The universe of basidiomycetous ground fungi

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Although pileate saprobic ground fungi are primarily appreciated for their contributions to the bill of fare, their role in the mineralization of organic residues and xenobiotics in soil should not be underestimated. Enormous differences in their interactions with soil microorganisms and nonhost plants impair their artificial transfer to natural substrates. The paper reviews the impact of emanations from competing soil microorganisms, whole natural sods, and decaying plant material on mycelial growth and fruiting of some representative soil basidiomycetes; the rate of successful field inoculations with sterile spawn, start substrates, and transplanted pieces of natural fairy rings; factors contributing to soil fungistasis; and the problems of fungal succession enforced by nutrient depletion in, and the autotoxification of, the colonized substrate. Finally, the role of plant emanations on the activity of fungal oxidoreductase enzymes and the rate of Polycyclic Aromatic Hydrocarbon degradation, as well as fungal influence on heavy-metal uptake by herbs will be discussed.

Keywords saprobic soil basidiomycete; substrate preference; fruiting; plant microbe interactions; plant and microbial volatiles; field inoculation; soil fungistasis; oxidoreductases; PAH; heavy metals

1. Substrate preferences of non-symbiotic basidiomycetous ground fungi

Unlike the ubiquitous populations of bacteria and the group of mitosporic and ascomycetous soft-rot fungi, basidiomycetes contribute little to the degradation of crop residues in, and thus to the maintenance of, the fertility of arable soils [1]. With their active contribution to the growth of timber and their outstanding efficacy in its complete mineralization, the ecological groups from ectomycorrhizal, plant residue degrading, tree root and stem pathogenic, to slash mineralizing basidiomycetes give a unique example of familiar cooperation. The release of oxidoreductase enzymes which catalyze the opening of aromatic rings in lignin and xenobiotic structures independently or via redox mediator compounds [2-4] denotes more or less all ecological groups [5-8]. This is best characterized by their abilities to transform a set of 5 polycyclic aromatic hydrocarbons (PAHs) with 3 to 5 benzene rings. Groups of 8 wood-degrading, 3 wood- and straw-degrading, 20 terricolous, 21 ectomycorrhizal, and 5 mitosporic soil fungi made a mean of 52.1; 69.1; 23.5; 13.2; and 12.6 %, respectively, of the PAHs dissipate from solution [9]. Similarly, groups of 8 wood-degrading, 7 terricolous, 10 ectomycorrhizal, and 9 mitosporic soil fungi reduced the absorbance A_{340} of soil humic substances by 53.1; 27.5; 17; and 19.4 %, respectively [10] to indicate the order of the enzymatically based fungal access to lignocellulosic and humic soil constituents under monoxenic conditions. In-vitro decay of beech timber is initiated by wood and litter degraders but not by ectomycorrhizal fungi [11].

Soil access by wood-decay fungi. Fungal spread in natural soils is not only impaired by the drop of laccase and peroxidase activities to 0.04-2.7 % of those in timber or sterile spawn and the frequent absence of manganese peroxidase [2]. It is also influenced by conducive and allelopathic exhalations of microorganisms and plants as well as by soil fungistatic effects (see below). Killing of competing microorganisms by saprobic wood-decay fungi such as *Gymnopilus, Hypholoma, Kuehneromyces*, and *Pleurotus* sp. in timber substrates [12, 13] is as common as the repression of bacteria by *Pleurotus ostreatus* and their propagation by *Hypholoma fasciculare, Stropharia rugosoannulata* and other fungi in soil [2, 14, 15]. Fungal resource capture may therefore go along with the repression and the possible digestion [16, 17] of the autochthonous microflora sensitive to its antibiotics [18]. Insensitive populations may be tolerated or included into catabolic and nutritional cooperations [19]. The low competitive ability excludes tree pathogenic basidiomycetes [12, 20] which are adapted to the colonization of the internally near-sterile living wood [21, 22] from growth and nutrient acquisition in a non-sterile habitat [23-25]. The competitively stronger slash-degrading white and brown rot saprobes [12, 20] expand into soil to complete their nutrient supply (Table 1) [2, 20, 23]. In practice, inoculated timber sections drive dense and fleshy coronar mycelia 10-25 cm wide into the surrounding soil of mediate but not excessive C_{org}. Mycelia degenerate gradually after 2-3 yr but persist in the wood blocks for > 5-10 yr. They undergo lysis immediately when timber as the main source of carbohydrate and energy is being removed [2]. Fungal colonization of soil can, even in the case of ectomycorrhizal basidiomycetes [26], result in a drop of bacterial counts and metabolic activities. This results in lower dissipation rates of 3- to 4-ring PAHs which are convenient substrates of bacteria, whereas the higher-condensed PAHs are left to, and degraded by, soil basidiomycetes [2, 27, 28].

