil quality in order to

sustain productivity of crops. Agricultural systems that sustain or enhance soil quality through creation of higher biodiversity can provide sustainability to production of crops and often partially substitute for nutrition that is currently being managed through external chemical inputs.

So far consensus exists only to a limited extent on the importance of utilizing microbial biodiversity indices as a measure of soil quality. Currently, several different indices for microbial diversity have been established, but it is very difficult to know which index is most suitable for a given situation. To address this question, more in depth research is needed to determine the most suitable microbial indicators and how they should be interpreted. Moreover, while we have documented shifts in soil microbial communities in response to various conditions, we have yet to determine if depressions in microbial diversity begets a shift in soil quality or if the extent of microbial functional redundancy is so great that the link between microbial diversity and function is weak, and whether these relationships shift in response to different disturbance intensities. The related challenge is to develop quantitative relationships between any apparent functional redundancy and genetic diversity. Despite the debate that functional redundancy is not commonly existent, exceptions may occur. For example, it was once thought that AMF were functionally redundant given a lack of host specificity, but it has been demonstrated that AMF provide different benefits to the different plant hosts.

Another important concern regarding assessment of microbial diversity for soil quality monitoring are the issues of sampling, sample preparation, and handling for analyses. Most microbial analyses are very sensitive to water content and temperature, thus sample collection and storage become major barriers for many analyses. As new protocols are developed to include microbial diversity in the suite of soil quality indicators, specific guidelines for sample collection and preservation must be standardized to facilitate comparisons among independent studies. Should samples be stored moist at a low temperature, processed immediately, or air dried before analysis? Will it be more efficient and cost effective to pursue enzymatic measures or genetic profiles considering that commercial soil-testing laboratories will ultimately be called upon for soil quality assessments? These are difficult questions to be answered because they involve the human element and bias, but must be addressed before microbial indicators will be as easily incorporated into soil quality assessment as current physical and chemical indicators.

9 Conclusion

The diversity of microorganisms in agro-ecosystems is immense but critical to maintaining ‘good’ soil quality because they are involved in so many important soil processes. With an increased number of monitoring programs utilizing microbial diversity, composition and function as an indicator for evaluating soil quality, comprehensive comparisons among geographic zones and cropping systems will both strengthen our understanding of links between microbial diversity and function, and

develop regional standards for microbial fingerprints associated with 'good' soil quality. The judicious use of biological inputs including inoculums, manures, cover crops, and plant residues is recognized as a practical way to promote a healthy soil and support sustainable crop production. To guide the use of these materials and to achieve the desired change in microbial communities, the first step will be to confirm critical linkages between specific soil microbial groups and critical soil functions. Then, baseline parameters such as soil respiration, organic carbon pool, and soil enzymes that are routinely utilized worldwide for monitoring soil quality can be incorporated into an overall soil health assessment programme. However, we advise that factors that highly influence soil microbial community composition e.g. soil pH, texture, and water content be incorporated into the monitoring programs to avoid false conclusions regarding association between microbial diversity, function and soil quality. Although recent advances in molecular techniques for analysis of soil microorganisms have occurred, we emphasize that exclusive use of a single technique in a monitoring program may provide biased and distorted interpretations of microbial diversity, emphasizing the importance of establishing common standards among soil monitoring programs. Likewise, coordination among independent research programs to develop a minimum common database (MCD) and methods standardization, such as has been demonstrated by the National Ecological Observatory Network in the United States, would facilitate greater understanding of microbial diversity, function, and soil quality, and increase its accessibility to both growers and policy makers across a broader geographic scale.

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