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## Review article

# Role of pathogens, signal recalcitrance, and organisms shifting for ecosystem recuperation. A review

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**Abstract** – Nature ability to adapt to ecosystem changes such as cultivation depends upon microbial interactions with plant, animals and humans. A such organisation is made possible in particular by signal exchanges, horizontal and vertical transfers of genetic material from one organism to another, the efficient use of pathogens and environment in food web interactions, the ability to metabolic modifications of shifting, and the potential to assume dormancy under unfavorable conditions. So far industrial agriculture has led to pollution and declines of biodiversity and soil carbon. The biodiversity of agricultural fields can be improved by several processes such as DNA-uptake; viruses and horizontal gene transfers; animals carrying propagules, spores, cysts and seeds from less disrupted environments; and sexual reproduction. Within weeks soil water retention capacity, nutrients availability, communication, and high biomass production is improved. In less perturbed but unfertilized, shifting cultivation systems a return to original productivities needs about 50 years.

**genetic-chemical signals / environmental cues / informational ecology / self-organisation / host-control / biofilms / anabolism / catabolism / defence / cryptobiosis / food web interactions**

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## 1. INTRODUCTION

Ecosystems, disrupted by fire, volcano eruptions, storms, flooding or to a lesser extend perturbed by faunal predation, browsing, soil compaction due to root growth or grazing, return to their initial productivity by orderly successions of herbivore-carnivore, detritus based above- and belowground

food webs (Wardle, 2002). Manmade activities like ploughing, fertilization, pest management, mining, urban development or industrial waste disposals shatter agro-ecosystems and may cause carbon debts, e.g., of 702–3452 Mg CO<sub>2</sub> ha<sup>-1</sup> in palm- and soybean-biodiesel farms and enhance atmosphere-, ground- and water-pollution. On the other hand, it is observed that agricultural sites regain high biomass productivities much faster than traditional, unfertilized shifting cultivation systems

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where the soil is turned over with hoes for a few years' cultivation after having areas cleared of the original steady state vegetation (Addiscott, 1995; Benckiser, 1996; FAO, 1999; Parry et al., 1999; Buckley and Schmidt, 2003; Benckiser, 2007a; Crutzen et al., 2007; Vogel and Babel, 2007; Fargione et al., 2008; Searchinger et al., 2008; Martinez-Inigo et al., 2009; Benckiser, 2010). Shifting cultivation systems need about 50 years, fertilized agricultural sites only weeks to recuperate and to return to high productivities.

About  $10^{10}$ – $10^{11}$  bacteria, sub-grouped into 6000–50 000 species, and about 200 meters fungal hyphae per gram soil care for about 5 to 80% of the annual plant nitrogen- and for about 75% of the phosphorus-demand (van der Heijden et al., 2008). Agricultural and natural biomass productivities rely on these recycler communities. Ratios between agricultural and natural biomass productivities ranging between 0.1 for Zaire and 1.07 for Benelux states reflect the quantum leaps in agricultural yields, honed during the last 5000 years, and indicate a positive influence of agricultural measures on the self-organized and host-controlled microbial activities and shifting (Esser, 1994; Benckiser, 1997; Honermeier, 2007; Valentine, 2007; Benckiser, 2007a; Ganapathy et al., 2009).

New methods, developed through the last decades, brought a variety of new insights into nature's recuperation concepts, usually studied on the plant and animal level with recognition of microorganisms in nutrient recycling processes (Benckiser, 1997; Benckiser and Schnell, 2007; Wardle, 2002; Nannipieri et al., 2003; Kolter and Greenberg, 2006; Fuchs, 2007; von Lützow et al., 2007; van der Heijden et al., 2008; Bahn et al., 2009). Resourceful ideas have been liberated about the transitory nature of soil pore space environments and signal transfers, metabolic soil functioning, the self-organized and host-controlled interactions of above- and belowground food webs, environmental networks, and the remarkable abilities of horizontal gene transfers practicing microorganisms to form communities that conduct the portrayed life sustaining biochemical processes.

