Plant–microbe interactions as drivers of ecosystem functions relevant for the biodegradation of organic contaminants

Thomas Fester, Julia Giebler, Lukas Y Wick, Dietmar Schlosser and Matthias Kästner

The plant organism and associated microbial communities can be seen as a sunlight driven hotspot for the turnover of organic chemicals. In such environments the fate of a chemical will not only depend on its intrinsic structural stability toward (bio-)chemical reactions and its bioavailability but also on the functional effectiveness and stability of natural microbial communities as main drivers of natural attenuation of chemicals. Recent research demonstrates that interactions between plants and microorganisms are crucial for the biotransformation of organic chemicals, for various processes affecting the bioavailability of such compounds, and for the stability of the affected ecosystem. Practical bioremediation approaches, therefore, should encompass integrated measures targeting functional vegetation as well as functional microbial communities. Good examples for a successful practical approach are constructed wetlands, where an artificial, simplified ecosystem is used for the detoxification of organic contaminants. While such systems have considerable practical success, they are often treated as a black box and a sound mechanistic understanding of functional resilience and of the 'reactive power' of such plant–microbe ecosystems is poor. This situation has to change, if progress in the application of bioremediation is to be made.

Addresses
Helmholtz Centre for Environmental Research – UFZ, Permoserstrasse 15, D-04318 Leipzig, Germany

Corresponding author: Wick, Lukas Y (lukas.wick@ufz.de)

Introduction

Bioremediation is widely regarded as a preferred method for the natural attenuation of chemicals of human and environmental concern (consecutively termed as 'contaminants') and there is intense research aiming at improving its performance [1•,2]. Most approaches are focusing on single genes, organisms or groups of organisms, as exemplified by the term 'phytoremediation'. However, effective turnover of contaminants as of any other chemical should be seen as a function of the complete ecosystem and thereby depends on the functional stability and the interactions of a large range of organisms in a given environment. In particular many of the processes connected to plant–microbe interactions (Figure 1) can be regarded to be of crucial importance for understanding and managing terrestrial ecosystems challenged by organic chemicals.
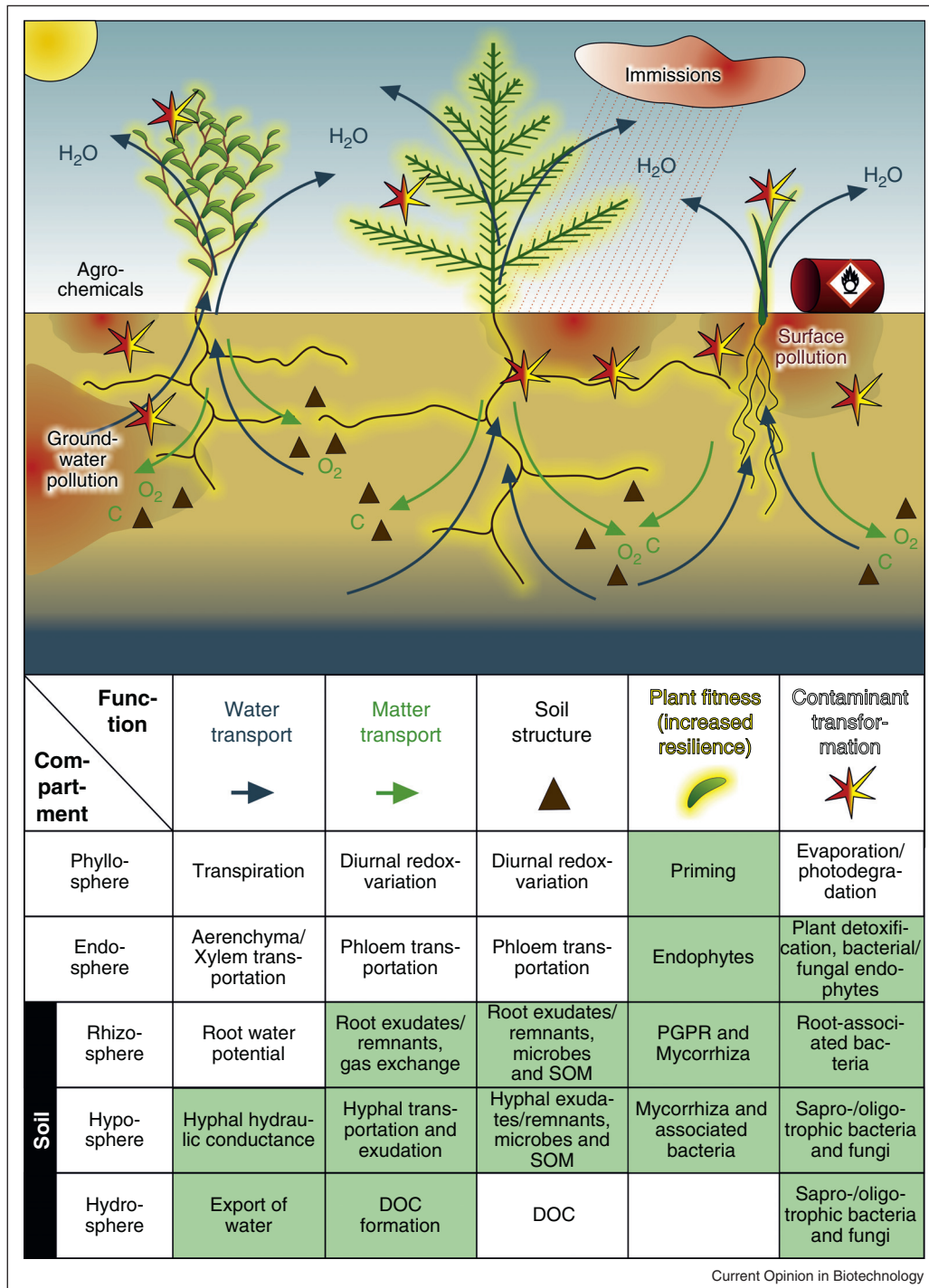
The keyword 'plant–microbe interaction' covers a wide range of interactions (Figure 2). While this review focusses on mutualistic interactions, it tries to include the whole range of interdependencies from obligately symbiotic to purely saprotrophic microorganisms. This includes mycorrhizal fungi and close bacterial symbionts (*Rhizobium*, *Frankia*), bacterial and fungal endophytes, as well as numerous saprotrophic or oligotrophic fungi or bacteria colonizing the rhizosphere. In all cases plant-derived carbon is exchanged against benefits comprising improvements in plant mineral nutrition, plant tolerance of biotic and abiotic stress, and plant hormone regulation. While there is an increasing amount of research analyzing the interactions of plants with algae, nematodes or protists, this review will mostly focus on the plants' interplay with bacteria and fungi.

