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Interactions between Bacteria and Fungi on Aquatic Detritus – Causes and Consequences

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Abstract

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Bacteria and fungi dominate the decomposition of aquatic plants, a major process in the carbon and nutrient cycling in many aquatic systems. Although phylogenetically distant, bacteria and fungi often live in close proximity with each other. Since these microorganisms also have similar ecological functions, interactions have developed between them. This thesis explores the nature of such interactions, and the potential effects on key components of the decomposition process. The thesis includes a critical assessment of the ergosterol method for determination of fungal biomass, a survey of the environmental factors determining the distribution and taxa numbers of litter-decomposing bacteria and fungi in lakes, and a number of experiments on the interactions between bacteria and fungi. In all the experiments performed, fungi responded to bacterial presence through antagonism, although different fungal strains, bacterial communities and substrates were used. The antagonism seemed to be caused by interference competition for substrate. The fungal effect on bacteria was less consistent. Bacterial growth was suppressed, unaffected, or even enhanced by the presence of fungi. Fungi contributed more to extracellular enzyme production than bacteria, and bacteria were probably able to assimilate intermediate decomposition products formed through the activity of extracellular enzymes of fungal origin. Thus, the effect on bacteria from interacting with fungi was determined by the balance between competition and benefit from excreted enzymes. Bacteria and fungi also used different size fractions of the organic matter, according to their different enzymatic capacities. Hence, bacteria appeared to assimilate low-molecular-weight compounds, while high-molecular-weight compounds were utilized primarily by fungi.

In brief, the ecological interactions influenced the growth and hence also the biomass development of bacteria and fungi, which affected enzyme activity as well as utilization of dissolved organic matter. Therefore, I suggest that interactions between bacteria and fungi influence degradation of plant litter in aquatic systems.

Keywords: bacteria, fungi, decomposition, antagonism, extracellular enzymes, competition, macrophytes, dissolved organic carbon (DOC), ergosterol

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To my parents, with love

List of papers

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals.

- I Mille-Lindblom, C. & Tranvik, L.J. 2003. Antagonism between bacteria and fungi on decomposing aquatic plant litter. *Microb. Ecol.* 45: 173–182.
- II Mille-Lindblom, C., Fischer, H. & Tranvik, L.J. Antagonism between bacteria and fungi: substrate competition and a possible trade-off between fungal growth and tolerance towards bacteria. *Submitted manuscript*.
- III Romani, A.M., Fischer, H., Mille-Lindblom, C. & Tranvik, L.J. Interactions of bacteria and fungi on decomposing litter: differential extracellular enzyme activities. *Manuscript*.
- IV Fischer, H., Mille-Lindblom, C., Zwirnmann, E. & Tranvik, L.J. Contribution of fungi and bacteria to the formation of dissolved organic carbon from decaying common reed (*Phragmites australis*). *Submitted manuscript*.
- V Mille-Lindblom, C., Fischer, H. & Tranvik, L.J. Litter-associated bacteria and fungi – a comparison of biomass and communities across lakes and plant species. *Submitted manuscript*.
- VI Mille-Lindblom, C., von Wachenfeldt, E. & Tranvik, L.J. 2004. Ergosterol as a measure of living fungal biomass: persistence in environmental samples after fungal death. *J. Microbiol. Methods* 59: 253–262.

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Abbreviations

ANOVA	Analysis of variance
B	Bacteria
C	Control
CO ₂	Carbon dioxide
DAPI	4',6'-diamindino-2-phenylindole hydrochloride
DGGE	Denaturing gradient gel electrophoresis
DNA	Deoxyribonucleic acid
DW	Dry weight
DOC	Dissolved organic carbon
F	Fungi
FPOC	Fine particulate organic carbon
HMW	High molecular weight
HPLC	High performance liquid chromatography
LMW	Low molecular weight
MMW	Medium molecular weight
PCA	Principal component analysis
PCR	Polymerase chain reaction
RDA	Redundancy analysis

Introduction

Background

Emergent macrophytes in lakes

In the vast majority of the world's lakes, the area of the littoral zone is larger than that of the pelagic, since most lakes are small and shallow (Wetzel 1990). In terms of productivity, the littoral dominance is even more pronounced; in fact, the emergent macrophytes of lake littorals are among the most productive plant communities in the world (Wetzel 1983). Hence, the organic matter produced by the littoral vegetation can literally drive lake metabolism. A typical emergent macrophyte is *Phragmites australis* (common reed), which has a worldwide distribution. *Phragmites* and many other emergent macrophytes have supporting tissue containing the recalcitrant structuring molecules cellulose, hemicellulose and lignin, wherefore most of its biomass remains ungrazed and instead enters the detritus pool (Farmer and Morrison 1964, Polunin 1984).