## 2. PERTURBATIONS, ADAPTATIONS AND SURVIVING

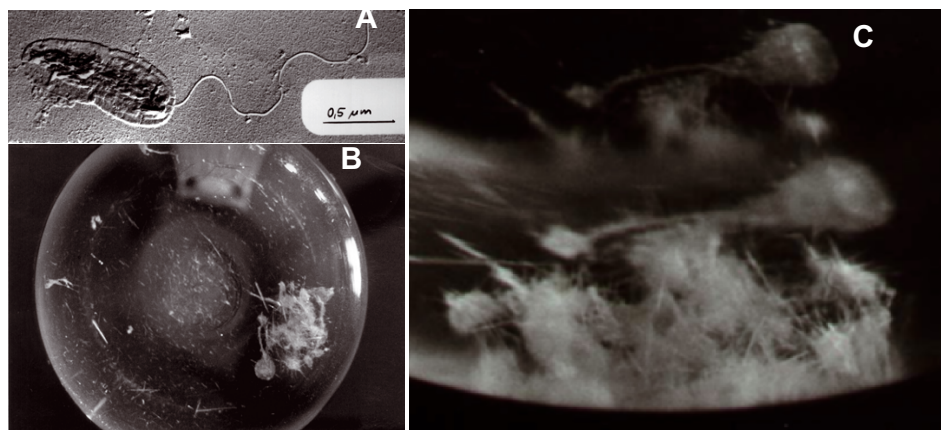
### 2.1. Information exchange

Biological information, stored in sugar-phosphate backbone genomes, replicates along template strands in opposite direction. Bases join matching bases on templates and form new identical DNA. Adaptation on environmental changes is achieved by mutations or genetic information received from outside. A crucial role in receiving genetic information from outside play DNA or RNA containing viruses and virus derived transposable (jumping) elements (TE) having genome sizes between 0.0046 (*Escherichia coli*, 0.3%) and 5.0 piko-grams (*Zea mays*, 60%; Tashiro et al., 1987; Suttle, 2005; Biemont and Vieira, 2007; Goldenfeld and Woese, 2007; Wolfe et al., 2007). Viruses, considered as gene repository and memory of a community, replicate either lysogenic in

host genomes or are lytic by bursting the host cell. The error rates during replication are high and consequently the genetic diversity of viruses exceeds that of eu- and prokaryotes together. The host-integrated viral DNA is occasionally shattered, disintegrates, the host cell starts reproducing virus particles, bursts, and releases not only the virus particles but also quantitatively important amounts of nutrients into the surrounding environment. Metabolism around the virus particles resumes. Matter-, ATP- and heat-gradients emerge. The system moves away from its previously status (Rubi, 2008). Microbes, plant roots and animals are attracted. New virus-host interactions can develop. Genetic information is transported. Vehicles are besides viruses (transduction), virus RNA based transposable elements, freed and uptaken DNA (transformation), horizontal gene transfers among bacteria (conjugation) and sex among eukaryotes (Goddard et al., 2005). All these genetic vehicles play a vital role in colonizing biochemical niches and in replenishing continually the genetic variability. New capabilities are obtained (Benckiser, 2007a) as documented by a sudden conversion of harmless *E. coli* strains into hemorrhagic fever causing bacteria (Karch et al., 2005) or by a three times more often occurring virus-*Staphylococcus aureus* dependent pneumonia than primary viral pneumonia (Tashiro et al., 1987). Increasingly found are antibiotic resistant bacterial strains. Antibiotics excreted into an environment may cause species redundancy (Naeem, 1998). All these interacting activities are increasingly understood (Knight, 2004; Kolter and Greenberg, 2006; Tebbe and Schlöter, 2007).

Masterly bacteria exchange up-taken viral or freed DNA among each other and are thus the most promiscuous replenishers of ecosystem meta-genomes. Almost daily are newly formed bacterial species detected (Vogel et al., 2009) and only recently it has been observed that animals engulf whole plastids and integrate them, though it is without doubt that sex among animals cares majorly for genetic information exchange (Rumpho et al., 2008).

Pro- and eukaryotic cells communicate not only on the gene level. A broad variety of signals like non-coding RNAs, bis-(3'-5')-cyclic dimeric guanosine monophosphate (c-di-GMP), 2-heptyl-3-hydroxy-4 quinoline (PQS), c-adenosin monophosphate (cAMP), homoserine lactones, epigenetically changed chromatin structures, methylated or acetylated histones, methylated cytosine, matrix slimes (polysaccharides), extracellular products consisting of polysaccharides, proteins and nucleic acids (EPS), flagellin, environmental cues activating hundreds of hidden genes, quorum sensing (gene expression in dependency of cell density), and stochastic, mostly non-deterministic fluctuations, "noise" add to the information exchange in nature (Matasuyama et al., 1992; Kessin et al., 1996; Darby et al., 2002; Rao et al., 2002; Sourjik and Berg, 2004; Mashburn and Whiteley, 2005; Branda et al., 2006; Hartmann et al., 2007; Kubicek et al., 2007; Hengge, 2009). Noise appears to be a universal information carrier, though the next state cannot fully be foreseen. Plants secrete a huge number of communicators, inter alia hormones for attracting and manipulating growth promoting microbes in their rhizospheres (Ratering et al., 2007). Biofilms formation is the visualized result (Falk and Wuertz, 2007).



*P. aeruginosa* strain B 8a, isolated from waste water effluent with HCB-agar (TEM picture A) and tested for HCB-degradation in a mineral salt medium (pH 7.3, 30 °C; 150 mg cold HCB, 6 mg U-<sup>14</sup>C-ring labelled HCB  $l^{-1}$  added in hexane that was withdrawing by evacuation) under a reduced O<sub>2</sub>-atmosphere and in presence of NO<sub>3</sub><sup>-</sup> (3.2 mg N  $l^{-1}$ , alternative electron acceptor; 10% O<sub>2</sub>, v/v). After about 4 months of incubation strain B 8a suddenly started to form a biofilm around the HCB-crystals (B and C; pictures made 5 month after the start of incubation). Several hexane extractions unveiled that the bacterial biomass detained about 8,5% of the radioactivity (13 mg  $\pm$  1.03) and only 0.07 mg or 0.048% was found as <sup>14</sup>CO<sub>2</sub> (Benckiser, 1980). Though degradation of HCB, a very recalcitrant, ozone depleting, bio-accumulating, as fungicide since 1981 (Stockholm convention) banned substance, is not confirmed until today it was found that energy gaining dehalorespiration occurs among strictly anaerobic syntrophic consortia but also among several anaerobic bacterial isolates and seems to be universal and increasingly understood (Holliger *et al.*, 1999; John *et al.*, 2009; Ravishankara *et al.*, 2009).