With reference to bioremediation of organic contaminants this review aims at presenting recent findings regarding the role of plant–microbe interactions in (i) degrading organic contaminants, (ii) increasing the bioavailability of organic chemicals in soil, and in (iii) practical approaches to bioremediate organic compounds.

The potential of plant-associated microorganisms for the biotransformation of organic contaminants

Prokaryotic and eukaryotic microorganisms can utilize organic contaminants as carbon and energy sources, or co-metabolize them in the presence of suitable growth substrates. Given the oligotrophic nature of soil, plant-derived carbon (e.g. from root exudates or remnants) is a crucial driver of such (co-metabolic) processes. Contaminants thereby can serve as electron donors becoming oxidized under both aerobic and anaerobic conditions, where various electron acceptors other than oxygen can enable anaerobic respiration processes. Moreover, halogenated organic compounds can also serve as terminal

Figure 1

| Compartment \ Function	Water transport ➡	Matter transport ➡	Soil structure ▲	Plant fitness (increased resilience)	Contaminant transformation
Phyllosphere	Transpiration	Diurnal redox-variation	Diurnal redox-variation	Priming	Evaporation/photodegradation
Endosphere	Aerenchyma/Xylem transportation	Phloem transportation	Phloem transportation	Endophytes	Plant detoxification, bacterial/fungal endophytes
Rhizosphere	Root water potential	Root exudates/remnants, gas exchange	Root exudates/remnants, microbes and SOM	PGPR and Mycorrhiza	Root-associated bacteria
Hyposphere	Hyphal hydraulic conductance	Hyphal transportation and exudation	Hyphal exudates/remnants, microbes and SOM	Mycorrhiza and associated bacteria	Sapro-/oligotrophic bacteria and fungi
Hydrosphere	Export of water	DOC formation	DOC		Sapro-/oligotrophic bacteria and fungi

Current Opinion in Biotechnology

Processes and compartments involved in bioremediation of organic contaminants. Processes connected to plant–microbe interactions are marked in green color. SOM, soil organic matter; DOC, dissolved organic carbon; PGPR, plant growth promoting rhizobacteria.

electron acceptors, either supporting growth in dehalorespiration or becoming incidentally dehalogenated due to lacking enzyme specificity in co-metabolic processes. Both growth-supporting and co-metabolized organic chemicals can be degraded to CO_2 and H_2O, whereas oxidative anaerobic co-metabolism or reductive dehalogenations represent biotransformations commonly resulting in organic metabolites.

