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BELOWGROUND BIODIVERSITY AND SUSTAINABILITY OF COMPLEX AGROECOSYSTEMS

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INTRODUCTION: DIVERSITY IN SIMPLE AND COMPLEX AGROECOSYSTEMS

Diversity of components and interactions distinguishes complex agro-ecosystems from the simple agro-ecosystems which have replaced them in most of the temperate zone. In the tropics farmer decisions on agro-ecosystems have retained more similarity with natural ecosystems, but a strong trend towards specialization exists. As part of a re-appreciation of agroecosystem complexity, functional aspects of belowground diversity deserve more attention.

The complexity of agroecosystems is largely based on farmer decisions Farmer decisions on complex agroecosystems can be grouped as choices on the 'planned diversity', on the management of 'associated diversity' and on the harvest regime for the various components (which may include elements of the 'associated diversity' category) (Swift and Ingram, 1996; Vandermeer *et al.*, 1998). Planned diversity includes deliberate choices for intercropping (patch level), crop rotations and diversity of farm enterprises. Associated diversity is a result of the interaction between farm management and the landscape context of the farm. Belowground biodiversity is usually in this latter category. Whereas the harvested components are directly linked to the way agroecosystems productivity is measured and evaluated by the farmer in the short run, the non-harvested components play a key role in the functioning of the agroecosystems, its sustainability and long term productivity (Figure 1).

Society at large may evaluate agroecosystems by a range of criteria which extend beyond those of the farmer (Giller *et al.* 1997), and embrace a variety of scales including global issues such as biodiversity conservation and contribution to global warming. For example, the maintenance of soil organic matter and a viable soil resource generally depends on sufficient organic inputs to the soil, which requires that a substantial part of total biomass production is not harvested but is returned to the soil on site.

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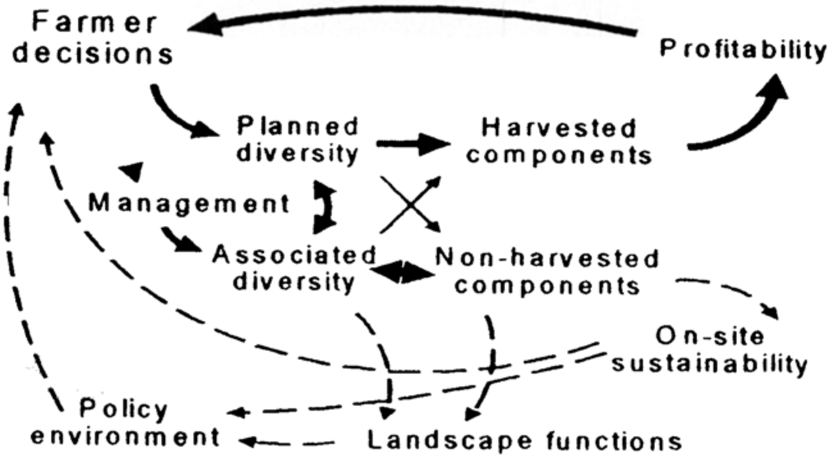

Figure A conceptual scheme of relations in agroecosystems complexity and function (modified from Swift and Ingram, 1996).

Starting from the highly diverse farms in a true subsistence economy, a dominant trend during 'development' is one of simplification and specialization. Such specialization is based on externalization of functions of farm components:

- range of subsistence products: market supply replaces production by all households,
- pest control: chemical solutions replace local ecological ones,
- soil fertility maintenance: chemical fertilizer inputs replace local 'service' components,
- insurance: social and market-based insurance schemes replace the stabilizing effect of farm diversity,
- institutional factors: land tenure can be claimed by other means than trees as markers.

The benefits of specialization are based on 'economies of scale' where mechanization, specialized know-how and marketing are involved and on exploiting comparative advantages of the local production situation. This simplification has a pronounced effect on field and farm-level diversity, but not necessarily on regional and national level diversity. It is first of all a change in 'grain size', a shift in the 'segregate - integrate' continuum (Figure 2).

While this trend to specialization is a marked aspect of 'development', it has clear drawbacks as well as direct financial benefits. There is a range of driving forces, the balance of which can lead to a net decrease or increase of agro-ecosystem complexity (Table 1). The overall trend towards specialization has made the agro-ecosystems vulnerable to:

- climate variability,
- pest outbreaks and weed invasion,
- decreasing tolerance of society at large of the environmental side-effects of chemical inputs and the energy needed to produce them,
- loss of environmental service functions at the landscape level, such as the regulation of stream and sediment flows, and increasing conflicts with downstream land users.