**Figure 1.** Biofilm formation around hexachlorobenzene (HCB) crystals.

## 2.2. Biofilms or the organizing of protection, survival and growth promotion

Water is solvent in all metabolic active cellular systems and hydrophobic compounds having the tendency to exclude water are essential for biological compartmentalization. Since the bioavailability of hydrophobic compounds is generally limited, microbes have developed various physiological mechanisms to degrade hydrophobic organics (Ottow, 1997), inter alia biofilm formation at solid material-liquid interfaces (Fig. 1).

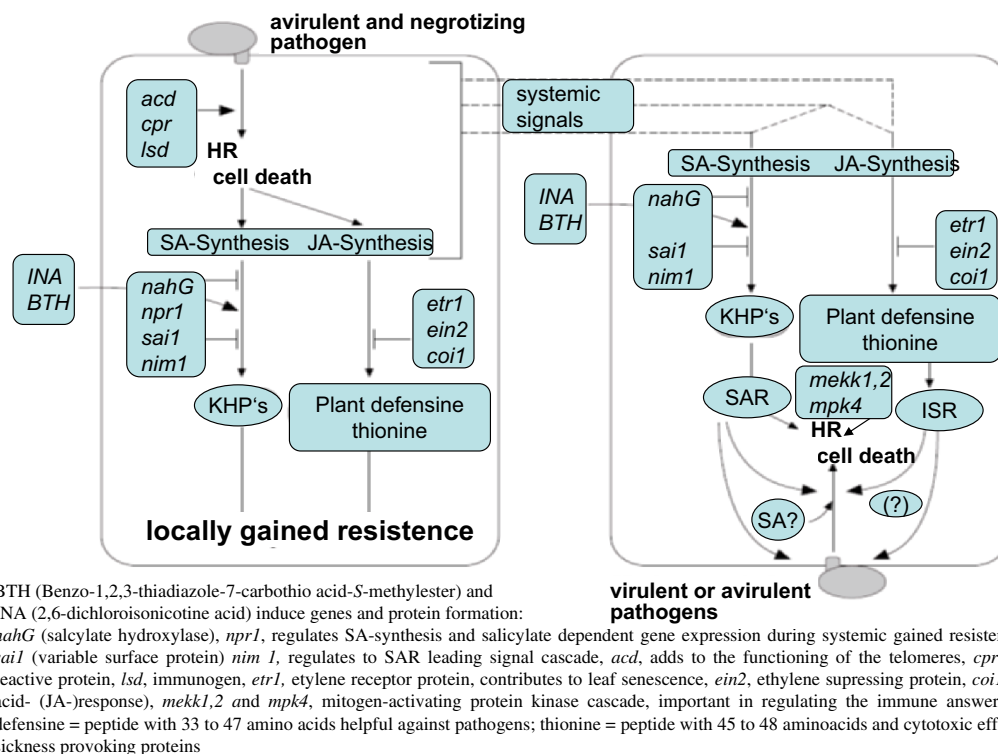
Biofilms, considered as cybernetic units of increasing auto cognizance, are wide-spread in nature and are generally initiated at less favoured growth conditions. (Ben-Jacob, 2003; Morris and Monier, 2003; Falk and Wuerzt, 2007). Biofilm forming organisms must have the following capabilities: they should be able to

- recognize solid surfaces;
- attach to them with the advantage not being separated from extra cellular enzymes and hydrolyzates;
- synthesize and excrete extra cellular polymeric substances (EPS, matrix slimes) for a self-organized embedment;
- form a fine-structured environment with solid/liquid, liquid/liquid, solid/gas, and liquid/gas interfaces, void spaces and channels in the EPS layers that a multitude of nutrients and soluble carbon compounds can pass and nourish the embedded cells; and
- receive information from outside that adaptation to a new life style can be organized.

The biofilm organization improves the internal information exchange and hereby EPS and matrix slimes not only act as mechanical buffers but also as signal carriers for hundreds of hidden genes. In the inner part of biofilms immobilized anaerobes can proportional to their activities and protected from desiccation, UV, bactericides and predation ferment on a  $\mu$ m scale at aerobic conditions outside. The plurality of phase transitions and developing oxygen-, nutrients-, proton-, electron-, ATP- and heat-gradients increases. Biofilm and surrounding micro-environment move far away from a thermodynamic equilibrium (De Beer, 1999; Yoon *et al.*, 2002; Morris and Monier, 2003; O'Toole, 2004; Benckiser, 2007a; Ratering *et al.*, 2007; Rubi, 2008).