Figure 2
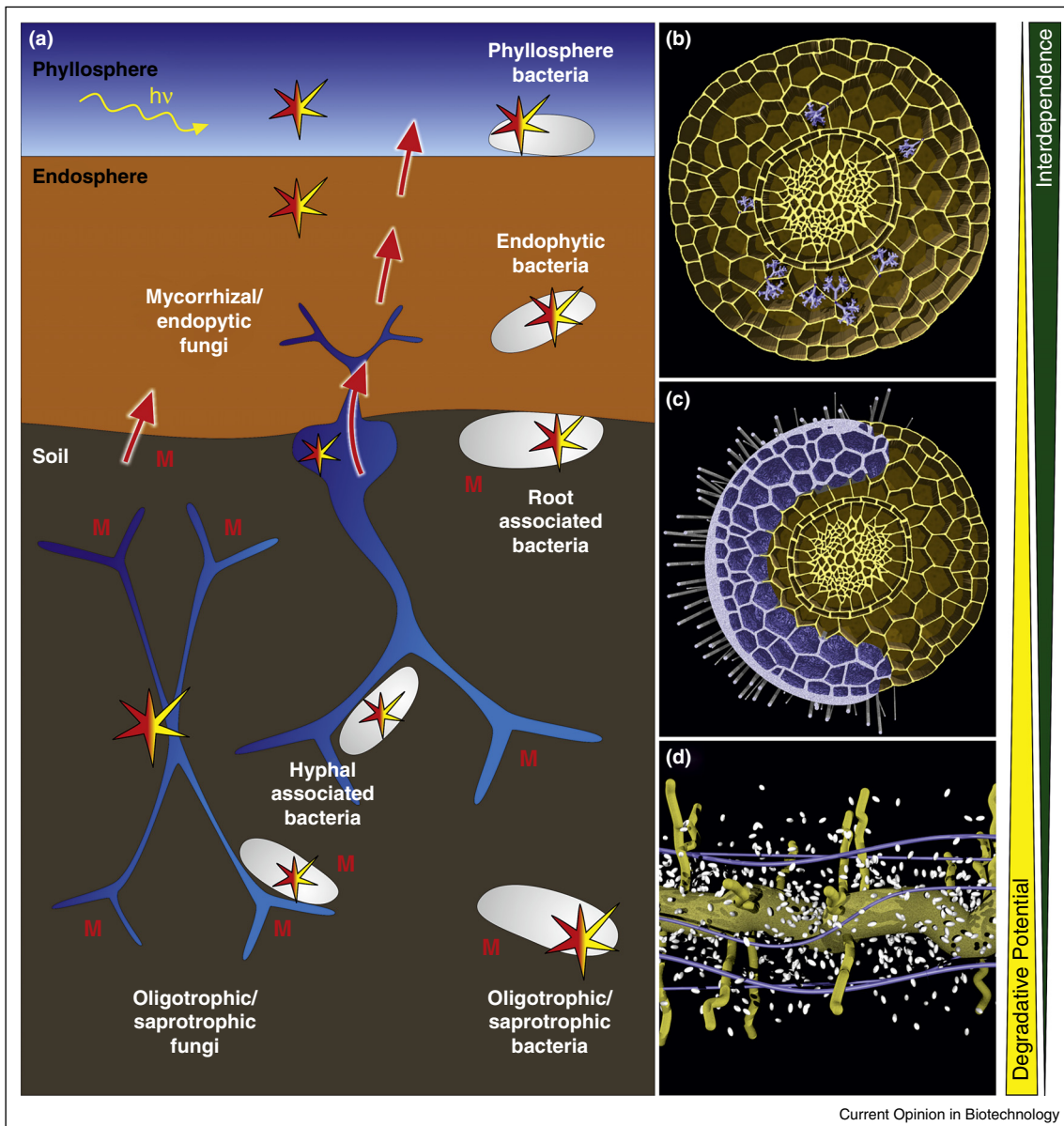
Mobilization and degradation of organic contaminants by plant roots and associated microorganisms (in white); **(a)** schematic summary: important transport routes of organic contaminants are indicated by red arrows, mobilization of organic contaminants by a red 'M', transformation of organic contaminants is indicated by a yellow/red star, and fungi are depicted in blue (see also Figure 1). **(b–d)** Illustrations of typical interactions. (b) Arbuscular mycorrhizal fungi are forming arbuscules (highly branched hyphae constituting the main symbiotic interface) in individual root cortical cells in a root cross-section. (c) Ectomycorrhizal fungi are colonizing intercellular spaces in a cross section of a root tip. (d) Microorganisms colonizing the rhizosphere (depicted not according to their real size).

Mycorrhizae probably comprise the most prominent and closest forms of mutualistic plant–fungal interactions. Regarding the biotransformation of organic contaminants, ectomycorrhizae (ECM) have been most frequently investigated. Pure cultures of ECM fungi were shown to degrade various chloroaromatics, polycyclic aromatic hydrocarbons (PAH), and explosives such as 2,4,6-trinitrotoluene (TNT). An enhanced compound degradation was occasionally monitored in symbiosis of ECM fungi with plants [3••]. An enhanced dissipation of PAH and atrazine was also reported for arbuscular mycorrhizal fungi (AMF), although AMF have been less frequently investigated for bioremediation purposes than ECM [3••]. Pure cultures of ericoid mycorrhizal fungi were shown to degrade chloroaromatic herbicides [3••]. A few studies have demonstrated that colonization by AMF can increase the uptake of PAH by plant roots [4,5]. However, studies addressing the potential role of

mycorrhizal associations for the degradation of organic chemicals rarely go beyond monitoring their dissipation from the experimental system, leaving the question 'who is doing what' largely unresolved. Moreover, mycorrhizal associations were not always found to be beneficial for phytoremediation of contaminants [6], hence requiring analysis of the boundary conditions for a successful employment. Similar to mycorrhizal fungi, fungal endophytes have been reported to promote PAH removal from planted soil [7]. Metabolization and detoxification of plant defense compounds have been demonstrated for these fungi [8], and the production of contaminant-degrading enzymes by such organisms [9•] suggests a certain potential for the breakdown of organic contaminants.

In general almost all fungi attack organic contaminants oxidatively under aerobic conditions, despite the existence of very rare reports describing anaerobic fungal contaminant degradation [3••,10]. In addition, fungi primarily co-metabolize organic contaminants, that is, often depend on plant-derived carbon sources (like root exudates or root remnants). Fungal growth on contaminants seems to be restricted to compounds with rather simple monoaromatic (e.g. phenol, *p*-cresol, toluene) or aliphatic (e.g. *n*-alkanes) structures [3••]. Saprotrophic wood-decaying and soil litter-dwelling basidiomycetes, causing a white-rot decay type of lignocellulosic matter, possess a particular potential for the co-metabolic mineralization of a wide range of organic contaminants. This is due to the unspecificity of the catabolic radical reaction machinery primarily 'invented' for lignin degradation (enzymatic combustion), which involves a range of extracellular (peroxidases, multi-copper oxidases) and intracellular enzymes (e.g. cytochrome P450 monooxygenases) [3••]. Recent genome studies have demonstrated that ectomycorrhizal fungi lack lignin-modifying peroxidases known from lignin-degrading saprotrophic *Agaricomycetes*, whereas other potential candidate enzymes for organic contaminant breakdown (laccases/multi-copper oxidases, P450s) are present [11,12•]. This suggests a lifestyle-related, less distinct potential for the catabolism of organic contaminants in biotrophic compared to saprotrophic fungi.