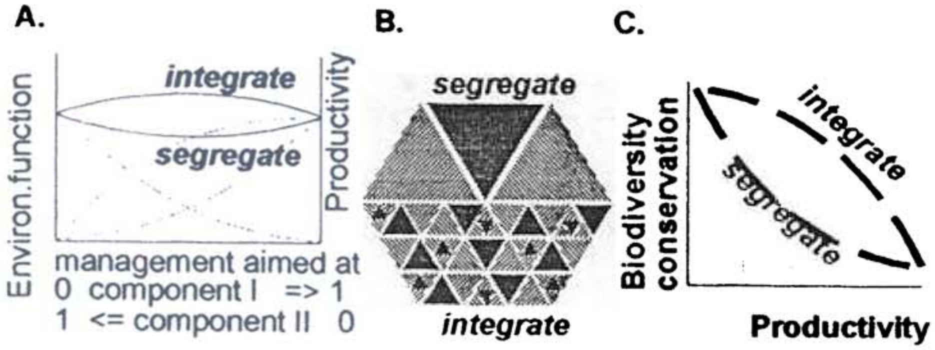

Figure 2. Segregated or integrated solutions to multiple objective problems may include the same components and total diversity, but differ significantly in interactions and local diversity.

Although simplified systems may indeed be superior from a farmers perspective, it is also possible that a bias is introduced by agronomic research which has an adequate tool-box of experiments and models for technology development in monocultures, but which is less able to deal with more complex systems. Similarly, models of mixed forests are widely available and used for teaching, but have hardly become used in practical forest management, where monocultural stands still predominate (Vanclay and Skovsgaard, 1997). Maybe specific forms of more complex systems would indeed be better for the farmer, but the knowledge base for evaluating this is incomplete. This is a challenge to research to first of all re-appraise the current complexity and then develop a tool-box for technology development while maintaining the complexity. A range of driving forces can be distinguished for either a reduction or enhancement of the complexity of agro-ecosystems.

Table 1. Driving forces for reduction and enhancement/re-emergence of agroecosystem complexity

Reducing	Enhancing
mechanization, which restricts the opportunities for planned mixed cropping, especially at the transition from manual field operations to draught-animal traction, with further reductions at the transition from animal to tractor-based systems	recognition and selection of plant-plant combinations which exhibit true complementary in resource use and may thus have real agronomic advantages
intensification of land use, aiming for higher economic outputs per hectare, reducing the thresholds for 'weediness'	'appropriate technology' developments in mechanization which allow higher labour use efficiencies without a strong drive for simplifying field plant combinations
further market integration of the farm household, inducing specialization and its ensuing segregation	extensification of land use, as occurs in later stages of economic transformations of (formerly) agricultural economies, when returns to labour are higher in other sectors of the economy
the use of 'hybrid' germplasm which is not conducive to local selection and depends on a continuous external source of 'quality seeds'	the continuous introduction of new germplasm, maintaining or enhancing the 'transient diversity' aspect of the farms (as new germplasm is generally only locally 'new', this type of activity may reduce diversity at global scale), effective rewards from society at large by effective policies for maintaining complexity in as far as it is valuable to interest groups beyond the farm
extension services and 'projects' which tend to reduce between-actor variation, especially in combination with 'planning' and 'models' in the sense of 'blue-prints'; such models are usually enforced by credit schemes leaving few options, if not by social pressure	Development of models which allow more location-specificity in development options, adjusting credit schemes to the real qualities of the site and real objectives of the farmer instead of 'blue prints'.

The complexity and diversity of existing agroecosystems can be based on one or more of the following reasons, operating at different scales. At plot/field level these include:

- 'planned diversity' based on deliberate mixing of plant species (mixed cropping, intercropping, mixed pastures, agroforestry technologies, mixed tree planting) and/or plants and animals,
- tolerating 'associated diversity' consisting of spontaneous dispersal and regeneration at plot level (maintaining volunteer plants which are not 'weedy' enough to be worth taking them out, allowing insects and other animals to stay on below a 'pest threshold'),
- 'transient diversity' due to farmer experimentation and attempts to include new components; some of the components present may be remnants of the past, some current income-earners and others part of a 'trial and error' attempt to cater for the future.

At farm level, additional complexity arises from the multiple objectives and plant functions for a farm household. These multiples objectives can be met in an integrated approach by complexity at plot/field level, in a segregated approach by maintaining between-field diversity on farm, or by participation in a market economy and specialization in sectors of comparative advantage (segregation at a higher scale).

At village/community/watershed scale, the presence of multiple actors, all with their own objectives, constraints and ideas (related to gender, age, family size, resource endowment) adds to overall diversity and complexity. In the landscape mosaic interactions between fields and farms will have impacts on the 'associated diversity', as it modulates dispersal and migration processes, especially for the higher levels of the food web.

FUNCTIONAL BELOWGROUND BIODIVERSITY

Human interest in belowground biodiversity may be based on a number of perceived functions. We propose to group these under 7 headings, each with a number of questions which are likely to be of interest to natural resource management policy (Table 2). The ranking 1...7 reflects our rough assessment of the likely interest of society at large in soil biota, but we are not aware of more formal valuation efforts.