Colonization of non-fermented lignocelluloses. Other than the initially near-sterile timber blocks [21, 22] with their fungal- and bacterial-growth limiting shortage in nitrogen [29], sawdust and straw substrates of an enormous surface:mass ratio invite random microbial contaminants to enter [30]. These substrates are therefore not colonized by the competitively weak wood-decaying pathogens [20]. In contrast, the competitively stronger wood-decay saprobes (Table 1) and waste-substrate fungi such as *Agrocybe, Coprinus*, and *Stropharia* spp. colonize compact slash pieces and non-fermented straw/sawdust under indoor conditions to the same extent [20, 31]. Formation of basidiomes by wood-

decay fungi however is preferentially restricted to compact timber pieces and tree stumps and their coronar soil mycelia. Fruiting of *Agrocybe* and *Stropharia* spp. is confined to grassland and to straw and shredded timber deposited on soil [32]. This behaviour may be caused, in part, by the ability of wood-decay fungi to fruit unexceptionally far from soil under sterile conditions [33]. In contrast, numerous ground fungi of the genera *Agaricus, Agrocybe, Coprinus*, and *Stropharia* are obligately bound to soil. They fail to reproduce under strictly sterile conditions or persist in the button state [34]. Similarly, the commercial mushroom *A. bisporus* depends on (casing-) soil associated bacteria and streptomycetes to form mature basidiomes [35, 36]. Successful fungal repression of the fast-growing primary sugar fungi in shredded timber, and of *Coprinus fimetarius*, mitosporers, ascomycetes [30] and "green moulds" [37, 38] in non-fermented grain straw may be a determinant of substrate preference. The possibility of catabolic and nutritional cooperation with the substrate bacteria [19] such as those propagated by *S. rugosoannulata* within its vegetative thallus [2] may also be of relevance. The use of the innumerable *Pleurotus* spp. [39, 40] in mushroom production on grain straw deserves attention, too. Their frequent failure of colonizing non-fermented straw substrates pre-infected by fungal competitors and bacteria [30] can be circumvented with untreated and high-yielding combinations of 70 % (v/v) leafwood dust and 60 % of field pea or rape straws harvested in the brown (not green) and therefore widely sugar-fungus-resistant state [32].

Fermentation of lignocellulose and muck substrates. Mass production of commercially cultivable basidiomycetes with high fruiting potential but low competitive ability and mould-susceptible spawn materials (e.g., *Agaricus lanipes* [32] and *Macrolepiota rhacodes* [41]) depends on the use of autoclaved lignocelluloses with excessive supplements of hydrocarbon- and protein-rich seed meals and food wastes [42]. Mushroom species of higher competitive ability get on with fermented substrates. Fermentation allows for the synthesis of carbohydrate-, mineral-N-, and protein-rich plant residues with animal faeces and fertilizers to CNPK optimized and comparatively mould-resistant lignocellulose substrates of highest mushroom yield potential whose microfloras tolerate the basidiomycete of choice. Due to their insufficient self-heating potential, rice and wheat straw may be amended with alfalfa straw, corn cobs and stalks, cotton waste, peanut hull, and wastes of tropical crops [42, 43]. The moistened and lime-amended substrates ferment in open-air piles for 3-7 d, reach 60-70° C in their center, and are turned over several times. A subsequent pasteurization at 50-65° C for 8-16 h precedes inoculation with mushroom spawn [30, 42]. Wheat/alfalfa straw substrates lost cellulose (9 %) and hemicellulose (19 %) relative to the content in lignin but gained 77 % in their hydrolytic-enzyme digestibility during fermentation [30]. The initial random fungal contaminants were replaced by mesophilic yeasts and thermophilic fungi at > 40° C, accompanied by successions in the bacterial populations. Fungi vanished during pasteurization [30]. Formulations of *A.-bisporus* composts comprise, beside the regional cereal straws, manure from horse, cattle, pig, and chicken beside wastes of the food industry and CaNPK mineral fertilizers [42]. Microbial consume of soluble C and N and the partial degradation of cellulose, hemicellulose, and protein during composting [44] results in deposition of the carbon, protein, and mineral enriched dark-brown substances of live and degraded microbial fractions [45] which are utilized by the cultivated fungus [16,17]. Microbial succession from mesophiles to thermophiles [42, 46] and the disappearance of fungi during pasteurization contribute to make composts selective for *A. bisporus* and other coprophiles (Table 1). Mushroom compost from horse manure on wheat straw had to be intensely homogenized with A01-A1-layer forest litter from leafwood and conifer stands to be colonized by *A. aestivalis, A. macrocarpus, A. porphyrizon*, and *Lepista nuda* [47,48].