In contrast to fungi, bacteria deploy more specific enzymes for contaminant transformation, involving also alternative electron acceptors thereby extending the microbial activity beyond oxygenated zones [13]. The structural similarity of most xenobiotics to natural compounds (e.g. root exudates) and the ability for a rapid genetic adaptation generate an almost unlimited genetic versatility for degradation among bacteria [14], even toward non-natural chemical structures. Thus, retarded elimination of contaminants by bacteria in soil is generally due to unfavorable conditions for the respective degraders [15,16•]. The heterogeneous and often oligotrophic nature of soil, in particular in anthropogenically over-burdened soils, stratifies the bacterial range of action due to physical or chemical entrapment (of bacteria, contaminants or essential nutrients), unmet niche-requirements or inhibitory effects (e.g. high contaminant concentrations or the presence of co-contaminants) [17•]. Organismic interactions with other bacteria, with plants or fungi have been identified as important factors affecting the net-degradation performance of a community. The plant genotype and physiological status, for instance, determine the composition of the bacterial rhizosphere community [18,19], which might be either favorable or repellent for potential contaminant degraders. This impact is particularly important in the case of endophytic bacteria, which can transform contaminants taken up by plants to a certain extent [9•]. However, their contribution to the overall contaminant dissipation when compared to rhizosphere bacteria might be poor due to low (phylo-) genetic diversity and cell numbers.

'Microbial logistics' as promoter of biodegradation

Plants and their biotic/abiotic environment constitute a multitude of heterogeneous habitats for microbes. Some of these habitats may contain toxic mixtures of compounds or lack nutrients, water and/or appropriate terminal electron acceptors needed to support microbial communities capable of remediation. Similar to the problems of human transport logistics an effective flux of matter and energy between the point of origin and the point of consumption is needed for the well-being of microbial catalysts and the effective turnover of environmental chemicals ('microbial logistics'). Little is known, in this respect, about processes in the phyllosphere, one of the largest microbial habitats with an estimated surface area of $4 \times 10^8 \, km^2$ [20]. In the rhizosphere, by contrast, microbial turnover is often limited by the tendency of many chemicals to escape the aqueous microhabitats of most degraders, and to interact with the solid soil matrix or to accumulate in soil organic matter. A recent concept [21] measures bioavailability of a chemical by its *chemical activity* (i.e. its chemical potential to partition into organisms at equilibrium), and bioaccessibility as a chemical's fraction that is reversibly bound and can undergo rapid release into the aqueous phase. In bioremediation such approaches define operational physico-chemical endpoints, that is, degradation rates and maximal fractions of a chemical to be biodegraded, respectively. Yet, such a concept poorly accounts for the fact that bioavailability emerges from highly dynamic physical, chemical and biological interactions that shape the spatio-temporal exposure of individual organisms to chemicals in an environment. Confronted with this spatio-temporal heterogeneity in soil, many bacteria have developed evolutionary adaptations that help them to cope with an unfavorable (too high or limited) availability of chemicals. These adaptations include physiological

characteristics (e.g. the release of surface-active vesicles [22] or cellular swimming modes allowing to tactically follow water and airborne chemical gradients [23•]). Mycelial fungi, on the other hand, are often less sensitive to soil heterogeneities than bacteria [24], as long as soil environments are not extensively disturbed. By developing structures of high fractal dimensions that optimally exploit the three-dimensional space, they have adopted a unique life style that is adapted to environmental changes [25••]. The morphology and cytoplasmic streaming in mycelia reflect an effective foraging strategy that combines explorative expansion under poor nutrient conditions with growth in optimal environments. Hyphae thereby cross air–water interfaces, bridge air-filled soil pores, and may grow into soil pores with a diameter as little as 2 μm. They influence soil structure through electrostatic, adhesive and enmeshment mechanisms and have strong impact on organic matter decomposition. They also transport N and P nutrients, shape soil water infiltration properties by producing large quantities of hydrophobic compounds (hydrophobins) or help to extract soil water from pores under dry conditions [26]. Mycorrhizal fungi are also able to utilize hydraulically lifted water from plants to obtain nutrients in extremely dry soils and are thought to be mediators of infochemicals for bacteria and plants [27,28]. Not surprisingly bacterial–fungal interactions and their biotechnological applications have become a prominent topic in microbial ecology [3••,29••]. Particularly in soils, bacterial–fungal interaction mechanisms have improved our understanding of complex ecosystem dynamics [30,31]. Fungi are known to facilitate bacterial growth, alter bacterial community structures or promote the activity of 'fungiphilic' bacteria in the hyphosphere [32]. Mycelial networks may also serve as dispersal vectors ('fungal highways' [33]) for a wide range of bacteria and enable their (random or tactic) access to otherwise unattainable soil habitats [27] or mobilize a wide range of PAH by vesicle-bound cytoplasmic transport ('hyphal pipelines') [30]. Given the fact that 10–30% of the host plant's net carbon fixation is deposited in the rhizosphere and ends up in spatially dense mycorrhizal networks, fungal logistic networks may be of crucial importance for the degradation of organic contaminants in the rhizosphere; in particular as fungi often attack organic compounds using a range of unspecific extracellular oxidoreductases in mostly co-metabolic processes. By using simulation models that describe such highly complex dynamics in a simplified manner, key interactions can be disentangled and, with the help of ecological theory, the biodegradative effectiveness be simulated *in silico* [34•,35].

Plant associated microorganisms — the unseen majority in phytoremediation

As outlined above and similar to plant biomass production in terrestrial ecosystems in general [36], plant microbial symbionts may constitute the 'unseen majority' in 'phytoremediation' of organic compounds. Plants have an enzymatic potential for biodegradation of organic contaminants of their own (green liver concept [2]) and are clearly driving many important processes (water flux, carbon flux, redox conditions). They have a strong impact on soil microbial communities even under conditions of strong contamination [31] and they are often responsible for the architecture and mechanical stability [32] of a given system. Nevertheless, in reality, plant associated microorganisms often seem to be the real players mediating the plant impact on contaminant transformation.