Research on belowground biodiversity has only recently started and both the concepts and methods still require a lot of attention. A priority setting is needed to focus the few resources available for this type of work. The items 2 and 3 may currently represent the highest commercial value, but the land use related to items 1 and 4...6 affect a much larger number of people, including the majority of smallholders involved in agriculture. Research on item 1 and 4 can provide the background for the more specific function 6 and will provide the background to questions on (re-) introduction of soil biota (5). Therefore, items 1 and 4 are seen as first priorities for publicly funded international research.

Table 2. Seven direct and indirect reasons for human interest in maintaining belowground biodiversity, and related questions on natural resource management

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1. Soil biota as contributors to soil fertility, maintenance of nutrient cycles and soil structure:
    - 1.1 Are basic processes of decomposition and mineralization affected by agricultural management practices?
    - 1.2 Does N_2 fixation and/or mycorrhizal infection contribute significantly to the N and P economy of the system and increase economic return on a sustainable basis?
    - 1.3 Is the economic efficiency of the system increased by maintaining an organically and biologically driven component to the nutrient cycles (as compared with reliance on inorganics alone)?
    - 1.4 Are negative impacts on the surrounding environment, e.g. by pollution of ground- and surface water and by emission of greenhouse gases, reduced or elevated in systems with organically and biologically driven nutrient cycles?
    - 1.5 Which contribution is made by soil macrofauna to soil conservation by increasing water infiltration and reducing surface run-off (deep-burrowing (non-pigmented) earthworms are the prime example) and how can this contribution be increased?
    - 1.6 Which contribution is made by maintaining soil structure as a favourable environment for (tree) crop roots and thus reducing the need for soil tillage, and how can this be further increased?
2. Soil as a source of genes, microbes and other soil biota for (*ex situ*) use in pharmaceutical industry or other biotechnology applications (this may represent the highest direct market value, but probably depends on soils in 'extreme environments' rather than 'normal' soils in agricultural use):
    - 2.1 Are current regulations of access to the belowground gene resource adequate?
    - 2.2 Are current activities in line with reasonable expectations of the real value?
3. Soil biota as producers of edible products (e.g. mushrooms), either *in situ* or *ex situ*:
    - 3.1 Are current harvest levels sustainable under current *in situ* management?

   3.2 Can soil biota be 'domesticated' for increased production in semi-natural or man-made environments?

4. Soil biological capital, concerns on overall land degradation and global homeostasis:
   4.1 Is there a 'soil biological capital' which is lost due to specific land use types and which restricts potential future usage of this land?
   4.2 Which aspects of land use are largely responsible for loss (or maintenance) of soil biological capital: conversion of forests, slash-and-burn and other techniques for land clearing, amount and quality of organic inputs, use of agro-chemicals?
   4.3 What is the role of soil biota and their diversity in global homeostasis by maintaining balance in the global C and N cycles and dissipating carbon sequestered in photosynthesis and nitrogen fixed by microorganisms or industries? specific attention may be needed for the greenhouse gasses methane and nitrous oxide which can be oxidized in soils in the neighbourhood of production sites, before they reach the lower atmosphere?
5. Benefits and risks of (re-)introduction of soil biota,
   5.1 Can symbiontic inoculants (*Rhizobium*, mycorrhizal fungi) be targeted to those soils and crops/trees where a real response can be expected?
   5.2 How can quality control be provided for the considerable number of inoculants available commercially?
   5.3 Can we assist farmers and land managers in a better judgement of whether and where the use of general microbial inoculants ('biofertilizer') is worth the money spent on it?
   5.4 What are risks and benefits of (re-)introduction of soil meso- or macrofauna (e.g. earthworms, dungbeetles)?
   5.5 How can we assess the risks of releasing genetically modified soil (micro)organisms?
6. Soil biota as antagonists and suppressants of 'soil-borne diseases', reducing the need for agrochemicals,
   6.1 Which soil-borne diseases are directly influenced by land use practices, including organic matter management?
   6.2 Can generalizations be made on antagonism and suppression beyond the specifics of well-known diseases?
7. Soil biota as a valuable component of the biosphere in their own right, reflecting an important part of the evolutionary history of the biosphere,
   7.1 How important is this 'intrinsic value' argument relative to the more direct values presented by 1...6?
   7.2 Does the 'intrinsic value' argument lead to specific conservation efforts beyond points 1...6?

Whilst the study of soil biology has a long history, including the famous studies by Darwin (1837, 1881) on the role of earthworms in soil formation, the links between the diversity of the soil biota and the functional values they are perceived to have is poorly established (Giller *et al.*, 1997). The study of belowground biodiversity per se is indeed a relatively new focus. The obvious difficulties of method in obtaining inventories of belowground diversity have hampered such investigation. But as such studies procede, driven by the new concerns about biodiversity loss and global change (Point 4), it becomes more and more apparent that biodiversity belowground is significantly in excess of earlier predictions and often greater than that aboveground (Giller, 1996; Eggleton *et al.*, 1995).