Planted habitats. Most fairy-ring-like fungi from grassland and forest soils form mature basidiomes only under non-sterile conditions [34]. The concentric or arc-like mode of spread they display is principally typical of all filamentous fungi which expand centripetally from an inoculum. The presence of free fairy rings on grassland and of tethered ones around woody plants [49] indicates the availability of continuous substrate areas large enough to allow for undisturbed fungal spread over several consecutive years [50]. Free *L.-nuda* rings in timber forests may use the plant residue deposits in a conducive state of pre-degradation (see below) whereas those in grassland may also go back to the fungus' facultative necrotrophism to climatically weakened autumnal grasses [51]. *Agaricus xanthodermus* fruits abundantly in tethered rings of *Acer campestris* L. trees. Its mould-resistant mycelia colonize natural soils *in vitro*, but its numerous primordia stagnate [unpublished]. *Agaricus campestris* from free grassland rings behaves alike [52]. Its hyphae have been shown to expand into root cortical cells of ryegrass (*Lolium perenne* L.) [53]. The mycelium of *Agaricus arvensis* colonizes grass roots, too [54] and could not be transplanted to grassland soil [53] or sterile mushroom compost [55]. Factors transforming this competitively weak and easily moulding organism into the stable, fast-growing and fleshy fungal thallus of fairy rings in sward root zones are as unknown as in the case of ectomycorrhizal basidiomycetes. Quite the same applies to the fairy-ring fungus *Marasmius oreades* [34]. Its dense mycelia degrade 20-35 % of apparently senescent sward roots upon the release of laccase [56]. A fast-growing *A.-lanipes* isolate from a fairy ring tethered to *Fagus sylvatica* fruited excessively on sterile media but moulded in contact with natural soils [32,34]. Two conspecific isolates from *Picea abies* showed weekly mycelial growth rates < 1mm on malt extract agar and could not be transplanted to spawn media. The fleshy mycelia in fairy rings of *A. langei* associated with cocksfoot grass (*Dactylis polygama* Horvátovszky) under *Picea abies* yielded two annual flushes of its extremely delicate mushrooms, exuded laccase and monophenol oxidases, and killed by 50 % of the associated roots. This vigour is once more not reflected by its agar mycelia and their weekly growth rates below 1 mm [unpublished]. Whether growth and competitive ability of the critical mycelia normalize in the presence of fairy-ring associated herbs and trees should be studied aseptically *in*

vitro. Comparative techniques convince in the case of ectomycorrhizal basidiomycetes [57]. It has been suggested that the living plant root is at least part of the ecological niche of several *Agaricus* spp., too [53, 54].

Farmlands. Tilling arable soils comprises the fragmentation and subsequent lysis of basidiomycetous mycelia upon the separation of foraging hyphae and strands from nutrient-rich local resources. Fragmentation may be less disastrous to sclerotia-forming basidiomycetes such as *A. porphyrizon*. Its epidemic fruiting in horse-manure fertilized *Daucus carota* beds could be reproduced by spawn inoculations of carrot cultures and other crops [58] (see below). Similarly, the vegetative knots formed by *Volvariella speciosa* could contribute to secure the appearance of its basidiomes between consecutive field crops of wheat, rape, maize, and grasses [unpublished]. The excessive spread and fruiting of *A. fissuratus* in timothy grass (*Phleum pratense* L.) field cultures however is the more surprising. Its extremely moulding mycelium lacks any competitive ability to microbial competitors [34]. Survival strategies of mycelia such as those are not understood.

Table 1 Several non-symbiotic and widely non-pathogenic basidiomycetes with (temporary) activities in natural soils.

Main substrate	Fungal species	References
Timber segments	*Kuehneromyces mutabilis* (+++); *Pleurotus ostreatus* (+++)[a]; *Bjerkandera adusta* (+++); *Hypholoma fasciculare* (+++); *H. capnoides* (++); *H. sublateritium* (++); *Gymnopilus sapineus* (++); *Coniophora puteana* (+); *Phanerochaete velutina; Pholiota squarrosa* (+); *Serpula lacrymans* (+); *Trametes hirsuta* (+); *T. versicolor* (+)	23, 59-61
Non-fermented straw/sawdust	*Agrocybe dura; A. praecox; Coprinus comatus; Marasmius peronatus; Stropharia aeruginosa; S. coronilla; S. cubensis; S. hornemannii; S. rugosoannulata; S. semiglobata, Volvariella volvacea*[a]	28, 32, 42
Fermented lignocell-ulose and muck substrates	*Agaricus bisporus; A. edulis; A. blazei; A. subedulis; Coprinus comatus; Leucoagaricus leucothites* *Agaricus macrocarpus*[b]*; A. aestivalis*[b]*; A. porphyrizon*[b]*; Lepista nuda*[b]	32, 42, 47, 48, 62-65
Grassland and forest soils	*Agaricus arvensis*[c]*; A. campestris; A. langei; A. lanipes*[c]*; A. xanthodermus; Lepista nuda; Marasmius oreades*[c]	32, 52, 53, 56
Field crops	*Agaricus fissuratus*[c]*; A. porphyrizon; Volvariella speciosa*	34, 58

+++…+, Descending quantity of coronar soil mycelia. [a] Mass production also on non-fermented and fermented lignocelluloses. [b] Cultivation on *A.-bisporus* compost amended with forest litter. [c] Fungal spawn not mould-resistant.