Decomposition is slow for such refractory matter, and in addition, *Phragmites* detritus has low concentrations of nutrients, which further slows down the degradation (Gessner 2000). The low breakdown rate results in a more or less continuous metabolism of macrophyte litter. In combination with the immense amount of litter, this continuity is important for ecosystem stability for the otherwise highly fluctuating availability of organic carbon in lakes (Wetzel 1995).

As in most other ecosystems, the majority of the plant litter decomposition is carried out by microorganisms (Dickinson and Pugh 1974). Saprotrophic decomposition is a key process in all ecosystems, and is thought to be the second largest flux in the global organic matter cycling, next to primary production (Sturner and Elser 2002). Decomposition regulates for example the duration of nutrient immobilization in biomass and the quality of the released products. For simplicity, budgets used for estimation of decomposition are usually based on carbon. Microbial decomposers release mineralized products in gaseous form as CO₂ and generate intermediate decomposition products in the form of dissolved organic carbon (DOC) and as fine particulate organic carbon (FPOC) (Baldy and Gessner 1997, Gessner et al. 1999). Little is known about the amount and composition of the FPOC that accumulates during decomposition. The quality of the produced DOC is determined

by e.g. the configuration of the substrate and the enzymatic capacity of the saprotrophs (Sinsabaugh 1994, Cleveland et al. 2004, Scully et al. 2004).

Microbial decomposers in aquatic systems

The two groups of microorganisms of greatest importance for decomposition are bacteria and fungi. In aquatic macrophyte litter, fungal biomass generally exceeds that of bacteria considerably, typically constituting above 90% of the total microbial biomass (Newell et al. 1989, Kominkova et al. 2000, Findlay et al. 2002). Usually, fungi also have a higher production than bacteria, and hence perform the major part of the decomposition (Kuehn et al. 2000, Gulis and Suberkropp 2003a). Still, bacteria have been reported to contribute significantly to decomposition. Bacterial turnover times can be considerably shorter than for fungi, and hence their contribution to decomposition may be larger than implied by their biomass (Findlay and Arsuffi 1989, Baldy and Gessner 1997, Hieber and Gessner 2002).

Running water

Most of the aquatic research concerning microbial and especially fungal decomposers has been performed in woodland streams, which can receive high amounts of terrestrial leaf litter. Fungi have been recognized as a link between the terrestrial litter and invertebrate detritivores (Bärlocher 1985). In streams, the predominant saprotrophic fungi are the aquatic hyphomycetes, a polyphyletic group also called Ingoldian fungi (Suberkropp and Klug 1976, Chamier et al. 1984), which are typically anamorphs (asexual stages) adapted to life in water (Deacon 1997). They have prerequisites for rapid growth and reproduction when substrate availability is high (Gessner and Chauvet 1994, Gessner and Chauvet 1997). Fungal hyphomycetes are well-adapted to life in streams, for example through their branched spores, that attach like anchors to new substrata (Bärlocher 1992, Deacon 1997). Thus, fungi have been reported as fast colonizers of leaves that fall into the water. After an early fungal peak that often occurs within weeks unless the leaves are very recalcitrant, fungal biomass generally declines. Bacterial biomass on the other hand tend to stabilize or increase throughout decomposition (Findlay and Arsuffi 1989, Gessner and Chauvet 1994, Baldy et al. 1995, Weyers and Suberkropp 1996).

Standing water

Although generally slower than for terrestrial leaves in streams, decomposition of plant litter in lakes and wetlands can be largely performed by fungi, which dominate microbial biomass and production correspondingly to the situation in streams (Newell et al. 1989, Kominkova et al. 2000, Kuehn et al. 2000, Findlay et al. 2002). Fungal decomposition of emergent macrophytes can be substantial already in aerial parts during the standing dead phase, i.e.

before the plants break and fall into the water (Kuehn and Suberkropp 1998, Gessner 2001, Verma et al. 2003). Fungal decomposers of macrophytes in standing water are generally dominated by ascomycetes, and although they are not easily identified, more than 200 taxa of freshwater ascomycetes have been reported, most of them from plant detritus (Shearer 1993). Many of these species also occur in terrestrial habitats. The littoral zone represents the interface between terrestrial and aquatic habitats, and hence the decomposers are probably adapted to alternating submergence and aerial exposure (Shearer 1993). Bacteria contribute to plant litter decomposition also in standing waters (Anesio et al. 2003). As in streams, they are generally less important than fungi for decomposition (Gaur et al. 1992a, Newell 1993, Kominkova et al. 2000), even if contrasting results are reported from some systems (e.g. Gaur et al. 1992b).