There is remarkably little detailed evidence that agricultural intensification (in a broad sense, including an increase in the fraction of time that land is cropped, the use of fertilizer, pesticides, mechanization and/or control of soil water content by irrigation and drainage) results in a loss of biodiversity in soil (Giller *et al.*, 1997) or whether thresholds of biodiversity change, significant in terms of the function described in Table 2 can be detected (Swift *et al.*, 1996). Initial studies on the macrofauna, particularly earthworms (Fragoso *et al.*, 1997) have shown that significant changes in soil biodiversity do indeed occurr under land use change (Lavelle and Pashanasi, 1989) and that these can have functional consequences (Pashanasi *et al.*, 1996). A particularly interesting example is given by Fragoso *et al.* (1997) who showed that conversion of Amazonian rainforest to pasture can lead to reduction of earthworm diversity to the extent that only a single species survives resulting in soil compaction due to its massive surface casting activity. Significant impacts of land use change on the termites and nematodes have been shown for the Cameroon rainforest (Eggleton *et al.*, 1996; Hodda *et al.*, 1997) and significant shifts in system carbon fluxes have been anticipated. Swift *et al.* (1998) have summarised a number of other studies across a range of environments. Part of the soils used for temperate zone agriculture, however, can be mistreated to a remarkable extent and yet crops continue to support crop yields close to their theoretical maximum provided external inputs replace biological functions.

In the last ten years a number of initiatives have been taken within tropical environments, to fill these gaps and contribute to elucidation of the questions raised in Table 2. Giller *et al.* (1997) proposed a number of hypotheses and questions that need to be answered within such research. A comprehensive approach is being taken to investigate the relationship between land use change and soil biodiversity in Indonesia, Cameroon, Brazil and Peru by the Alternatives-to-Slash-and-Burn (ASB) project, a consortium of scientists was formed, working on soil macrofauna as well as soil microbial properties in a range of land use types (from forest to 'degraded' lands). The main hypotheses underlying this work relate below- to aboveground biodiversity and overall C balance of land use systems, so the work is carried out as part of an integrated survey. It is pioneering work which is likely to yield a number of surprises. The first step will focus on 'land use change' (the large steps, 4.1), to be followed later (4.2) by research on the management options within a given land use type (mulch management, aboveground diversity of crops and 'weeds', re-introductions).

The diversity belowgound is huge comprising a wide array of fungi, bacteria, protists and representatives of the majority of terrestrial invertebrate phyla. No survey can realistically hope to cover all groups. The approach in the ASB project has therefore been to concentrate on a sub-set of taxa. These have been selected largely on two criteria - that they have significant and relatively well defined functions of significance at the ecosystem scale or beyond; and that they are methodologically accessible for biodiversity studies. These groupings are shown in Table 5.

There is as yet little evidence to guide us in determining the extent of soil biodiversity that should be maintained in an agroecosystem or other land use in order to obtain the benefits described in Table 2. The only exception to this generalisation is the case of nitrogen-fixing bacteria (Point 4) which have been studied sufficiently to derive some insights into the value of their benefits, although even here there is still a large area of uncertainty (Giller and Wilson 1991). The challenge remains both to evaluate the benefits of soil biodiversity and to develop the means for its conservation and management. Soil organisms can be manipulated directly (e.g. by inoculation) or indirectly through soil management ('planned diversity', tillage, selective pesticides etc) or plant and organic matter mangement (Swift *et al.* 1998). This implies the development of an integrated approach to soil management analogous to the IPM concepts in pest control (Woomer and Swift, 1994; Brussaard, 1997). That such practices should be an explicit part of agroecosystem design may seem an obvious priority, but it is still far from being incorporated into the conventions of agricultural development.

LINKS BETWEEN ABOVE- AND BELOWGROUND DIVERSITY

Plants can affect the functioning of the belowground ecosystem via litter quality, quantity and timing (with the directly soluble leachates affecting the microflora and the more structural components providing substrate for 'comminutors'), root exudates and turnover, the soil water balance and microclimate in the surface layer. Plant diversity can lead to a wider array and/or a more continuous supply of substrates for the belowground system. In return, the belowground community provides a number of 'environmental services' for the plants; the functions in mineralization and decomposition are broad-based and there is little evidence that specific groups are needed, or that more diverse systems function better from a plant's perspective. Current models of belowground food-webs are reasonably successful in predicting the time pattern of N mineralization for a given structure of the foodweb and abundance of functional groups, but even in the most intensively managed and simplified agro-ecosystems mineralization of organic residues still functions (De Ruiter *et al.*, 1995). Specific relations occur in the symbionts, diseases and their antagonists and it is here that belowground diversity may facilitate aboveground diversity.