2. Production of fungal inoculum

Vigorous pure culture isolates of basidiomycetes are established by plating plectenchyma pieces of several mm^3 in volume, excised aseptically from the upper stipe-pileus region, on 2.5-% malt extract agar slants. Outgrowing mycelia are maintained in test tubes Ø16 mm on 2.5-% malt extract agar (saprobic and ectomycorrhizal ground fungi) and on barked leafwood twig segments Ø1.5-3x9-12 mm embedded in malt extract agar, respectively (wood and straw degrading fungi), at 2° C. Mycelia from agar slants or liquid standing cultures (2.5 % malt extract, 0.2 % casein peptone solution) serve as inocula for sterile-spawn substrates in 1- to 2-L glasses (Table 2). Pure culture techniques and fungal spawn production are extensively reviewed by Chang and Miles [42].

Table 2 Receptures of sterile spawn for mycelial transfer of wood-decay and ground fungi to raw substrates.

Constituents	Fungi	Substrates
100 % leafwood dust (*Fagus* sp. preferred); 100 g $(kg\ DW)^{-1}$ sugar; 50g $(kg\ DW)^{-1}$ wheat flour; 200 % DW^{-1} water	Wood decay fungi	Fresh cuts of tree stem sections
70 % (v/v) leafwood dust; 60 % rape or pea straw chaff; 3 % DW^{-1} $CaCO_3$ (Spanish white)	Wood decay fungi	Timber blocks, straw and sawdust
90 % (v/v) wheat straw; 30 % leafwood dust; 3 % wheat flour	*Stropharia, Agrocybe*	Straw, sawdust
80 % (v/v) rape or pea straw; 30 % garden soil; 3 % wheat flour; 1 % sugar	All saprobic ground fungi	Straw, soil, mushroom composts
50 % (v/v) leafwood litter, horizons A01-A1; 50 % bean straw	*Lepista nuda*	Soil, composts

3. Herbaceous plant covers and the development of basidiomycetous ground fungi

Within herbaceous plant covers, non-symbiotic and (widely) non-pathogenic soil basidiomycetes have not only access to humic substances [10, 66, 67], dead plant material, senescent sward roots [53, 54, 56], and even to root cortical cells (*A. campestris*) [53]. Apart from the large number of metabolic products leached from the wetted sound plant [68], roots

exude readily metabolizable sugars, aliphatic and aromatic acids, amino acids, amides, phenolics, enzymes, proteins, sterols, siderophores, purines, vitamins, hormones, and biosurfactants [69-71]. They make up the 2-4 % [72] to more than 40 % [73] of the plant's daily exuded (^{14}C) net assimilate. The classes of volatiles from root and shoot resemble those released by fungal pure cultures [74, 75] and comprise mainly C_6 to C_{18} saturated and unsaturated aliphatic hydrocarbons and their derivatives such as acids, alcohols, aldehydes, ketones, esters, ethers, and exceptionally N and S containing compounds as well as variable mixtures of terpenoids and aromatics from plant essential oils [68, 76, 77]. They easily penetrate into soil or dissolve in soil water [78, 79]. Up to 80 % of root exudates are volatile [80]. With the microbial degradation of plant material, a huge number of low-MW hydrocarbons, alkaloids, terpenes, benzenes, phenols, and heterocyclic compounds are generated, liberated [68, 81, 82] or consumed and transformed from volatile precursors [83, 84]. They are sometimes used as sole sources of carbon and energy even by basidiomycetes such as *Phanerochaete chrysosporium* [85, 86] and can apparently induce microbial enzymes (see below). Soil basidiomycetes elicit stress responses in herbs [87] not only by phytotoxic antibiotics such as the fasciculol derivatives of *H. fasciculare* [88]. They could also increase the exudation of primary and secondary, stress-related metabolites from roots. This was shown for mitosporers and ascomycetes [89]. Several of the secondary metabolites are allelopathics with antimicrobial and phytotoxic properties [82, 90].

Attempts to place allochthonous microorganisms in the interacting world of natural soils to repress plant pathogens [18], improve crop plant nutrition [91], or control xenobiotic-hydrocarbon, mineral-oil [2, 92, 93] and heavy-metal contaminations [94] continue for more than 50 yr with little success [93]. In these attempts, the white mycelia of basidiomycetes visible with the naked eye can serve as model organisms. In a respective test series in 1-L vessels, only 2 of 17 natural unplanted top soils, irrespective of pH and C_{org} content, supported satisfactory mycelial growth when spawned with 15 spp. of *Agaricus, Coprinus, Lepista, Macrolepiota, Marasmius*, and *Stropharia* [95]. Grassland soil from the surroundings of a natural *L.-nuda* fairy ring was most conducive. Soils rooted by legumes and grasses promoted vegetative mycelia of several *Agaricus, Coprinus, Macrolepiota*, and *Lepista* sp. and inhibited *Agrocybe* and *Stropharia*. Other mycelia flourished only in the presence of 1 to 2 out of 11 plant species, whereby a (conducive) plant effect could switch to inhibition when tested on another source of top soil. In addition, fungistatic activities diminished in plants after flowering and fruit set [95]. Juvenile plant roots maintain a state of surface sterility by liberating volatile inhibitors [96] which occur particularly abundant in pea [97]. In further test trials, natural turf pieces and artificial single-plant sods with the adhering soil were placed on 1.5-L soil samples spawned with *Agaricus* and *Lepista* spp. The sods acted primarily as a cover to limit the outflow of inhibitory volatiles produced by the soil itself. Apart from some stimulatory leguminous crops, mycelial development was neither promoted by possible plant root exudates nor by volatile whole-plant exhalations [98]. In the simulated edaphosphere of herbaceous plant roots, mycelia of 12 soil basidiomycetes were generally inhibited by excess CO_2 released from soil and plant cover (up to 30–50%), by exhalations of whole sound ryegrass (*Lolium perenne* L.) sods (by 90%), and by volatiles produced or set free from certain microbial populations on aerobically decaying ryegrass residues (100% inhibition by half the fungi) [99], a fumigatory effect confirmed by Larkin and Griffin [100]. Inhibition changed with species and age of the plant [99]. Minor volatile concentrations stimulated mycelial growth [99, 101].