Embedded cells lose virulence (O'Toole, 2004) what not explicitly means less defence as the *Caenorhabditis elegans-Yersinia pestis* example or likewise the fruiting body formation of the gliding bacterium *Myxococcus xanthus* and the social amoeba *Dictyostelium discoideum* unveil (Kessin *et al.*, 1996; Darby *et al.*, 2002). *Y. pestis* seals with an electron dense biofilm matrix the mouth of attacking nematodes. Self-aggregating bacteria and protozoa like *M. xanthus* or *D. discoideum* form fruiting bodies to protect inside residing cells from being ingested by worms.

Plants export 5–50% of their photosynthates into their rhizo- and phyllospheres for attracting bacteria, archaea and fungi, stimulating biofilm formation, matter and information fluxes, and finally the mutual nutrition (Trofymow *et al.*, 1987; Hansel *et al.*, 2001). Small and larger animals graze



**Figure 2.** Induction and expression of systemic gained resistance, adapted from [Mauch-Mani and Metraux, 1998; Ausubel, 2005; Stein *et al.*, 2008; Badri and Vivanco, 2009; Santner and Estelle, 2009].

The scheme shows how induction and expression of systemic gained resistance and the systemic answer on a virulent or necrotic attack, on pathogenic organism might occur. The complexity is only halfway understood and our daily increasing knowledge adds continually to the presented scheme.

on rhizo- and phyllosphere biofilms and employ the engulfed microbes (Brune, 2006; Benckiser, 2010).

### 2.3. Plant-animal-host microbe interactions

It is meanwhile well-known that bacteria, archaea, protozoa, chytrids, fungi and various worms including their viruses co-operate in a symbiotic or parasitic way with plants and animals. Secreted extra-cellular materials help to connect better photosynthesis, inorganic nutrition and information exchange. Signal compounds originated from intercellular or intracellular living microbes and transferred into the cytoplasm of plant cells or the blood streams of animals/humans are increasingly identified (Stone and Coulter, 1932; Lundberg *et al.*, 2004; Stein *et al.*, 2008). An estimated 80% of plants associated bacteria excrete auxine (indole acetic acid, IAA) that stimulates cell division and cytokinin that retards senescence. Such exudates extend the microbial access to the plant nutrients pool (Jones and Dangl, 2006). *Pseudomonas syringae*, *Xantomonas campestris* or *Rhizobium spp.* use a type III secretion system to inject inter alia coronatine, a jasmonic acid mimic, into plant cells for suppressing salicylic acid, important in systemic resistance (Fig. 2).

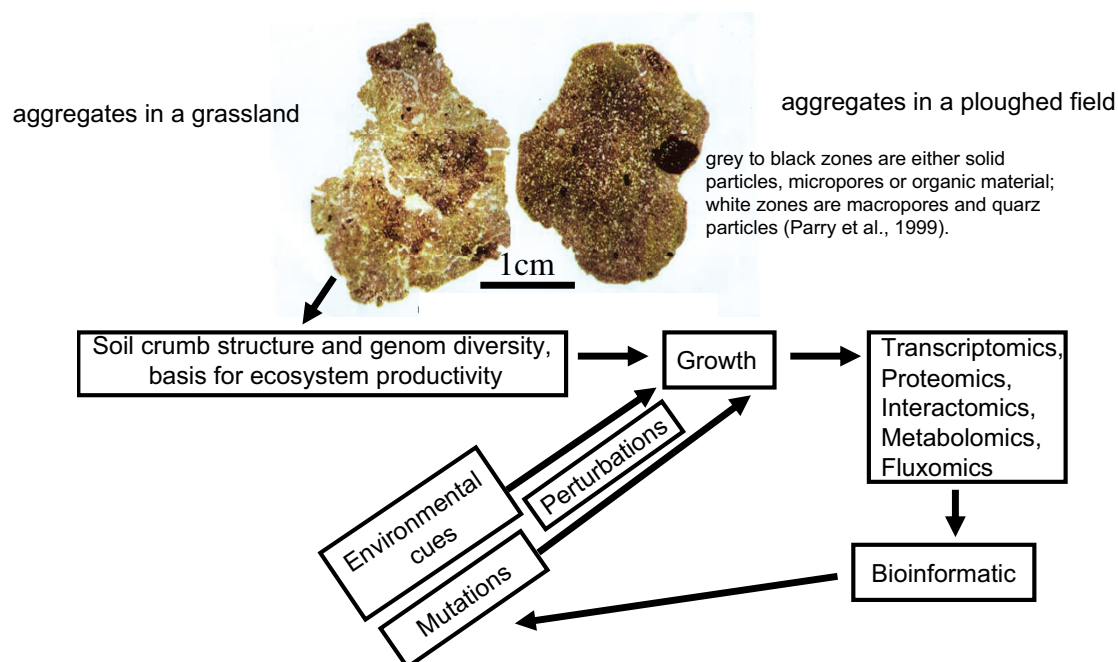
Plants lacking a phagocytosing immune system that detects signals from foreign bodies and directs destruction of

the invader as in animals respond on foreign attacks with a two branched system relying on systemic signals emanating from the infected site. The first branch consisting of trans-membrane pattern recognition receptors identifies molecules such as flagellin and other effectors common to many groups of pathogenic and non-pathogenic microbes. The second branch produces nucleotide-binding, immunity activating leucine-rich proteins (NB-LCR) which enable to react on invaders. Inter- and intracellular spaces of roots, stems and leaves or intestines inhabiting microbes act as mediators between the in- and organic world and especially sessile organisms (bacteria, plants) must molecularly recognize abiotic and biotic signals in order to organize competition between non-parasitic and parasitic microbes and to improve and stabilize immune system, nourishment and health (Fig. 2).