Table 3. Effects (=>) of plant diversity (PD) on belowground biodiversity (BB)

	Aspect	Effect	Soil organisms	
PD	Litter quality and timing	Leachates	Microflora	BB
		Structural material	Comminutors. Engineers	
	Root quality and timing	Rhizosphere effects: C-supply, Enzymes, pH, Aeration, N-mineralization	Rhizosphere microflora + related mesofauna	
		Food source	Rhizovores	
		Symbionts	Symbionts	
		Soil structure	Microflora	
	Water balance	Drying cycles => structure	all	

Table 4. Effects (<=) of belowground biodiversity (BB) on plant growth (PG)

	Effects	Functions	Groups	
PG	Resources	N, P mineralization	Comminutors, microbes, mesofauna	BB
		N_2 fixation	*Rhizobium*, *Azospirillum*, etc.	
	Uptake efficiency	Mycorrhiza formation	Mycorrhizal fungi	
		Soil structure => Root growth	Ecosystem engineers	
	Biotic relations	Root turnover, plant death	Rhizovores	
		Protection against diseases and rhizovores	Antagonists	

Table 5. Main functional groups of soil organisms; the **bolded** groups are included in the TSBF Soil Biodiversity Network in the ASB project

Soil Organisms	Engineers and Comminutors	Decomposers and Foodweb	C, N and P Transformers	Acquisition and Manufacture Symbionts	Rhizovores, Plant Parasites and Diseases	Antagonists and Suppressants
Macrofauna	**Earthworms, termites**	**Ants, cockroaches, millipedes, centipedes**				
Mesofauna	Enchytraeids	**Nematodes (omnivores, bacterivores, fungivores, predators),** collembola, mites			Termites (plant parasitic)	
Microfauna		Protozoa				
Fungi		**"Microbial biomass", platable fungi, subtrate-specific groups**		**Mycorrhiza (endo and ecto)**	Soil-borne pathogenic fungi	Parasitic fungi, nematophagous fungi
Protista						
Bacteria			Methanogens and **methanotrophs, nitrifyers** and denitifyers, P-solubilizers	***Rhizobium***, *Frankia*, *Azotobacter*, *Azospirillum*	Soil-borne pathogenic bacteria	Parasitic bacteria

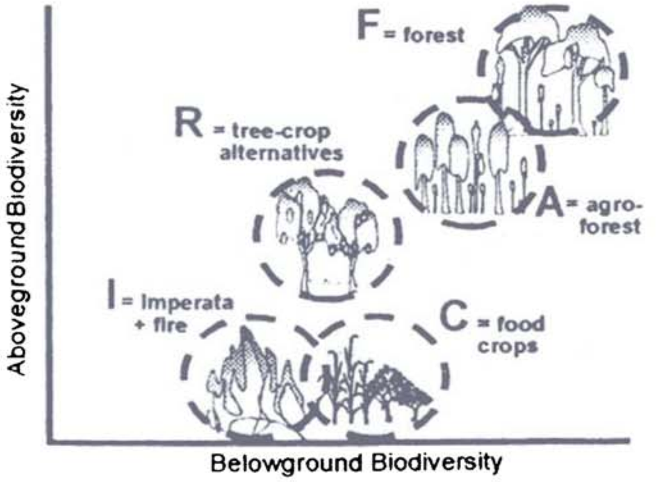

Figure 3. Hypothetical relationship between below- and aboveground biodiversity during intensification of land use in the tropics.

Causal links between aboveground (plant) diversity and belowground biodiversity are likely to exist (Table 3), but probably involve considerable time lags. Little is known of how long it takes for the belowground ecosystem to respond to even such drastic changes as a conversion of forest to crop or grassland. For re-introducing aboveground diversity ('rehabilitation of degraded lands') the lack of specific groups of soil organisms may limit potential aboveground (plant) diversity (Table 4), but little hard data exist. Functional relations between above- and belowground biodiversity, mediated by roots, are likely to involve time-lags and may show 'hysteresis' (Figure 3). Soil organisms tend to have less effective means of dispersal than most aboveground organisms and may thus become a rate-limiting step for ecosystem adjustment in as far as they are critical for the functioning of aboveground vegetation. This is most likely to be the case for specialized obligate symbionts such as mycorrhizal fungi and specific rhizosphere organisms. The rate of establishment of plant-parasitic nematodes was recently shown to be a major determinant of the primary succession in sand dunes in the Netherlands (Van der Putten *et al.*, 1993), which had been previously interpreted on the basis of nutrient availability.