This was confirmed in further tests with plant-soil microcosms. Volatile hydrocarbons released from herbaceous plants and from unplanted soil substrates improved the mycelial density of *A. macrocarpus* and *Clitocybe* sp. but repressed their primordial formation extremely, whereas growth and fruiting of *A. bisporus* were not touched by the presence of plants [102]. Volatiles in their role as microbial nutrients, toxins, and hormonal compounds interfere thus with all physiological processes of microorganisms and plants as well as the integrity of walls and organelles of the cell [68, 76, 102, 103]. Mycelia of *A. porphyrizon* and *L. nuda* confirmed the extreme fungal sensitivity to the presence of adjacent plants, but with contrary responses. In 2-L/6-L vessels, fungus-colonized horse manure/forest litter substrates of 1.2/4 L were in neighbourhood to, but not covered by, soil planted to ryegrass, parsley, and several legumes. Their root systems were restricted to the soil. The primarily volatile emanations from roots and eventually from associated microorganisms reduced the mycelial quantities in the compost significantly between 16-80 % and the mushroom fresh weight by 66 % to the unplanted control. Contemporarily, the number of (smaller) basidiomes and of fertile vessels increased [58]. *Agaricus macrocarpus* fruits under sterile conditions. The sole applications of bacterial suspensions from sods of *Deschampsia flexuosa* reduced its yield by 17 % [34, 47].

4. Field inoculations

In general, re-inoculation of basidiomycetous ground fungi fails if they are spawned into compost heaps, grasslands, plant monocultures, and timber forests from which they had been isolated [34, 41, 53, 62]. *Coprinus comatus* resists grassland inoculations but appears voluntarily on freshly deposited turf soils within urban sites for a decade. It shares the preference for sites treated with liquid manure or animal excrements with *L. nuda*, *A. bisporus,* and *A. macrosporus*. *Lepista nuda* rejects garden compost piles but colonizes pure deposits of leaves and grasses in a state of progressive self-fermentation. Replacing sterile spawn by excised sods from *L.-nuda* fairy rings with their conducive microflora is no improvement [unpublished].

In 200 field inoculations [104], sterile spawn was inserted into 1-m-long furrows or in 1-L carrier substrates covered by plastic foil and the local soil. The transfer of *A. praecox* by furrows and wheat straw-sawdust carriers into unplanted soils, meadows, field crops, and forest stands was successful to 100 %. The fungus fruited in 2 of 76 cases on grassland. It preferred fresh and rotten lignocellulose residues and grew best at the base of straw piles. *Coprinus comatus* was transferred to grassland via carrier substrate. The fungus colonized the latter but failed to fruit and expand into grassland soils. Inoculations with *L. nuda* via furrows and carrier substrates were successful at a rate of 31.3 %, with 11 % of the sites bearing basidiomes. Colonies >30 to 150cm in diameter persisting for at least 2 yr were restricted to timber forests on mottled sandstone [104].

5. Soil fungistasis

Soil fungistasis originally defined by Dobbs and Hinson [105] refers to the failure of viable fungal spores to germinate in natural soils. The nutritional hypothesis ascribes fungistatic effects to the lack of those external nutrients which spores need to germinate. The inhibition hypothesis involves fungistatic substances into stunting of nutrient-independent spores [106]. Appropriate nutrients overcome this inhibition. In the focus of interest is nevertheless a control of soil-borne plant diseases by an active management of soil suppressiveness [107]. The feature of "general suppressiveness" denotes more or less all natural soils whereas "specific soil suppressiveness" is aimed at single pathogens [108]. Fungistatic effects of natural soils impair the spread of nearly all basidiomycetous ground fungi with mould-resistant inocula, too, and can be modified by presence of plants (Section 3).