Differences between bacteria and fungi

Bacterial and fungal saprotrophs have similar functions in the sense that they decompose plant litter, but they are in most other aspects very different organisms. Bacteria are prokaryotes, unicellular organisms lacking a cellular nucleus as well as other organelles. Fungi are eukaryotes, and phylogenetically very distant from bacteria. In many features, their requirements for and means of growth and reproduction are also widely different (Deacon 1997, Madigan et al. 1999). Bacteria are suspended in or attached to a substrate while the fungal saprotrophs, which typically are filamentous, penetrate into the substrate with their hyphae.

Extracellular enzymes

In order to decompose plant litter, saprotrophic microbes produce extracellular enzymes. The most relevant enzymes from this aspect involve those that break down the plant fibers (cellulases, hemicellulases, pectinases, phenoloxidases, chitinases) as well as enzymes important for microbial acquisition of nitrogen and phosphorus (peptidases, ureases and phosphatases) (Sinsabaugh et al. 2002). Fungi in general have a more forceful enzymatic capacity than bacteria (Kirk and Farrell 1987). Many terrestrial fungi, in particular basidiomycetes, are well-known for having remarkable enzymatic capacities, and can therefore degrade even highly recalcitrant, lignin-rich detritus, such as wood (Kirk and Farrell 1987, Deacon 1997). Several of the fungal species generally considered to be terrestrial can also be found in aquatic systems, but also truly aquatic species have been shown to produce a wide range of enzymes (Zemek et al. 1985, Shearer 1992, Abdel-Raheem and Shearer 2002), some even lignin degrading enzymes (Fisher et al. 1983, Shearer 1992, Bucher et al. 2004a, Bucher et al. 2004b). Being filamentous, fungi more frequently inhabit relatively large units of particulate organic matter, while negative correlations have been reported between particle size and bacterial biomass and production (Sinsabaugh and Findlay 1995). Ex-

tracellular enzyme activity has been found to correlate positively to particle size (Jackson et al. 1995, Sinsabaugh and Findlay 1995), again suggesting fungal dominance in their production. However, production of cellulolytic and xylanolytic (hemicellulolytic) enzymes has been reported to occur also in bacteria (Robb et al. 1979, Tanaka 1993, Sala and Güde 2004). In a few cases, bacteria have shown to contribute to the degradation of lignin, either as primary decomposers (Benner et al. 1984), or through mineralization of intermediate products released through fungal activity (Rüttiman and Vicuna 1991). Decomposition of *Phragmites* has been found to relate to activity of cellulolytic and xylanolytic enzymes, which can be produced by both bacteria and fungi (Tanaka 1991, Tanaka 1993).

Decomposition products

Differing in their abilities to produce extracellular enzymes, bacteria and fungi presumably deliver different decomposition products. Several studies have contributed to the knowledge about microbially mediated mass loss and breakdown rates (e.g. Baldy and Gessner 1997, Gulis and Suberkropp 2003a), but few have examined the contribution of specific microbial groups to mass loss and formation of decomposition products (Gessner et al. 1999). A small number of studies have investigated formation of specific decomposition products, for instance during lignin degradation (Opsahl and Benner 1995, Dittmar and Lara 2001), but the roles of different microbes were not considered. It is possible that bacteria benefit from the enzymatic activities of fungi, since a large fraction of the soluble products of decomposition is exported rather than metabolized by fungi (Sinsabaugh and Findlay 1995, Baldy and Gessner 1997).

Ecological interactions

Synergism and antagonism

Ecological interactions between two organisms or populations can either be positive (synergistic), negative (antagonistic), or lack effect. The interaction can influence both parts in a similar way (bilateral) or differently. Competition would be the typical example of bilateral antagonism. Ecological interactions have developed between bacteria and fungi during the long time of co-occurrence. The most famous illustration of microbial antagonism is the production of antibiotic substances such as penicillin by certain fungi. There are also useful applications for bacterial antagonism against fungi, for instance as biological control agents of fungal plant pathogens (Weller 1988). Synergism occurs whenever at least one of the interacting organisms benefit from the other. If the synergetic relationship is bilateral, it is called mutualism. As an example of synergistic relationships between bacteria and fungi,

the beneficial effect from some bacteria on establishment of mycorrhiza can be mentioned (Founoune et al. 2002).