Phytoremediation of organic contaminants has been described for the water compartment (employing constructed wetlands, CWs) and soil compartment. CWs are artificial systems consisting of a basin with water-logged soil filters usually planted with helophytes (plants with an aerenchyma for active oxygen pumping into anaerobic sediments [37•,38]). CWs are efficient, low-cost treatments systems but, similar to natural wetlands and depending on management measures, may have methane production as unfavorable side effects [39]. In comparison to soil phytoremediation, waste water treatment by CWs can be considered as a state of the art remediation technology based on ecological principles, as they encompass plant-mediated and microorganism-mediated contaminant removal strategies and allow interactions among the various partners [plant-induced formation of oxic–anoxic interfaces with diurnal spatial changes due to light (and dark) driven metabolic processes]. Besides domestic and industrial waste water treatment, CWs have recently been applied also to remove contaminants from contaminated groundwater [40•,41•].

Similar to CWs, plant-based soil remediation is less expensive and less energy-demanding than, for example, physical and chemical treatments. In addition, plants may alleviate erosion and improve soil carbon sequestration. Bioremediation on marginal lands may be combined with biofuel production [42]. However, phytoremediation is often considered as slow and incomplete, due to limitations in plant-metabolic capacity, in rooting depth and due to seasonality of plant growth [43]. As a consequence, phytoremediation is currently believed to be restricted to 'moderately hydrophobic' compounds.

Inclusion of microorganisms interacting with plants in phytoremediation schemes is increasingly regarded as an option for dealing with inherent weaknesses of the plant organisms [1•]. For trichloroethylene (TCE) contaminated groundwater, for instance, it was shown that the contaminant was eliminated partially by microbial degradation within the rhizosphere [44]. The application of various endophytic bacteria, for example, for the degradation of hydrophobic compounds [45,46] or for improving plant N-supply (diazotrophic endophytic bacteria) or the plant's supply with P, Fe or hormones (plant-growth-promoting-rhizobacteria, PGPR) [42,47] has also been

proposed. Several reports showed that PGPR may increase plant fitness and root and shoot biomass at a given site [48•]. In addition, they may promote the elimination of contaminants. One additional important issue when regarding plant–microbe interactions is intra-species and inter-species communication in the rhizosphere operating either by direct contact or by chemical 'long-distance' signaling [49].

While many current research approaches promote the application of isolated elements derived from the complex rhizosphere interplay for tackling problems in phytoremediation (designer-plants, designer-microbes or nano-technologies [1•,2,46,50,51•]), reports on respective real-world pilot-scale remediation facilities are rare. Older, more integrative approaches (soil treatment using ligninolytic fungi [52] with stable coupling of partially reduced amino-metabolites into the humus matrix [53] or the addition of high amounts of electron donors for anaerobic processes [54]) appear to be technically more successful. The inclusion of interacting microbial consortia of degraders, but also of biodegradation-improving mature composts [55•,56] may point toward ecological approaches for soil remediation and should be more focussed in future research.

One aspect hardly considered when reflecting on the application of specific microorganisms, are effects referring to ecosystem stability. AMF, for instance, are at the same time stabilizing soil structure as well as host plant performance under stressful conditions [57]. A similar stabilization of host plants under stress conditions has been described for PGPR [58] and fungal endophytes [9•] and even phyllosphere microorganisms have been described to strengthen plant defense (priming, [59•]). A complete ecosystem's approach targeting ecotoxicological effects of organic contaminants and the alleviating effects of microorganisms is currently lacking [60••], however, and respective analyses are only focused on specific keystone species, like AMF [61] or on a subset of the ecosystem, like soil microbial communities [62•].

Perspectives

Plants and their interactions with microbial communities are crucial for transporting and transforming organic contaminants and for stabilizing affected ecosystems. While the importance of the rhizosphere becomes increasingly acknowledged, other compartments, like the phyllosphere [20], are largely neglected. In order to obtain a systemic understanding of the multitude of compartments and processes and to manage the large areas of terrestrial ecosystems affected by organic contaminants in a rational way, multidisciplinary research will be necessary. Key aspects to be studied will comprise interactions between organic contaminants and plant or microbial diversity, an integrated view on matter flux and organismic distribution, and an improved understanding of

contaminant interactions with the physico-chemical environment in the various compartments.

References and recommended reading
Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Abhilash PC, Powell JR, Singh HB, Singh BK: **Plant–microbe**
• **interactions: novel applications for exploitation in multipurpose remediation technologies**. *Trends Biotechnol* 2012, **30**:416-420.
This opinion paper highlights three novel bioremediation approaches: transgenics, low-input 'designer' plants and nanotechnology suggesting biotechnological engineering as a potential solution to former drawbacks in soil remediation.

2. Van Aken B, Correa PA, Schnoor JL: **Phytoremediation of polychlorinated biphenyls: new trends and promises**. *Environ Sci Technol* 2010, **44**:2767-2776.

3. Harms H, Schlosser D, Wick LY: **Untapped potential: exploiting**
•• **fungi in bioremediation of hazardous chemicals**. *Nat Rev Microbiol* 2011, **9**:177-192.
A comprehensive review of the metabolic and ecological capacities of fungi for the bioremediation of organic chemicals, metals, metalloids and radionuclides.

4. Sun Y, Ling W, Liu J, Zong J: **Effects of arbuscular mycorrhizal fungi on the uptake of phenanthrene and pyrene by *Alfalfa***. *J Agro-Environ Sci* 2012, **31**:1920-1926.