In general, chemical and physical parameters alone do not explain the (frequently fungus-specific) suppressiveness of a given soil [52, 106, 107]. Antagonistic effects such as selective nutrient depletion, shift to unfavourable pH, E_h, and a_W values, production of toxic phenols, ketones, and alcohols, and the formation of antibiotics [109] make resident microorganisms the main players in soil fungistasis, although constellations of the most efficient microbial species can not yet be named [107]. Their key role is indicated by several facts. Sterilization of soils results generally in a loss of fungistasis [107]. Among 21 top soils inoculated with *L. nuda*, only 3 allowed the resulting mycelia to survive for > 20 wk. The number of conducive soils increased to 16 after peak-heating at 90° C for 30 min with the mycelial densities rising to the 10- to 20-fold. The conduciveness of peak-heated soil was further improved by the addition of soil from a natural *L.-nuda* fairy ring [104]. Although these data suggest solely the disappearance of fungistasis together with the soil's resident microflora, temperature treatment means also the destruction of heat-sensitive antibiotics and the transformation of the microbial biomass to readily available fungal nutrients [16, 17]. It means further a temporary end to the microbial production of soil volatiles [98] which are conducive at low, and toxic at higher concentrations [99, 101]. It stops microbial formation of soil fumigants upon the aerobic composting of grass residues [99] and the derivatization of crucifer-residue released glucosinolates [100, 110]. It means less of the simple and allelopathic volatiles released from composts [74].

In studies of Postma *et al*. [111], a conducive soil became suppressive after 5 subsequent cauliflower crops inoculated with their pathogen, *Rhizoctonia solani*. In this process, successive soil inoculations with the pathogen contributed more to the development of suppressiveness than the presence of the plant. The authors surmised *Lysobacter* spp. but not several mycoparasitic and competitive fungi to be the active agent. In the commercial production of *K. mutabilis* and *P. ostreatus*, inoculated tree stem sections are inserted into bed soil (Section 1) for culture cycles of 3-6 yr. Establishment of further cultures in the spent bed soil results in drastic yield reductions and a depressive growth of the fungal mycelia from the timber block into the surrounding soil [112]. Inhibitory effects of spent bed soils and spent mushroom substrates [113] against consecutive monocultures with the same fungal species point to effects of autotoxification. This principle could also explain the observations of Postma *et al*. [111]. Like most basidiomycetous ground fungi examined, wood-decaying fungi such as above enrich colonized soil with organic-N derived NH_4 in concentrations up to the 3- to 5–fold [56, 114]. Resulting emissions of ammonia under alkaline conditions have been recognized as the only known abiotic determinant [115] of soil fungistasis.

In an assay of 23 ground fungi on 12 unplanted top soils, fungal growth correlated positively with the soils' C_t Ca K Mg content and negatively with microbial CO_2 evolution as an indicator of microbial activity. Pasteurization and autoclaving increased mycelial growth and life span in soils pH 6.6–8.2. Growth of pH-sensitive but not of pH–tolerant fungi was inhibited on the Ca-deficient soils pH 4–4.4 (–5.6) and was not improved by autoclaving. The pretended fungistasis of acid soils to pH-sensitive fungi was controlled by N P K mineral (pH not altering) or organic (pH increasing) fertilizing as well as by neutralization with NaOH or $CaCO_3$. Although microbial competition was mortal to 33% of the fungal mycelia inserted into natural unplanted soils, further seriously antifungal effects beyond those pretended by low pH conditions and shortage in mineral macronutrients were not identified [52].

6. Influence of plant emanations on fungal enzymatic and catabolic activities

In-vitro activities of constitutive fungal exoenzymes such as laccases, Mn-independent peroxidases (PO), and Mn-dependent peroxidases (MnP) are greatly stimulated by the presence of adequate enzyme substrates and redox mediator

compounds such as Mn(II) [2-4] (see also Section 1). Conditions determining activities of root-surface PO [116] and cytosolic laccases of sterilely grown herbaceous plants are poorly understood. Exudation of PO increased in minerally fertilized, water-stressed, and dying plants [117]. Contemporarily, increases in cytosolic (shoot) PO for the control of reactive oxygen species which are generated in response to biotic and abiotic stress have received wide attention [118, 119]. The synchronously increasing formation of Mn(III) in stressed plant tissue has been attributed to reactions of PO with plant phenolics [120] many of which are formed under stress conditions [118, 121]. The presence of a MnP variant in plants has not been postulated [87, 122].

Changes in activities of the respective fungal and plant enzymes were studied in pairings of 6 soil saprobes and 2 ectomycorrhizal fungi with the laccase-deficient white mustard (*Medicago sativa* L.) non-host plants in sterile microcosms [87]. The poor laccase production of the saprobes *A. arvensis, A. porphyrizon, Lepista nebularis, S. rugosoannulata*, and *H. fasciculare* (group-5) on glucose-salt medium increased to the 2.2- to 2290-fold in the presence of liquid and volatile plant emanations. Activities of PO in the culture fluid rose to the 21-fold and comprised possibly fungal and plant-root derived enzymes. MnP was formed by 2 fungi and experienced little stimulation by the plant. Pairings of *A. porphyrizon*/white mustard accelerated the dissipation of the polyaromatics phenanthrene and anthracene from solution whereby plant PO, supported by fungal redox mediator compounds, played a role in the degradation of phenanthrene, anthracene, and fluoranthene [87].