As herbivory and its belowground counterpart of rhizovory (Van Noordwijk *et al.*, 1998) exert a considerable selection pressure, it is understandable that plants spend a considerable part of their energy and nutrient resources on making 'secondary metabolites' which play a primary role in making plants less attractive as food (Brown and Gange 1991). Several of the antinutrinutional factors such as silica needles and polyphenolics continue to inhibit comminution and decomposition. Such relations have been poorly quantified so far, but recent observations (Min Ha, *pers. comm.*) of limited earthworm activity under *Tephrosia candida* fallow, a species with a high rotenon content, may give an explanation for the surface accumulation of its litter. Crop domestication has often led to a reduction of these substances to increase the harvestable yield and consumption value. Interestingly, where the labour efforts required to guard crops from herbivores without chemical defense exceed the labour required for removing the toxins in food processing, as in 'bitter cassava' preferred by African farmers for out-fields, plant chemical defense properties may be retained during domestication. Decomposition may be accelerated in agroecosystems and there be less need for maintaining an assembly of specialists.

Partly decomposed remains of root systems can facilitate subsequent plant roots and their symbionts. In acid soils in the humid tropics old tree root channels can be important for crop root penetration, water infiltration and nitrogen management (Van Noordwijk *et al.*, 1991). Decaying roots of a previous forest vegetation provide a micro-environment facilitating nodule development of subsequent tree plantations (Figure 4).

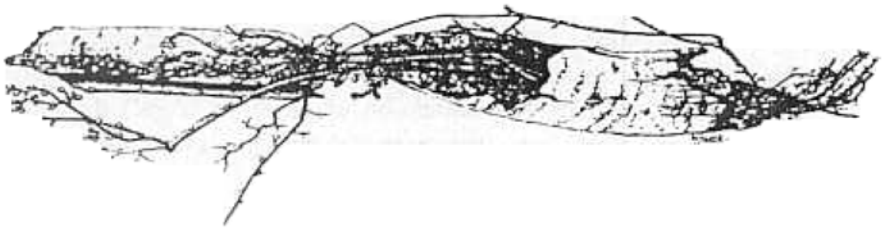

Figure 4. *Acacia mangium* growing in decaying tree root from the previous forest vegetation in southern Sumatra (Indonesia). Inside this old tree root, the *A. mangium* roots had many root hairs and were profusely nodulated, while nodulation in mineral soil was far less (drawing by Wihyono).

FUNCTIONAL ATTRIBUTES OF PLANNED AGRO-ECOSYSTEM DIVERSITY

A dominant trend in land use change globally is still the replacement of diverse natural ecosystems by simpler man-made ones and the on-going replacement of diverse 'traditional' agricultural systems (e.g. multiple cropping) by simpler, more specialized ones, based on specialization (less species, monocultures, simple rotations) in coarser grain landscape mosaics. A reverse trend, to re-diversify agricultural systems, is often perceived as desirable ('integrated agriculture', 'agroforestry'), but is an exception on a global scale as yet. It remains an open debate whether this trend to spatial segregation is based on a real superiority of such specialized land use types, or on the limited capacity of research to develop effective alternatives strengthening complexity and integration (Sanchez, 1995; Vandermeer *et al.*, 1998).

Planned diversity of agro-ecosystems can aim at larger total resource capture (Cannel *et al.*, 1996; Van Noordwijk and Garrity, 1995) and/or at reduced risk if the components have a partially different response to environmental variability (Van Noordwijk *et al.*, 1994; Van Noordwijk and Ong, 1999). Root architecture (Van Noordwijk and Purnomosidhi, 1995) has long been recognized as important in determining the success of mixed stands of trees or trees and crops (see references to the work of Coster in the 1930's in Van Noordwijk *et al.*, 1996).

The conceptual scheme of Figure 1 attributed an important role to the non-harvested part of plant production. Apart from the root systems, non-harvested parts consist of crop residues. Giller and Cadisch (1995) discussed the conflicting selection pressures on leguminous components of crop systems, which are grown for their bean yield as well as positive effects on subsequent crops. Crop domestication and selection towards a higher harvest index increases the direct value, but reduces the indirect benefits; if the nitrogen harvest index (fraction of total biomass N which is in the harvested products) exceeds the fraction of total N derived from atmospheric N fixation, the legume will start to have a negative rather than positive effect on the overall N balance.