5. Gao YZ, Cheng ZX, Ling WT, Huang J: **Arbuscular mycorrhizal fungal hyphae contribute to the uptake of polycyclic aromatic hydrocarbons by plant roots**. *Bioresour Technol* 2010, **101**:6895-6901.

6. Joner E, Leyval C, Colpaert J: **Ectomycorrhizas impede phytoremediation of polycyclic aromatic hydrocarbons (PAHs) both within and beyond the rhizosphere**. *Environ Pollut* 2006, **142**:34-38.

7. Cruz-Hernandez A, Tomasini-Campocosio A, Perez-Flores LJ, Fernandez-Perrino FJ, Gutierrez-Rojas M: **Inoculation of seed-borne fungus in the rhizosphere of *Festuca arundinacea* promotes hydrocarbon removal and pyrene accumulation in roots**. *Plant Soil* 2013, **362**:261-270.

8. Zikmundova M, Drandarov K, Bigler L, Hesse M, Werner C: **Biotransformation of 2-benzoxazolinone and 2-hydroxy-1,4-benzoxazin-3-one by endophytic fungi isolated from *Aphelandra tetragona***. *Appl Environ Microbiol* 2002, **68**:4863-4870.

9. Li HY, Wei DQ, Shen M, Zhou ZP: **Endophytes and their role in**
• **phytoremediation**. *Fungal Divers* 2012, **54**:11-18.
A comprehensive review of the diversity of contaminant-resistant/degrading endophytes and their role in phytoremediation of organic contaminants and heavy metals.

10. Wang G, Wen J, Li H, Qiu C: **Biodegradation of phenol and *m*-cresol by *Candida albicans* PDY-07 under anaerobic condition**. *J Ind Microbiol Biotechnol* 2009, **36**:809-814.

11. Martin F, Kohler A, Murat C, Balestrini R, Coutinho PM, Jaillon O, Montanini B, Morin E, Noel B, Percudani R *et al.*: **Perigord black truffle genome uncovers evolutionary origins and mechanisms of symbiosis**. *Nature* 2010, **464**:1033-1038.

12. Floudas D, Binder M, Riley R, Barry K, Blanchette RA, Henrissat B,
• Martínez AT, Otillar R, Spatafora JW, Yadav JS *et al.*: **The paleozoic origin of enzymatic lignin decomposition**

reconstructed from 31 fungal genomes. *Science* 2012, **36**:1715-1719.
A comparison of 31 fungal genomes suggests that lignin-degrading peroxidases expanded in the lineage leading to white-rot basidiomycetes of the *Agaricales*, and diminished in parallel lineages leading to brown-rot and mycorrhizal species.

13. Brune A, Frenzel P, Cypionka H: **Life at the oxic–anoxic interface: microbial activities and adaptations**. *FEMS Microbiol Rev* 2000, **24**:691-710.

14. Springael D, Top EM: **Horizontal gene transfer and microbial adaptation to xenobiotics: new types of mobile genetic elements and lessons from ecological studies**. *Trends Microbiol* 2004, **12**:53-58.

15. Kuiper I, Lagendijk EL, Bloemberg GV, Lugtenberg BJ: **Rhizoremediation: a beneficial plant–microbe interaction**. *Mol Plant Microbe Interact* 2004, **17**:6-15.

16. Segura A, Ramos JL: **Plant–bacteria interactions in the removal
•   of pollutants**. *Curr Opin Biotechnol* 2013, **24**:467-473.
A concise opinion article reviewing state of the art bioremediation and bioengineering strategies to improve the degradation efficiency of rhizosphere colonizing bacteria.

17. Tyagi M, da Fonseca MM, de Carvalho CC: **Bioaugmentation and
•   biostimulation strategies to improve the effectiveness of bioremediation processes**. *Biodegradation* 2011, **22**:231-241.
The sound review evaluates the effectiveness of recent bioremediation strategies with regard to contaminant degrading microorganisms and uncovers potential pitfalls as possible explanations of gaps between lab trials and field applications.

18. Berg G, Smalla K: **Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere**. *FEMS Microbiol Ecol* 2009, **68**:1-13.

19. Cook RL, Hesterberg D: **Comparison of trees and grasses for rhizoremediation of petroleum hydrocarbons**. *Int J Phytoremediation* 2013, **15**:844-860.

20. Morris CE, Kinkel LL: **Fifty years of phyllosphere microbiology: significant contributions to research in related fields**. In *Phyllosphere Microbiology.* Edited by Lindow SE, Hecht-Poninar EI, Elloitt VJ. St. Paul, USA: American Phytopathological Society; 2002:365-375.

21. Reichenberg F, Mayer P: **Two complementary sides of bioavailability: accessibility and chemical activity of organic contaminants in sediments and soils**. *Environ Toxicol Chem* 2006, **25**:1239-1240.

22. Baumgarten T, Sperling S, Seifert J, von Bergen M, Steiniger F, Wick LY, Heipieper HJ: **Membrane vesicle formation as a multiple-stress response mechanism enhances *Pseudomonas putida* DOT-T1E cell surface hydrophobicity and biofilm formation**. *Appl Environ Microbiol* 2012, **78**:6217-6220.

23. Krell T, Lacal J, Reyes-Darias JA, Jimenez-Sanchez C,
•   Sungthong R, Ortega-Calvo JJ: **Bioavailability of pollutants and chemotaxis**. *Curr Opin Biotechnol* 2013, **24**:451-456.
This opinion paper draws a concise link between chemotaxis and biodegradation rate of contaminants and suggests taking into account the capacity for chemotactic behavior of degrading bacteria in novel bioremediation approaches.