### 2.4. Soil pores and water availability

The soil pores diameter separates inhabitants by their body size and the thickness of soil pore water films determines microbial growth and biofilm formation (Figs. 1 and 3). Soil gas flux measurements exhibit that despite drying conditions microbial activities continue and environmental cues are important in co-ordinating a living together (Benckiser, 1996). A value describing the water availability in soils is the pF





**Figure 3.** Soil aggregates (environmental cues) and a broad variety of other ecosystem regulators control situation dependent the transcription of information, stored in the genomes, into mRNAs, the translation into proteins and other metabolic products, metabolites fluxes to the places of demand, and adaptation enabling to react on perturbations.

(Tippkötter et al., 2009). At a relatively low pF-value of 1.8 the soil pores water films in a Haplic Luvisol and a Stagnic Anthrosol were with 3.0 or 10.6  $\mu\text{m}$ , respectively, much thicker than earlier believed and might explain the continuing gas fluxes at drying conditions. In conserving water film thickness in soils the presence of colloidal dispersed nano-particles (fine clay) is seemingly of importance. During rainless periods the generally found bacteria densities of  $10^7$  to  $10^8$  cfu  $\text{g}^{-1}$  dry soil (e.g., Caesar-TonThat et al., 2007) and the grazing predators can be evidently longer active in the retained water than earlier believed and at returning rainfalls soil pores water films can be as thick as 30  $\mu\text{m}$  with microrheological effects (Tippkötter et al., 2009). At such conditions biofilm grazers like Chilopoda or Gamasid mites will be active and control developing biofilms (Benckiser, 1997). In addition to the water film thickness spatially fine-structured biofilms prolong cell activities at drying conditions and the prolonged continuing genetic information exchange under worst getting conditions may contribute to the extraordinary genomic diversity found in soils, rhizo-, phyllo-, and intestiospheres. In biofilms starting from one phenotype up to 60% differing cell and colony structures can be expressed (Ben-Jacob, 2003; Knight, 2004; Kolter and Greenberg, 2006). It is therefore difficult to trace the bacterial geno- and phenotypes abundance and the microbial plurality (evenness) in soils (Buckley and Schmitt, 2003; Schmeisser et al., 2003; van der Heijden et al., 2008; Jones et al., 2009). Only a low percentage of the assumed bacterial geno- and phenotypes abundance in soils is presently known. Indicated is a dominance of proteobacteria, low G+C, Gram positive bacteria, bacteria of the Cytophaga-Flavobacterium-

Bacteroides group, smaller fractions devoted to Actinobacter and archaea. Corresponding programs are on the way to get a more realistic picture of the microbial diversity in soils and other environments (Vogel et al., 2009).

## 2.5. Signal compounds, and animal specialists living on polymers

In order to survive under varying climatic and soil conditions especially sessile organisms as many bacteria, protozoa and all plants must release and integrate a broad spectrum of abiotic and biotic environmental signals, which for being recognized must surpass threshold concentrations (Shaw et al., 2006; Paterson et al., 2008). The surpassing of a threshold concentration is achieved by releasing signal compounds with an inherent recalcitrance or in high concentrations. Communicators with an inherent recalcitrance accumulate by resisting degradation and high concentrated released signal compounds are recognized even when proportions of them are disappearing. Flavonoids, having a variously substituted phenol nucleus and are involved in organizing the early development of symbiotic  $\text{N}_2$ -fixation, exemplify communicators with an inherent recalcitrance (Ottow, 1997). Besides flavonoids locally acting ethylene, nitrate, ammonium and a variety of other, mostly unidentified chemicals contribute to the early development of symbiotic  $\text{N}_2$ -fixation. Such signals are high concentrated released and are accordingly recognized (Benckiser, 2007b). Proteinaceous, biofilm preventing lactoferrins excreted by plants and secondary metabolites released

by bacteria, actinomycetes and fungi must also have a certain recalcitrance for being effective in controlling competitors (Ottow, 1997; Morris and Monier, 2003; Schroeckh et al., 2009). Such toxic compounds may cause species redundancy (Naeem, 1998).