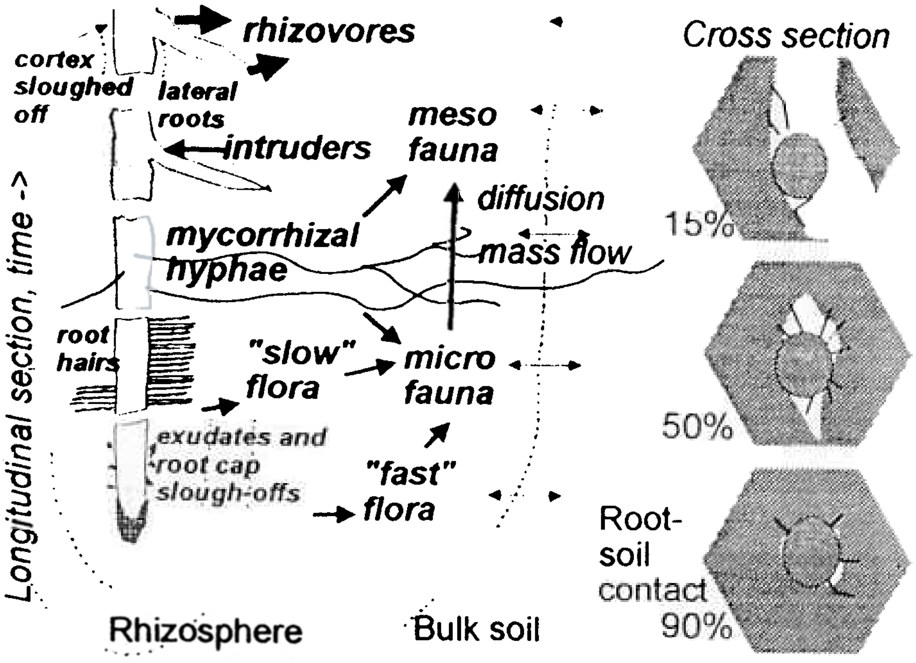

Figure 5. Schematic view on interactions between roots and biotic factors in the rhizosphere (based on Clarholm, 1985 and Dhillion, 1993) along a longitudinal section of the root representing changes in time (left side of the figure), and a cross section (right) highlighting the range of root-soil contact situations which is likely to exist in structured soils (Van Noordwijk *et al.*, 1993).

Agricultural production is possible without soil, soil organic matter or soil biota, if technical means are used to provide for the daily demands of water and nutrients of a crop (Van Noordwijk *et al.*, 1993). This means that no absolute thresholds exists for a gradual decline of the belowground resource base of agro-ecosystems. Yet, the technical means which can replace the functions of soil ecosystems are normally beyond the means of farmers, at least in most of the tropics (Van Noordwijk *et al.*, 1997).

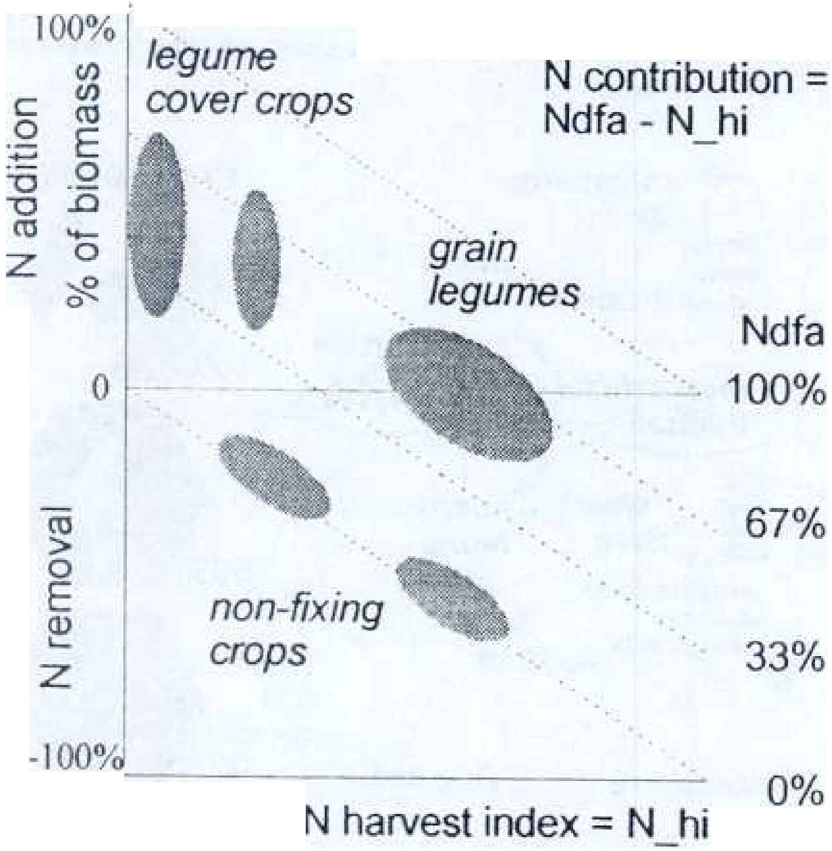

Figure 6. Relation between N harvest index, relative effectiveness of atmospheric N fixatin and net effect of a legume on the N balance of a cropping system (based on Giller and Cadisch, 1995).