24. Ritz K, Young IM: **Interactions between soil structure and fungi**. *Mycologist* 2004, **18**:52-59.

25. Heaton L, Obara B, Grau V, Jones N, Nakagaki T, Boddy L,
•• Fricker MD: **Analysis of fungal networks**. *Fung Biol Rev* 2012, **26**:12-29.
This review is a landmark in the conflation of experimental and model-based understanding of fungal network structures as it combines knowledge from biological observations with *in silico* network theory.

26. Allen MF: **Linking water and nutrients through the vadose zone: a fungal interface between the soil and plant systems**. *J Arid Land* 2011, **3**:155-163.

27. Furuno S, Pazolt K, Rabe C, Neu TR, Harms H, Wick LY: **Fungal mycelia allow chemotactic dispersal of polycyclic aromatic hydrocarbon-degrading bacteria in water-unsaturated systems**. *Environ Microbiol* 2010, **12**:1391-1400.

28. Barto EK, Weidenhamer JD, Cipollini D, Rillig MC: **Fungal superhighways: do common mycorrhizal networks enhance below ground communication?** *Trends Plant Sci* 2012, **17**:633-637.

29. Frey-Klett P, Burlinson P, Deveau A, Barret M, Tarkka M,
•• Sarniguet A: **Bacterial–fungal interactions: hyphens between agricultural, clinical, environmental, and food microbiologists**. *Microbiol Mol Biol Rev* 2011, **75**:583-609.
This comprehensive review attempts to bridge gaps among different research fields in which fungal-bacterial interactions are of high importance and seeks to achieve a novel unifying perspective of these interactions applicable in all fields.

30. Schamfuss S, Neu TR, van der Meer JR, Tecon R, Harms H, Wick LY: **Impact of mycelia on the accessibility of fluorene to PAH-degrading bacteria**. *Environ Sci Technol* 2013, **47**:6908-6910.

31. Ingham CJ, Kalisman O, Finkelshtein A, Ben-Jacob E: **Mutually facilitated dispersal between the nonmotile fungus *Aspergillus fumigatus* and the swarming bacterium *Paenibacillus vortex***. *Proc Natl Acad Sci U S A* 2011, **108**:19731-19736.

32. Warmink JA, van Elsas JD: **Migratory response of soil bacteria to *Lyophyllum* sp strain Karsten in soil microcosms**. *Appl Environ Microbiol* 2009, **75**:2820-2830.

33. Kohlmeier S, Smits THM, Ford RM, Keel C, Harms H, Wick LY: **Taking the fungal highway: mobilization of pollutant-degrading bacteria by fungi**. *Environ Sci Technol* 2005, **39**:4640-4650.

34. Banitz T, Johst K, Wick LY, Schamfuss S, Harms H, Frank K:
•   **Highways versus pipelines: contributions of two fungal transport mechanisms to efficient bioremediation**. *Environ Microbiol Rep* 2013, **5**:211-218.
Microbial simulation models were used to evaluate the effectiveness of mycelial networks as bacterial or contaminant dispersal vectors and to analyze the impact of these two mechanisms on biodegradation efficiency suggesting combined phenomena to be most effective.

35. Perez-Reche FJ, Taraskin SN, Otten W, Viana MP, Costa LD, Gilligan CA: **Prominent effect of soil network heterogeneity on microbial invasion**. *Phys Rev Lett* 2012:109.

36. van der Heijden MGA, Bardgett RD, van Straalen NM: **The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems**. *Ecol Lett* 2008, **11**:296-310.

37. Vymazal J: **Plants used in constructed wetlands with horizontal
•   subsurface flow: a review**. *Hydrobiologia* 2011, **674**:133-156.
Review on functions and desired properties of plants in constructed wetlands.

38. Garcia J, Rousseau DPL, Morato J, Lesage E, Matamoros V, Bayona JM: **Contaminant removal processes in subsurface-flow constructed wetlands: a review**. *Crit Rev Environ Sci Technol* 2010, **40**:561-661.

39. Kayranli B, Scholz M, Mustafa A, Hedmark A: **Carbon storage and fluxes within freshwater wetlands: a critical review**. *Wetlands* 2010, **30**:111-124.

40. Seeger EM, Reiche N, Kuschk P, Borsdorf H, Kaestner M:
•   **Performance evaluation using a three compartment mass balance for the removal of volatile organic compounds in pilot scale constructed wetlands**. *Environ Sci Technol* 2011, **45**:8467-8474.
The authors provide a detailed balance for the removal of volatile organic compounds from contaminated groundwater in constructed wetlands. In both treatments analyzed (with or without gravel), rhizosphere processes have the strongest impact on contaminant concentrations, followed by either plant uptake or volatilization depending on conditions.

41. van Afferden M, Rahman KZ, Mosig P, De Biase C, Thullner M,
•   Oswald SE, Muller RA: **Remediation of groundwater contaminated with MTBE and benzene: the potential of vertical-flow soil filter systems**. *Water Res* 2011, **45**:5063-5074.
The authors describe the successful application of vertical flow water filters (including a plant-based water filter) for effectively removing MTBE and benzene in a technical installation for treating contaminated ground water.

42. Weyens N, van der Lelie D, Taghavi S, Newman L, Vangronsveld J: **Exploiting plant–microbe partnerships to improve biomass production and remediation**. *Trends Biotechnol* 2009, **27**:591-598.

43. Vangronsveld J, Herzig R, Weyens N, Boulet J, Adriaensen K, Ruttens A, Thewys T, Vassilev A, Meers E, Nehnevajova E *et al.*: **Phytoremediation of contaminated soils and groundwater: lessons from the field**. *Environ Sci Pollut Res* 2009, **16**:765-794.