Fungal proteases degraded the glycoproteid, plant PO, to facilitate the sorption of fungal laccase to the root surface of white mustard in the presence of all laccase-positive fungi. Plant-stess related increases in shoot PO from 2.8- to 4.1-fold were exclusively elicited by group-5 saprobes and furnished proportionate increases in plant-phenolic mediated oxidations of Mn(II) to Mn(III). Root PO activities enhanced in the presence of all fungi to the 1.3- to 9.7-fold and comprised possibly PO of fungal origin [87]. *Agaricus bisporus* and the ectomycorrhizal *Hebeloma crustuliniforme* and *Suillus granulatus* did not respond to plant emanations with elevated laccase productions but solubilized apparently root-surface PO. These fungi failed to elicit stress-related PO increases (and possibly the *de-novo* synthesis of phenolics) and prevented thus Mn(III) formation in several tissues [87]. Mycorrhizal fungi avoid eliciting typical defence responses in their host plants, too [90]. The reduced or altered expression of host PO after root mycorrhizal colonization has also been interpreted as an active suppression of host defence [123, 124].

The interaction of white mustard with soil mycelia of *S. rugosoannulata* under non-sterile conditions resulted in comparable stress-related increases in shoot PO and Mn(III) content and the sorption of fungal laccase to the root surface [125]. Activity increases of laccase in the aqueous extract of the fungus-colonized soil in the order of 1.3 to 2.3 were not significant. This should be ascribed to the proteid-binding capacity of the soil itself, the competition of soil microorganisms for the respective root emanations, and the loss of stimulatory shoot volatiles to the open air. The mere presence of microorganisms may also interfere with enzymatic and catabolic performances of ground fungi. Contact with bacteria, fungi, and non-specific soil contaminants stimulated laccase production of white rot basidiomycetes *in vitro* [126]. The rate of leaf litter decomposition by *Collybia peronata in vitro* was 6-9 % higher after inclusion of the leaves' native microflora [127]. On the other hand, rates of lignin decomposition by white rot fungi diminished in the presence of mitosporic fungal competitors [128].

There is little insight into the nature of stresses exerted by non-pathogenic and non-symbiotic basidiomycetes on non-host herbs. Hyphal intrusion into root cortical cells by *A. arvensis* and *A. campestris* [53, 54], killing grass roots by *A. lanipes* [unpublished], and degradation of more or less senescent grass roots/shoots by *M. oreades/L. nuda* [51, 56] may be recognized as pathogen ingress. Below this level, phytotoxic metabolites such as fasciculols and fasciculic acids of *H. fasciculare* [88, 129], undissociated carboxylic acids [130] and fungal hydrogen cyanides [131] may be stress elicitors. The surface-active hydrophobins confer water-repellency to vegetative and generative structures of filamentous fungi and promote hyphal attachment to hydrophobic plant host structures. These proteins of around 100 amino acids in length are unique to fungal mycelia. Several hydrophobins are phytotoxic and act as elicitors of plant stress [132].

Siderophores, lipopolysaccharides, and hormonal signalling molecules such as IAA, ethylene, salicylic and jasmonic acids released by non-pathogenic rhizobacteria confer systemic resistance to plants [133, 134] due to their elicitor properties. They may also be the active ingredients in (mycorrhizal) fungal strategies [133, 135]. Other fungal metabolites referred to as effector proteins induce specific resistance genes of the plant which recognizes them as microbial "pathogen-associated molecular patterns" (PAMPs). They comprise fungal cell wall chitin and cysteine-rich proteins many of which cause severe plant defence responses [136].

7. Impact of fungal mats on mineral uptake of plants

Rules controlling plant metal homeostasis are poorly understood [137] but give room to manipulation. To increase uptake of potentially toxic heavy metals and radionuclides (HM) from contaminated soils by phytoextraction [138], several methods are being discussed. High soil applications of synthetic and phytochelants result in a non-specific and wick-like plant uptake of the excessively solubilized HM via root systems which have been damaged by the treatment [139, 140]. In another approach, continuous NH_4 applications stimulate biomass production and increase the plant's N_{org} content up to the toxic threshold of around 3 % by dry weight. Shoot concentrations of the (enzyme) metalloproteid-

associated transition metals, (Cd) Co Cu Mn Ni Zn increase near-linearly with N_{org} in the plant of higher dry weight. Uptake of the non-catalytic metals, Al Ba Cr (Fe) K Li Na Sr Ti U V increase little more than with the dry weight but not in concentration [141-143]. Soil applications of strong chelants such as cysteine or citrate in plant-root compatible concentrations support primarily the acquisition of Co Mn independent of N_{org} [144]. Carbohydrates applied to soil stimulate growth of N-consuming microorganisms and confine thereby the production of plant biomass and its content in N_{org} and the respective transition metals [142].

Uptake of elements by non-damaged plants increases frequently with their concentration in the soil solution but more with their adequate speciation [145]. Plants prefer free metal cations [146] and metal-mineral acid complexes [147] to the same extent. Humic and fulvic acid colloids however are by far the main ligands and matrices of (heavy) metals and actinides. In solutions of arable and forest soils pH 7.6/3.7, a mean of 46/87 % of polyvalent metals were coordinated with fulvic acids [148]. Stability constants (log K) of metal-fulvate and –humate complexes are in the 4.0/8.5 range at pH 5 to 5.5 and increase severely at neutral to alkaline conditions [148]. Metal complexes in the log K range ≤ 3 may ionize to < 5 % at neutral pH [149] and are thus highly plant-available.