Specialist in living on cellulose and lignin rich, recalcitrant substrates, are termites and harvester ants (Brune, 2006; Benckiser, 2010). Living on polymeric substrates affords exoenzymes to cleave complex structures into monomers, which can be channelled into the cytoplasm, and for narrowing the substrate immanent wide CN ratios communication with N<sub>2</sub>-fixing bacteria must occur. Highly specialized co-operations and processes, essential for life on earth like photosynthesis, respiration or N<sub>2</sub>-fixation, often or exclusively work host-controlled and less self-organized (Tamiaki et al., 2003; Benckiser, 2007a; Ganapathy et al., 2009). Co-operating recycling processes, e.g. in earthworms' intestines supplemented with nitrogen richer substrates like freshly decaying organic resources or excrements, on the other hand, work rather self-organized. Pre-digested, N-containing diets preferring earthworms enrich the up-taken food with mineral soil and gut fluids to maintain intestinal recycler communities (Makeshin, 1997; Whalen and Fox, 2007). Successional fungal species guide earthworms to find freshly decaying organic resources (Bonkowski, 2004). Earthworms contribute in average with 32% to the soil-C and N-turnover. In receiving sufficient nitrogen poikilothermic earthworms allow the co-operating intestinal communities more degrees of freedom than legumes N<sub>2</sub>-fixing bacteroids, perhaps because earthworms can survive by dehydrated, semi-biologically active cocoons at an intestinal malfunctioning.

## 2.6. Cryptobiosis and metabolic shifts

Pro- and eukaryotes survive long term stress situations at barely detectable metabolic activities or semi-biologically as dehydrated cells, spores, cysts, cocoons and seeds (Leubner-Metzger, 2005; Seki and Horikawa, 2007). Semi-biological specialists are water bears (*Tardigrada* spp.). Biofilm forming *Y. pestis*, the fruiting bodies forming *M. xanthus* or *D. discoideum* or the ample studied water bears reduce at unfavourable growth conditions the surface area by self-aggregation and internal controlled cell dehydration. At such events the cryoprotectant trehalose suspends the membrane and protein structures in high viscosity and the heat shock protein *hsp70* fold newly synthesized polypeptides correctly. The water bear metabolism similar as in tobacco plant seeds where the metabolism is 10–20 folds lower than during germination decreases to about 0.035% of its active stage.

Semi-biological, cryptobiotic or long term surviving is wide spread in nature and enables microbes, nematodes, some mites, and the cocoons of earthworms to resist agricultural measures. Larger animals, extinguished by agriculture, may return from adjacent less disturbed environments. Single cell organisms like bacteria, archaea, protozoa, algae, yeasts and some multi-cellular fungi survive unfavourable periods over certain times by switching between auto- and/or heterotrophic

metabolisms, e.g. from oxygen respiration to anaerobic respiration or fermentation. Anaerobic respirations and fermentations generate less ATP and need as prerequisite rather fertile conditions (Crawford et al., 2005; Ratering et al., 2007; Walter et al., 2009). Specialists in using organically stored energy very efficient are archaea. Horizontally or vertically desiccation-tolerance expressing genes received from, e.g., savanna or dry tropical forest organisms can enhance the survival of less dry-resistant organisms of temperate regions (Billi et al., 2000). High metabolic activities of dry-resistant organisms rapidly resume upon rewetting (Singh and Kashyap, 2006).

Photosynthesis-, <sup>13</sup>C pulse-chase- and N<sub>2</sub>-fixation-related studies exhibited that the presently known 89 genera of the domain archaea are better adapted to stress than the 1.400 known genera of bacteria, which prefer fertile conditions (Martin et al., 2002; Valentine, 2007; Badri and Vivanco, 2009; Lal, 2009; Maharning et al., 2009). An example for an adaptation to fertile conditions rhizobia species provide. During the early symbiotic N<sub>2</sub>-fixation stages they communicate with legumes via flavonoids, a Nod signal perception system and a Nod signal pathway network (Benckiser, 2007a, b; Bottomley and Myrold, 2007). At later symbiotic stages the individual, free-living status is given up and the still mobile, root nodules entering rhizobia are turned into an immobilized, host-controlled, well-nourished, N<sub>2</sub>-fixing, bacteroid status. The bacterial morphology and physiology has to adapt to a nutrient rich life. Only under such conditions they are enabled to fix N<sub>2</sub> in amounts needed by the hosting plant. Released from decaying nodules into the genetic storehouse of soils less fertile conditions have to be faced. Mobility regains and the conserved information combined with new information taken up from the genetic storehouse soil allow to adapt to less fertile conditions and to improve the N<sub>2</sub>-fixing potential in future N<sub>2</sub>-fixation cycles. Legumes, interested in efficient N<sub>2</sub>-fixation cycles, other plants in growth promoting relationships and animals in functioning intestinospheres have their co-operating microbial partners evolutionary adapted to more fertile conditions (Valentine, 2007). Archaea, on the other hand, possess less futile membranes than bacteria, conserve very efficiently small amounts of metabolically useful energy during several successful catabolic modes, hold exclusivity in case of methanogenesis, and thus out-compete bacteria in less fertile niches. Bacterial membrane structures allow a higher lateral diffusion. Because a low permeability would impair photosynthesis, respiration, N<sub>2</sub>-fixation, signal transduction and nutrients uptake the third domain eukarya has assumingly overtaken the bacterial membrane structure (de Vries and Schröder, 2002).