Interactions between decomposer bacteria and fungi

Naturally, interactions have developed also between saprotrophic bacteria and fungi, which have similar ecological functions and often live in close spatial proximity of each other. Synergism has been found to occur between saprotrophic bacteria and fungi, but the mechanism behind is not always known (Bengtsson 1992). For example, the excretion of extracellular enzymes can be beneficial also for other organisms than the producer, since the producer is not likely to be 100% efficient in assimilating the released product, as reported above for fungi. The enzymatic activity of fungi could also have an indirect effect. By softening the plant tissue and through penetration with hyphae, fungi may promote bacteria by increasing the accessible area of a specific substrate (Suberkropp and Klug 1980). There are even findings of bacteria adhering tightly to hyphae of mycorrhiza fungi and are thereby carried along with the hyphae (Nurmiaho-Lassila et al. 1997, Bianciotto and Bonfante 2002). Other bacteria exist as endosymbionts inside fungi (Bianciotto and Bonfante 2002, Minerdi et al. 2002).

However, interactions between saprotrophic microbes are not always synergistic. Although bacteria and fungi share limited resources and substrata, simple resource competition, or *exploitation* competition (Lockwood 1992), has been reported only sparsely (Gulis and Suberkropp 2003a). More often, when antagonism occurs between these organisms, “chemical warfare” seems to be used as a means of *interference* competition (Wicklow 1992). This involves the production of allelochemicals, and has been reported both from fungi (Platas et al. 1998, Gulis and Stephanovich 1999, Gulis and Suberkropp 2003b) and from bacteria (Møller et al. 1999, Wohl and McArthur 2001). However, the data for interactions between saprotrophic bacteria and fungi and in particular the ecological effects from such studies are still scarce.

Antibiosis, allelopathy and allelochemicals – some definitions

Antagonistic interactions between microorganisms involving excretion of substances can be referred to as either antibiosis or allelopathy. However, the term allelopathy has been used mainly when at least one part in the interaction was a plant (for a more detailed summary, see Fistarol 2004). The definition of antibiosis is somewhat vague, since it is sometimes used to describe a very specific relationship between two species, and sometimes a more general antagonism at a higher taxonomic level. Antibiosis and antibiotics are also closely associated with human medicine which can be confusing. I have therefore chosen to use the term “excretion of allelochemicals” in this thesis.

Aims of this thesis

The major aim of this thesis is to comprehend the nature of the interactions between bacterial and fungal decomposers of aquatic detritus. Additionally, the causes behind the interactions and their effects on enzyme production, degradation rate and decomposition products were studied.

Questions addressed in this thesis

- Do the domains of bacteria and fungi exhibit overall interactions, and, if so, are they antagonistic or synergistic? (Papers I, II, III and IV)
- What are the effects from ecological interactions on litter degradation rates and decomposition products? (Papers I and IV)
- Are there differences in production of major plant degrading enzymes between bacteria and fungi, and how is the enzyme production influenced by ecological interactions? (Paper III)
- Do bacteria and fungi compete for substrate, and can the outcome of competition be altered by pre-establishment of either group? (Paper II)
- Is there a trade-off between fungal growth and tolerance towards bacteria? (Paper II)
- What factors regulate bacterial and fungal decomposers in lakes? Are there any indications of ecological interactions between bacteria and fungi during decomposition in lakes? (Paper V)
- Is ergosterol a good indicator of living fungal biomass? Can bacteria have a role in its degradation after fungal death? (Paper VI)

Methods

Fungal biomass

The ergosterol technique

All true fungi have a membrane lipid called ergosterol, which is the major sterol in most fungi (Weete 1973, Deacon 1997). Ergosterol is rarely found in other organisms, except for small amounts in some algae and protozoa (Raederstorff and Rohmer 1987, Peeler et al. 1989). Since ergosterol is a component of cell membranes, it is correlated to fungal biomass. This combination of features qualifies ergosterol to be used as a biomarker for fungal biomass, and it is also considered to be specific enough for this use (Newell 1992). The ergosterol technique was developed in the late 1970's (Seitz et al. 1977, Seitz et al. 1979) and has increased in popularity since then. Prior to the use of ergosterol, fungal biomass was mainly estimated using microscopy techniques, which was tedious and imprecise, due to the embedded growth form of hyphae. Other biomarkers have been tested, for example ATP, chitin and glucosamine (Grant and West 1986, Ekblad and Näsholm 1996) but problems with specificity have been considerable (Suberkropp et al. 1993). The ergosterol protocol has been amended for use in various fields of ecological research (Lee et al. 1980, West et al. 1987, Newell et al. 1988) and it is also of economical importance since it can be used in food control, forestry and environmental monitoring (Salmanowicz and Nylund 1988, Pasanen et al. 1999, Padgett et al. 2000). For a detailed introduction to the use of ergosterol, see Paper VI.