In the past the concept guiding agriculture was 'the more roots the better crop growth', but evidence in simple agricultural systems has pointed that this is an overstatement (Van Noordwijk and de Willigen, 1987) and that the highest production may be obtained in systems with relatively small root systems, which (in absolute size) are smaller than the root systems obtained at suboptimal water and nutrient supply. In intercropping situations, however, more extensive root systems of the component species have value for the production of component species, as they modify competitive strength. Models such as WaNuLCAS (Van Noordwijk and Lusiana, 1999) can evaluate the total water and nitrogen capture by combined root systems, and may help in preventing 'over design' of the belowground component of more complex systems, as the carbohydrate costs of root systems are certainly not negligible (Buwalda, 1993). The superior resource capture abilities of trees tend to limit the opportunities for a close association of cros and trees on a patch scale, but when a partial spatial segregation is maintained (e.g. by using trees as border plantings, esp. on the downhill side of fields) the tree roots abilities for exploitation of local patches of fertility (Huxley, 1996; Caldwell, 1994; Van Noordwijk *et al.* 1996) may lead to a desirable level of 'lateral resource capture' (Van Noordwijk and Ong, 1996), reducing the leakiness of agroecosystem.

Extrapolation from small measurement units to landscape scale can not be based on the average values assigned to 'units', but should incorporate internal heterogeneity. Rooting patterns are important in exploiting as well as creating spatial heterogeneity of the soil (Fitter, 1994; Kooistra and Van Noordwijk, 1996; Van Vuuren *et al.*, 1996). The potential size of the root system of a single plant determines the scale at which plants can respond to heterogeneity. For a tree in an African parkland savanna this may be a circle with a radius up to 50 m, for a short lived annual one with a radius of 0.5 m or less (Van Noordwijk *et al.*, 1996). These differences between plants in scale of their operations have important consequences for experiments and data collection (Hauser, 1993).

Agronomic research methods are normally based on the fiction that there are internally homogeneous units in the landscape and that studying a few representatives of these units is a sound basis for 'scaling up' to the landscape scale. Internal homogeneity of experimental units may reduce the experimental error term when treatment effects are quantified, but often the implicit assumption is made that treatment effects would not be modified by internal heterogeneity. Van Noordwijk and Wadman (1992) showed that this assumption may have lead to substantial underestimates of the 'environment' - 'production' conflict in agricultural fertilizer use, as both the yield response curve and the nitrate pollution response curve depend on field level heterogeneity in factors determining N supply and demand to the crop. The resulting problem can be addressed in two complementary ways: at patch/field scale by reducing within-field variability with technical means and applying new information technology for 'precision farming', and/or at field/farm scale by maintaining a network of 'filter' elements which can mop up the left over resources flowing over or below the surface (Van Noordwijk *et al.*, 1998). The two approaches are complementary, but in tropical systems where the technical opportunities for precision farming are out of reach and the specific knowledge of farmers for implicit precision farming disappears, it may be a safe bet to retain and enhance a network of filter elements. Whereas field level practices specialize and deviate further from natural ecosystems, landscape level complexity in the form of mosaics can get additional functionality.

CONCLUDING REMARKS

The Maglus proposal that tries to establish the impacts of land use change on agrodiversity and specifically on the belowground aspects thereof, has to balance between three questions: does land use change indeed have effects on belowground organisms, does this matter for key soil functions and are these impacts perceived to be important by farmers or external stakeholders.

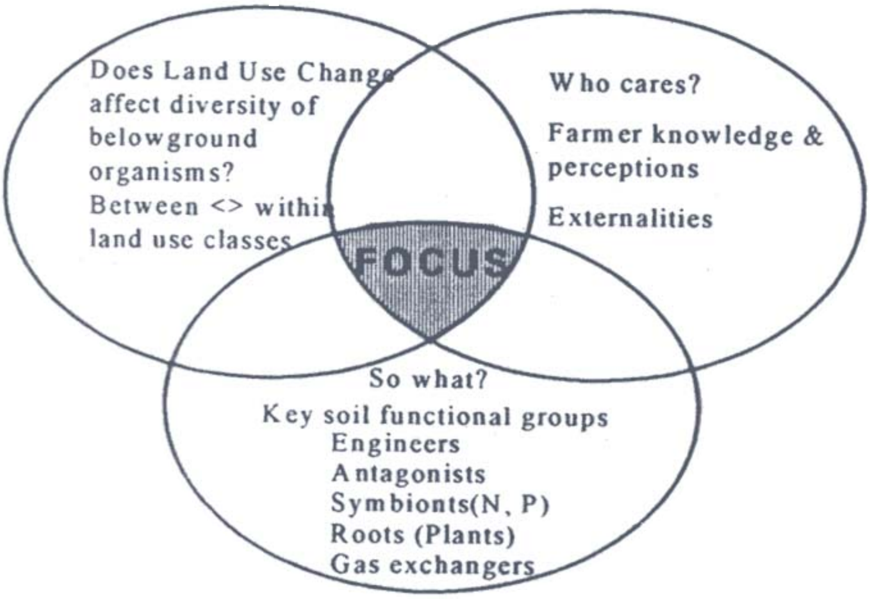

Figure 7. The focus of the Maglus project should be to help identify which real impacts of land use change on belowground biota have a direct effect on key soil functions that are relevant to farmers and/or external stakeholders; the three circles imply different approaches (biological surveys, experiments and models, studies of farmer knowledge and perceptions).

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