44. Weyens N, Taghavi S, Barac T, van der Lelie D, Boulet J, Artois T, Carleer R, Vangronsveld J: **Bacteria associated with oak and ash on a TCE-contaminated site: characterization of isolates with potential to avoid evapotranspiration of TCE**. *Environ Sci Pollut Res* 2009, **16**:830-843.

45. Stenuit BA, Agathos SN: **Microbial 2,4,6-trinitrotoluene degradation: could we learn from (bio)chemistry for bioremediation and vice versa?** *Appl Microbiol Biotechnol* 2010, **88**:1043-1050.

46. Van Aken B: **Transgenic plants for enhanced phytoremediation of toxic explosives**. *Curr Opin Biotechnol* 2009, **20**:231-236.

47. Marchand L, Mench M, Jacob DL, Otte ML: **Metal and metalloid removal in constructed wetlands, with emphasis on the importance of plants and standardized measurements: a review**. *Environ Pollut* 2010, **158**:3447-3450.

48. Batty LC, Dolan C: **The potential use of phytoremediation for**
• **sites with mixed organic and inorganic contamination**. *Crit Rev Environ Sci Technol* 2013, **43**:217-259.
In this review on phytoremediation, the authors emphasize in particular the importance of plant–microbe interactions and rhizosphere processes.

49. Badri DV, Weir TL, van der Lelie D, Vivanco JM: **Rhizosphere chemical dialogues: plant–microbe interactions**. *Curr Opin Biotechnol* 2009, **20**:642-650.

50. Rylott EL, Bruce NC: **Plants disarm soil: engineering plants for the phytoremediation of explosives**. *Trends Biotechnol* 2009, **27**:73-81.

51. Lorenz A, Rylott EL, Strand SE, Bruce NC: **Towards engineering**
• **degradation of the explosive pollutant hexahydro-1,3,5-trinitro-1,3,5-triazine in the rhizosphere**. *FEMS Microbiol Lett* 2013, **340**:49-54.
This publication demonstrates in mesocosm experiments that the application of rhizosphere bacteria containing a specific gene for contaminant degradation enhances degradation of the respective compound when compared to rhizosphere bacteria containing only an empty vector.

52. Weiss M, Geyer R, Russow R, Richnow HH, Kastner M: **Fate and metabolism of [N-15]2,4,6-trinitrotoluene in soil**. *Environ Toxicol Chem* 2004, **23**:1852-1860.

53. Weiss M, Geyer R, Gunther T, Kaestner M: **Fate and stability of C-14-labeled 2,4,6-trinitrotoluene in contaminated soil following microbial bioremediation processes**. *Environ Toxicol Chem* 2004, **23**:2049-2050.

54. Heiss G, Knackmuss HJ: **Bioelimination of trinitroaromatic compounds: immobilization versus mineralization**. *Curr Opin Microbiol* 2002, **5**:282-287.

55. Fernandez-Luqueno F, Valenzuela-Encinas C, Marsch R,
• Martinez-Suarez C, Vazquez-Nunez E, Dendooven L: **Microbial communities to mitigate contamination of PAHs in soil-possibilities and challenges: a review**. *Environ Sci Pollut Res* 2011, **18**:12-30.
A comprehensive review on state of the art bioremediation approaches including a large summary of known PAH degrading bacteria and fungi.

56. Loick N, Hobbs PJ, Hale MDC, Jones DL: **Bioremediation of poly-aromatic hydrocarbon (PAH)-contaminated soil by composting**. *Crit Rev Environ Sci Technol* 2009, **39**:271-332.

57. Smith SE, Facelli E, Pope S, Smith FA: **Plant performance in stressful environments: interpreting new and established knowledge of the roles of arbuscular mycorrhizas**. *Plant Soil* 2010, **326**:3-20.

58. Hayat R, Ali S, Amara U, Khalid R, Ahmed I: **Soil beneficial bacteria and their role in plant growth promotion: a review**. *Ann Microbiol* 2010, **60**:579-598.

59. Buxdorf K, Rahat I, Gafni A, Levy M: **The epiphytic fungus**
• *Pseudozyma aphidis* **induces jasmonic acid- and salicylic acid/nonexpressor of PR1-independent local and systemic resistance**. *Plant Physiol* 2013, **161**:2014-2022.
This publication provides evidence that a fungal phyllosphere organism (*Pseudozyma aphidis*) (1) directly inhibits fungal pathogenic organisms and (2) activates the plant defense system (priming).

60. Beketov MA, Liess M: **Ecotoxicology and macroecology — time**
•• **for integration**. *Environ Pollut* 2012, **162**:247-254.
The authors of this opinion paper state that ecotoxicological 'bottom-up' experiments are unable to answer urgent questions about the ecological effects of a given chemical. As a better approach to such issues they propose the adoption of a macroecological 'top-down' approach in ecotoxicological research.

61. Verdin A, Lounes-Hadj Sahraoui A, Fontaine J, Grandmougin-Ferjani A, Durand R: **Effects of anthracene on development of an arbuscular mycorrhizal fungus and contribution of the symbiotic association to pollutant dissipation**. *Mycorrhiza* 2006, **16**:397-405.

62. Griffiths BS, Philippot L: **Insights into the resistance and**
• **resilience of the soil microbial community**. *FEMS Microbiol Rev* 2013, **37**:112-129.
This review provides a definition of the terms resistance and resilience in ecological respect, before summarizing literature about the impact of disturbances on soil microbial communities. Subsequently the importance of various factors (e.g. biodiversity, adaptation, soil properties) for resilience of soil microbial communities is discussed.