In short, a combination of alkaline methanol and pentane or cyclohexane is used to extract the ergosterol through reflux followed by several purification steps. Finally, ergosterol is separated from other lipids using high performance liquid chromatography (HPLC). The protocol used in all papers of this thesis is based on procedures developed for soil (Davis and Lamar 1992, Ek et al. 1994), modified for plant litter use by optimizing sample weight and reflux time. A detailed description of the protocol is found in Paper I.

Stability of ergosterol after fungal death

Ergosterol is sometimes used as a measure of living biomass, based on the assumption of its fast degradation after fungal death. The validity of this assumption was addressed in Paper VI. The importance of the bacterial community for ergosterol degradation was also examined. The results of Paper VI showed that ergosterol was remarkably stable, in dead fungal tissue as well as when added in pure form. Addition of a natural bacterial community did not enhance degradation of ergosterol. On the other hand, when subjected to sunlight, ergosterol degraded very rapidly. Still, ergosterol is definitely the best biomarker for fungal biomass in most cases. However, these results suggest caution when using ergosterol as a biomarker for living fungal biomass, especially if samples have been subjected to sunlight to different extent.

Bacterial biomass

Bacterial abundance in natural samples is commonly quantified through staining with a fluorochrome and subsequent epifluorescence microscopy, after collection of the cells on a filter (Hobbie et al. 1977). For assessment of bacterial biomass, the volumes of the cells need to be measured. For water samples, the technique has been improved, and nowadays it is often possible to use flow cytometry and image analysis to reduce the time and effort required for the analysis (del Giorgio et al. 1996). Flow cytometry after staining with SYTO 13 (Molecular Probes) was used for the liquid samples in Papers I and II.

Biomass of litter-associated bacteria was measured in Papers I, III, IV, V and VI in this thesis. For such attached bacteria, detachment of the cells is necessary prior to analysis. Ultrasonication using a probe has shown to be an efficient method (Buesing and Gessner 2002), and was used before staining with SYTO 13 or DAPI. However, flow cytometry is problematic for bacteria associated with detritus, due to the presence of detrital particles. Therefore, I used epifluorescence microscopy for the analysis of litter-associated bacteria.

Microbial community analysis

Community analysis of fungi is reported in Paper III, and of both bacteria and fungi in Paper V. The methods used are similar, and are based on extraction, purification and amplification of DNA, followed by separation of DNA fragments. The protocols are described in detail in Paper V. In brief, a DNA purification kit is used for the extraction, which is followed by amplification through polymerase chain reaction (PCR) with primers specific for either bacteria or fungi. For bacteria, the 16S rDNA region is amplified, while the 18S rDNA region is used for fungi. In the final step, denaturing gradient gel electrophoresis (DGGE) is used for separation of the PCR products. DGGE is a fingerprinting method that presents information about the dominating taxa in a community.

Experimental set-up

For the experiments described in Papers I, II, III, IV and VI, bacteria and/or fungi were assembled from aquatic plant litter. The bacterial inocula used consisted of a mixture of natural bacteria, isolated through exclusion of fungi and other microorganism through centrifugation and filtration (Fægri et al. 1977, Møller et al. 1999), as described in Paper I. To produce fungal inocula free from bacteria, fungal strains were isolated on agar plates and purified in several steps.

For the experiments, 100-ml glass bottles were typically used for microcosms, and the substrate was *Phragmites* detritus in artificial lake water (Papers I, III and IV) or liquid nutrient medium (Paper II). When used in experiments, the organisms were inoculated either alone or in combination with other organisms.

Abbreviations for inoculated organisms

B	Bacteria
F	Fungi
F+B	Fungi+bacteria
C	Control (sterile, no organisms inoculated)

Other methods

Described above are the most important methods which are used in several papers in this thesis. In addition, a number of standard analytic methods were applied, for instance for water chemistry and litter quality. Simplified, rapid methods for analysis of microbial biomass have also been applied (Paper II). Methods for analysis of enzyme activity and quality of dissolved organic carbon (DOC) are described in detail in Papers III and IV, respectively.