Compost heaps, intensively studied by Jäckel and Kämpfer (2007), provide good nutrients and energy rich conditions for the recycler microflora at beginning of the composting process. Along compost development the nutrients are incorporated into the microbial biomass, CO<sub>2</sub> is enriching, and a shifting from a bacterial to an archaeal dominance is observed. During the recycling of faecal depositions of grazing animals or after fertilization of agricultural fields a similar microbial shifting can be assumed and needs to be studied in more

details (Singh et al., 2002; Grayston et al., 2004; McCulley and Burke, 2004; van der Heijden et al., 2008).

### 3. ECOSYSTEM RECUPERATION OR RESTORATION OF A HIGH PRODUCTIVITY

Much thicker water films in soil pores at drying conditions outside than earlier believed allow that bacteria and plants can prolonged incorporate photosynthesis derived C and fix nitrogen into their biomass. Faunal co-operations can prolonged disrupt polymeric structures by shortening the residence time of matter. Actinomycetes and fungi can prolong mining for phosphorus and all recycler organisms can prolonged transform stored energy into ATP and heat (entropy) (Maraun et al., 1998; Nannipieri et al., 2003; Bonkowski, 2004; Jäkel and Kämpfer, 2007; van der Heijden et al., 2008; Rubi, 2008; Tippkötter et al., 2009). Animals contribute to recuperating ecosystems by disrupting polymer structures, depositing excrements, and transporting ingested microbes and seeds over short and long distances. Besides air transported microbial and seed genomes animals are important vehicles in re-colonizing perturbed agricultural fields. The activity of metabolic specialists, fertilization related priming effects, the integrative role of animals and plants crucial for self-controlled matter/energy operations in rhizospheres and soils, and the cross-linked photosynthesis to an ecosystem functioning far away from the thermodynamic equilibrium is prolonged through soil pores water retentions, which are longer lasting than as earlier believed (Cabello et al., 2004). Price and Sowers, 2004; Scheublin et al., 2004; Franken and George, 2007; Maherali and Klironomonas, 2007; Ratering et al., 2007; Falkowski et al., 2008; van der Heijden et al., 2008; Esperschütz et al., 2009; Kool et al., 2009; Singh et al., 2009). Small, catabolically released molecules (e.g., methanol,  $H_2$ ,  $NO_3^-$ , ethanol,  $CH_4$ ,  $N_2$ ,  $NH_3$ ,  $O_2$ ,  $CO_2$  or  $H_2O$ ; per g fixed carbon 200–500 g  $H_2O$  is vaporized) can continue to be converted into less dissipative, polymeric structures (biomass). The transformation of solar energy into heat (entropy) slows down. Microbial metabolic activities and replications (abundances) can prolonged withstand geographical exposures (latitude, altitude, precipitation patterns), climatic changes, predation, and agricultural cultivation measures. Greenhouse gases releases into the atmosphere will be retarded and decline. Semi-biological life guaranteeing a periodic long term surviving finally enables to return to a water and nutrients dependent, synergistic, partly host-controlled working together that results in high, sustainable and economically produced biomasses.

To understand the noise dependent, synergistic, entropy balancing co-operations beyond ecosystem recuperation reasonably in their complexity is not that easy. Presently, it is known that members of the fungal families *Gigasporaceae*, *Glomeraceae*, experts in phosphorus-mining, co-operate with  $N_2$ -fixing rhizobia at the interphyla level. Such co-operations, embedded in manifold other soil processes, improve the own and the plant nutrition and make plants fit to counteract pathogens (Singh et al., 2009). To understand such complexities is future challenge (Schroeckh et al., 2009). Archaea,

about 30 years ago discovered, grow as bacteria under aerobic, anaerobic, phototrophic and lithotrophic conditions (Cabello et al., 2004; Ratering et al., 2007; Valentine, 2007). They can ferment, nitrify, denitrify, reduce  $H_2$ -dependent  $CO_2$  and sulphur, form  $CH_4$  and oxidize it anaerobically, couple proton reduction directly to proton translocation, and consume only a fraction of ATP from the net energy driving catabolism. With all these evolutionary developed capabilities archaea are stress-adapted and out-compete bacteria as soon as  $CO_2$  becomes major electron acceptor. The membranes of archaea, consisting of isoprenoidal alcohols instead of fatty acids esterified to a glycerol in bacteria, are less permeable to ions and energy loss. Archaea can reduce their energy demand drastically as the  $\Delta G' ATP$ -growth, -maintenance and -survival ratio of  $10^6:10^3:1$ , respectively, exhibits and possess several proton translocating ATP-synthases. They translocate only one ion per round of catabolism, maintain better a chemiosmotic potential, and can the stoichiometry of ion translocation better vary with the availability of energy from substrates than bacteria. The bacterial advantage is that they include pathogenesis into their growth concept (Fig. 2), grow inter-/intracellular (photosynthesis, respiration, mitochondria, symbiotic  $N_2$ -fixation as examples), synthesize extensively natural products (secondary metabolites, toxins), and survive as complex morphological structures (biofilms, spores) or dehydrated. In summary, archaea and mining fungi are superior adapted to chronic soil stress (lower net primary productivity), bacteria to fertile conditions (higher primary productivities; Esser, 1994; Grayston et al., 2004; van der Heijden et al., 2008).