Soil basidiomycetes improve the plant-availability of soil minerals by the release of carboxylic and amino acids which chelate preferentially proteid-associated transition metals [143, 150]. They reduce the size of metal-humic colloids to increase their mobility in the mass flow towards the root [151]. They contribute to soil acidification which results in the liberation of free metal cations by ion exchange and by chemical reactions of soil minerals with H^+ [152]. Nevertheless, extracellular polysaccharides, lipids, membrane proteins and fungal cell wall chitin [153-155] of fungal mats may sequester and precipitate metal cations from solution. Their intrahyphal and –bacterial complexation with metallothioneins, glutathione, polyphosphate, and oxalate, or their occurrence as protein-bound disulphides and metal-thiolate clusters [156-158] may interfere with their plant-availability [154]. Effects such a those may mimic the "protective effect" [159] mycorrhizal fungi exert on their host plant when HM complexed in this way can not pass from fungal structures into root cells. The plant must be able to re-complex metal cations of tolerable stability constants on their way from soil solution via (mycorrhizal mycelia), root symplast, apoplast, and xylem to shoot and vacuole [160].

In fairy rings of *Marasmius oreades*, degradation of 20 to 35 % of senescent plant roots in the presence of fungal laccase increased the content of dissolved organic carbon (3.74 x), hexose sugars (3.75 x), NH_3/NH_4^+ (5.1 x), NO_3^- (11.1 x), the number of aerobic bacteria (14.4 x), and the formation of the phytochelants, oxalic, citric, and malonic acids. Soil pH diminished by 1.5 units mainly due to nitrification and carboxylic acid production. Although the solubility of trace elements increased (6.1 x), the trace metal content in sound roots of grasses from the fungal region was as high as in roots of control plants. Shoot concentrations in Al, Cr, Fe, Ni, and Ti however diminished by more than 50 % due to inhibited root-to-shoot transfer under fungal influence [56]. Uptake of most of these elements is not under the control of shoot N_{org} [143, 144]. It was therefore concluded that particularities in complexation render their passage through root and xylem more difficult.

Stationary perennial mycelia of *H. fasciculare* and *K. mutabilis* were established in two field plots (4 m^2 each) on non-contaminated alluvial river sediments, using inoculated wood chips and stem sections of Europoean beech, respectively, as carrier substrates. Both mycelia raised the soil's NH_4 content to 300 %. Nevertheless, the growth-inhibited grasses of the *H.-fasciculare* plot lost 26 % in N_{org} but reached 60 % more in the sum of the metalloproteid-associated Co Cu Mn Ni Zn than the level of N_{org} made one expect. The buttercup (*Ranunculus acris* L.) vegetation dominating the *K.-mutabilis* plot was tolerant of fungal growth inhibitors. Its shoots contained 30 % more in N_{org} and 58 % more in the sum of the transition metals than control plants. It is concluded that the surplus in uptake of transition metals goes back to the action of strong chelants in the soil solution of which carboxylic acids, amino acids such as cysteine, and/or non-identified fungal ligands must be taken into account. Basidiomycetes can thus contribute to phytoextraction. Its efficacy is nevertheless impaired by fungal inhibitors of plant growth and N_{org} formation [114].

8. Conclusions

Basidiomycetous ground fungi try to select, promote, kill, and digest not only resident microorganisms of "dead" substrates. They damage plants by hyphal ingress, phytotoxic substances, and stress factors which call their rating as saprobes in question. They win and lose in their attempts of doing so, and little is known about the molecular basis of these attempts and their outcome. The direct visibility of hyphal growth, stunting, lysis, sclerotial, and basidiome formation make ground fungi optimum deputy organisms in ecological and physiological studies, e.g., in the following fields: nutritional and microbial basis of (pre-degraded) lignocelluloses which make them conducive to fungal growth, not only for edible fungi; simulated "field inoculations" with soils modified by organic and mineral fertilizing and by (artificially weakened) plants; overcoming soil fungistatic effects; the nature of fungal competitive ability and the inclusion of (the easily lost) volatiles in microbial interactions; how can fungal spores gain a foothold where (mould-susceptible) sterile spawn substrates fail; pretensions of fairy-ring fungi to come from the depressive growth on agar plates to the vigorous mycelia in grassland; survival strategies of fungi such as *Agaricus fissuratus* which lack any competitive ability; action of liquid and volatile emanations from microorganisms and plants on fungal life cycle; fungal enzymology in the presence of microorganisms and plants that modifies substrate catabolic efficiencies; fungal (volatile) antibiotics in ecology; nature of plant stress exerted by soil saprobes , e.g., to make plants host fairy ring

fungi; fungal (heavy) metal chelants and their impact on soil metal solubility and plant metal homeostasis; fungal gene induction by microbial and plant emanations and the resulting changes in the metabolome, to end an endless list of wishes.

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