Results and discussion

Microbial interactions

Bacterial presence reduce fungal growth

The interactions between bacteria and fungi were studied experimentally in Papers I, II, III, and IV. Fungi were always negatively affected by the presence of bacteria, expressed as deficient or completely reduced fungal growth. The extent of the bacterial influence differed between the experiments, as summarized in *Figure 1*. The possible difference between fungal strains in their response to bacterial presence was studied in Paper II. Indications of a trade-off between fungal growth and tolerance towards bacteria were found during this study of six different fungal strains. Hence, the strains growing best in absence of bacteria were most severely affected by bacterial presence, while those less restrained during co-existence with bacteria had lower growth rates in bacterial absence (*Figure 2*). A similar pattern was found for five strains used in Paper I, which is illustrated and discussed in Paper II.

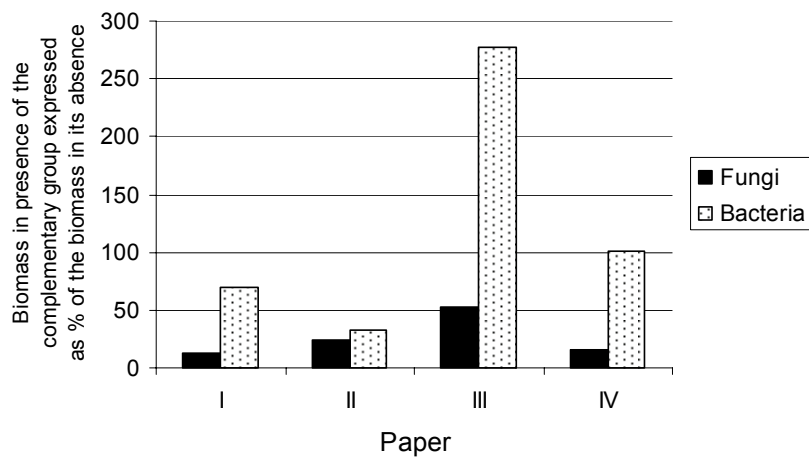


Figure 1. The biomass of bacteria and fungi during coexistence, expressed as percentages of the biomass in cultures where the complementary organism group was absent. This is a simplified figure; refer to the papers for information about biomass numbers, development and variation, and for details about the experiments.

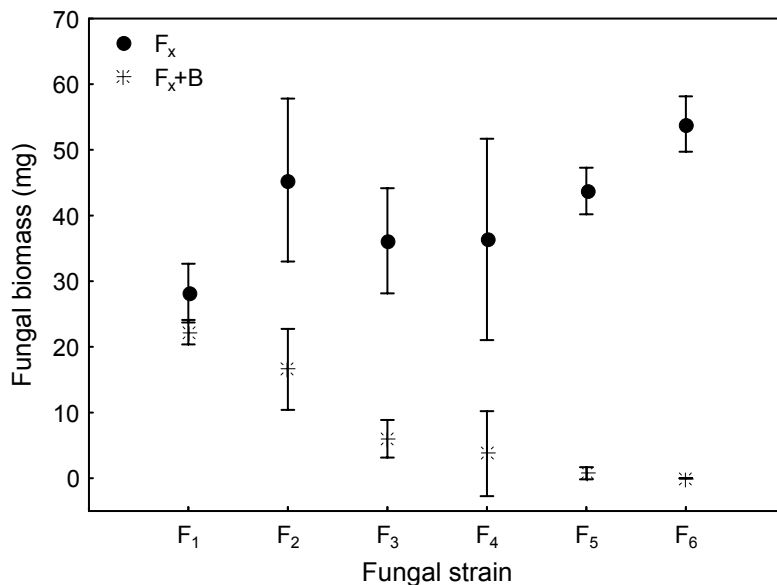


Figure 2. Fungal biomass after five days of growth in liquid nutrient medium in absence (F_x) or presence (F_x+B) of bacteria for six different fungal strains. For details refer to Paper II.

The most apparent reason for the antagonistic effect from bacteria on fungi is competition, and most likely the competition regards substrate (Lockwood 1992). Carbon competition was previously concluded to be the most probable reason for antagonism between bacteria and fungi (Møller et al. 1999), and competition is reported also in Paper II. It is possible that bacteria merely outcompete fungi for intermediate decomposition products (Suberkropp and Klug 1976). However, in the case of exploitation competition, a negative correlation would be expected between bacterial and fungal biomass, and such a pattern was not found. Also, the strength of the antagonism even at high substrate levels suggests this to be an inadequate explanation (Paper II). Similar conclusions were drawn in Paper I as well as in other studies of bacterial-fungal interactions, i.e. exploitation competition was regarded as an insufficient explanation (De Boer et al. 1998a, De Boer et al. 2003).