In nutrient rich environments like fertilizer-receiving agricultural fields cell-wall degrading, proteolytic, chitinolytic and cellulolytic *Bacillus amyloliquefaciens*, surfactin, iturin-like lipopeptides secreting *Pseudomonas fluorescens*, a variety of siderophores; antibiotics, such as pyrrolnitrin and phenazine-1-carboxylic acid, or respiration inhibitors like HCN releasing, growth promoting microbes contribute to a better nutrition and strengthen plant health by controlling pathogens (Leon et al., 2009). After fertilization (nutrients surplus) catabolic active, volatile compounds releasing bacteria dominate the system (Valentine, 2007). Shifts the system to low nutrients availabilities archaeal and fungal activities will dominate as many publications across the journals indicate. Research programs deciphering the bacteria/archaea genetic membrane and biochemical adaptation mechanisms and entropy balancing at varying nutritional and environmental situations are on the way and important in this context is the role of pathogens in stabilizing the immune system of plants and animals (Fig. 2; Stone and Coulter, 1932; Lundberg et al., 2004).

In the spirit of statistical mechanics and dynamical systems theory a returning to harmony (soil quality) after perturbations, a redeveloping of ecosystems to new levels of order, requires energy and information flows (Fig. 3; Green et al., 2004; Goldenfeld and Woese, 2007; Moore et al., 2007; Oberholzer and Höper, 2007). Surprisingly, not traditional, little perturbed, by orderly food web successions stabilizing agricultural shifting cultivation systems but agro-ecosystems maintained by



30 cm deep ploughing, sophisticated crop rotation programs including intercropping, and organic and/or mineral fertilizer inputs reach high biomass productivity levels faster (Esser, 1994; Addiscott, 1995; Wardle, 2002; Honermeier, 2007). An enhanced SOM-conversion accompanied by increased greenhouse gas emissions is seemingly the prize of fertilization and a faster returning to high productivities (Crutzen et al., 2007; von Lützow et al., 2007; Fargione et al., 2008; Searchinger et al., 2008). Agro-ecosystem mismanagements combined with climatic disruptions may fertile land deteriorate into deserts as it is already observed worldwide and much finer sampling scales are recalled. It is still difficult to differentiate between fertilizer-, soil type-, plant-, fauna- and agriculture-related effects on soil carbon declines (Cleeg et al., 2000; Green et al., 2004; Jones et al., 2006; Vogel et al., 2009). Still statistically explained in terms of a few environmental variables are substantial proportions of variation in species richness and functioning. Almost missing is a predictive theory of messaging molecules, signal transduction, integrated genome regulation, and synergisms in subsystems. Biologists, agriculturists, physicists, (bio-) chemists, and ecologists are challenged to fill this gap.

Breeders have already started to select low input varieties (Ruiz et al., 2008). Auxiliary microbes are on the agenda of researchers in order to connect photosynthesis and nutrients mining better (Gómez-Gómez and Boller, 2002; Benckiser, 2010; Brundrett, 2009). In near future exciting results about the manipulative power that synergistic systems can exert over each partner may be generated that more advanced and integrating ecosystem management concepts can be developed.

#### 4. CONCLUSION

Genes express or inhibit the action of other genes. Proteins, a broad variety of signal compounds and environmental cues control the functioning of organisms in ecosystems. Recombination, exposure to poisons, mutation, viruses and migrating animals are genetic vehicles caring for genetic variation and adaptation to changing conditions. Majorly small-sized organisms like bacteria, archaea, fungi, protozoa, nematodes and semi-biological cocoons of earthworms survive agricultural cultivation measures. Larger sized animals and their functions, extinguished by agricultural measures, may return from adjacent, less disturbed environments.

Better adapted to dung-urine returns are the 1400 known genera in the domain of bacteria than the 89 known genera in the domain of archaea. Archaea overtake leadership at energy and nutrients stress. Little understood are still the periodical modifications of intercommunicating bacterial, archaeal, fungal, plant and fauna based genomes, transcriptomes, proteomes, interactomes, metabolomes and fluxomes (Figs. 1–3). Little understood is further the fertility related shifting in between recycler communities. The domain archaea has evolutionary developed less futile membranes, exclusivity in case of methanogenesis, and the capability to conserve very efficiently small amounts of metabolically useful energy during several successful catabolic modes. The bacterial mem-

branes allowing higher lateral diffusions have been adapted to manifold co-operations with eukaryotes. Due to these morphological and physiological specifications bacteria out-compete archaea at more fertile conditions and vice versa archaea bacteria at nutrients stress. The organism shifting is seen as basis for a successful ecosystem returning to stability after perturbations. The third domain Eukarya has overtaken the bacterial membrane permeability, presumably because a low permeability would impair photosynthesis, respiration, signal transduction and nutrients uptake. The manifold interactions between microbes and plant-animal hosts including pathogenicity is a strong hint for understanding better nature's self-organized and host-controlled recuperation approaches. Exiting results can be awaited in future, the more, because new and rapidly developing methods applied to small scaled samplings allow increasingly insights into microbial and micro-faunal activities.

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