More likely, interference competition and adherent production of allelochemicals was involved in the studies by De Boer et al. (1998a, 2003) as well as in Papers I, II, III and IV. Correspondingly, plant pathogenic fungi are reduced when plants are grown in certain soils. Soil fungistasis was first discovered by Dobbs and Hinson (1953). The phenomenon is also called “suppressive soils” (Hornby 1983), and is caused by suppressive allelochemicals produced by bacteria (Alabouvette 1999, De Boer et al. 2003). In the studies included in this thesis, bacterial inocula produced at different

times, from different plants and aquatic systems all had a similar inhibiting effect on fungi.

Interference competition between different fungal species has been shown to be especially important during colonization of new substrates (Wicklow 1981, Wicklow 1992, Shearer 1993). Therefore, I compared simultaneous inoculation of bacteria and fungi to pre-establishment of either group (Paper II). If fungi were allowed to establish before bacterial inoculation, the suppressive effect of bacteria was almost eliminated. If bacteria were instead pre-established, fungi did not grow at all unless additional substrate was added.

It has been suggested that the nutrient content of the substrate plays a role in inducing production of antifungal compounds (Alabouvette 1999, De Boer et al. 2003). The effect of substrate concentration was studied in Paper II, where higher levels of substrate were found to have a positive effect on fungi, thus reducing the suppressive effect of bacteria. However, the fungal response does not reveal if this effect was due to reduced competition, lower production of allelochemicals in bacteria, or better fungal ability to overcome the bacterial aggravation when substrate concentration was high. Recent results have suggested that depletion of nutrients induced antibiosis (De Boer et al. 2003).

Variable influence from fungi on bacteria

The fungal effect on bacteria was less consistent. As seen in *Figure 1*, bacterial growth was suppressed, unaffected, or even enhanced by the presence of fungi. At first, the results seem mysterious, but at a closer look the answer to the inconsistency may lie in the availability of the substrate. The negative effect from fungi on bacteria was greatest when the microbes were grown on readily available liquid nutrient medium, and especially if fungi were allowed to pre-establish before bacterial inoculation (Paper II). However, also when recalcitrant *Phragmites* culms were used as substrate, fungi had a negative effect on bacteria (Paper I). In Papers III and IV, the substrate consisted of rather refractory *Phragmites* leaves, and bacteria were either enhanced or unaffected by fungal presence, respectively.

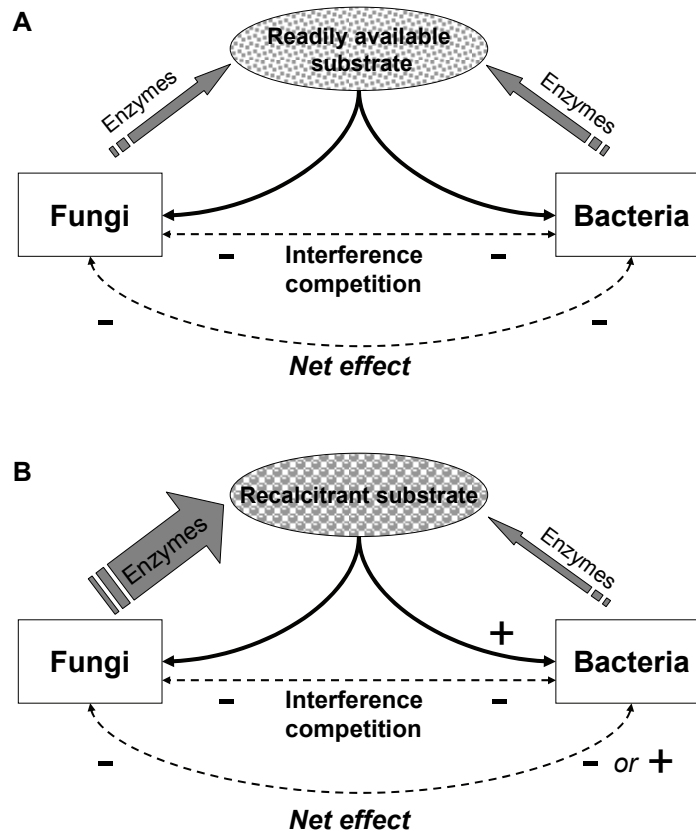


Figure 3. Conceptual model for the interactions between bacteria and fungi. Solid lines represent uptake of material while dashed lines symbolize interaction effects. A: When the substrate is readily available (as in Paper II), bacteria and fungi interact through interference competition, having a negative influence on each other. B: When the substrate is recalcitrant, fungi contribute more to degradation than bacteria, and thereby bacteria benefit from the intermediate decomposition product released by fungi. The net effect from fungi on bacteria is negative if the substrate is very recalcitrant, since the effect of fungal allelochemicals prevails over the profit in form of released substrate (Paper I). If the substrate is less recalcitrant, the profit equals (Paper IV) or exceeds the negative effect (Paper III).

I suggest a conceptual model, in which substrate availability explains the bacterial response to fungal presence (*Figure 3*). The presence of bacteria was always negative for fungi, as discussed above. Fungi in general have a greater enzymatic capacity than bacteria also in aquatic settings, as shown by direct comparisons of enzyme activities (Paper III) or indirectly (Jackson et al. 1995, Sinsabaugh and Findlay 1995). Most likely, fungi also produce allelochemicals as a means of interference competition (Platas et al. 1998, Gulis and Stephanovich 1999, Gulis and Suberkropp 2003b), which would have a negative effect on bacterial growth. Bacteria may profit from the activity of enzymes released by fungi, through uptake of intermediate decomposition products. For instance, fungi showed to contribute more to enzyme production (Paper III) while they were inefficient in uptake of small molecules (Paper IV).

On a readily available substrate, as the liquid nutrient medium used in Paper II, the entire enzymatic capacity of fungi is not employed, and the benefit for bacteria due to fungal enzymatic cleavage of macromolecules is minor or absent. Thus, on a readily available substrate, the net effect from fungi on bacteria is negative (*Figure 3A*).

On the other hand, on a more recalcitrant substrate, the bacterial profit from fungal enzyme production may overcome (Paper III) or balance (Paper IV) the negative effect from fungal allelochemicals (*Figure 3B*). If the substrate is very recalcitrant, as the *Phragmites* culms in Paper I, the bacterial profit from intermediate decomposition products is smaller than the negative effect from fungal allelochemicals, and hence the net effect is negative (*Figure 3B*). This is due to an overall lower degradation rate, resulting in a smaller transfer to bacteria of substrate mobilized by fungi. In conclusion, the experiments revealed that bacteria, although representing a minor part of microbial biomass, had a strong suppressive effect on fungi, while bacterial growth was suppressed, unaffected or enhanced by fungal presence, apparently depending on the substrate quality.

It could be argued that the different responses in bacteria reported in the different papers could be due merely to differences in antagonism between fungal strains, since in some of the papers one strain was used while in others several strains were used. Further on, Paper II did show dissimilar bacterial response to different fungal strains. However, the fungal strains which always caused suppressed bacterial growth (even though to different extent) in Paper II were stimulating bacterial growth in Paper III.

Other causes of antagonism

There are other possible causes than competition for antagonism between bacteria and fungi. For instance, pathogenic species that attack other microbes and cause cell lysis have been found among both bacteria (Kobayashi et al. 1995, Kopečný et al. 1996) and fungi (Thorn and Tsuneda 1992,

Tsuneda and Thorn 1995). When it comes to lysis of fungal hyphae, the target is often chitin, which is an important component of fungal cell walls (Cooke and Whipps 1993).

The results presented in this thesis do not suggest that lysis of living cells is a significant part of the antagonism, since the outcome was inhibition of growth rather than decrease of already present biomass. Similar results have been presented previously, when dune soil was investigated for signs of bacterial cell lysis of fungi (De Boer et al. 1998b). Hence, microbially mediated cell lysis seems to be a more specific trait, appearing in some specialized species in contrast to interference competition, which seems to be widespread and commonly occurring phenomenon in many ecosystems.

What about interactions in nature?

Paper V reports from a field study, based on sampling of three different macrophyte species in ten lakes representing a gradient in water chemistry. The aim was to compare the regulating effect from lake water chemistry and substrate quality on microbial biomass and communities and to elucidate microbial interactions. Microbial interactions may influence the distribution of bacterial and fungal biomass also on decomposing macrophytes in lakes. There was a trend towards opposite patterns for bacterial and fungal biomass on different plants. Previous research suggests that ecological interactions have a regulating role for bacterial and fungal decomposers in both stream and wetland habitats (Chamier et al. 1984, Shearer 1993, Buchan et al. 2003). Obviously, the conditions in nature are far more complex than in laboratory experiments, and this complicates data analysis.

Substrate quality was the most important regulating factor for bacteria and fungi. It has previously been shown to influence microbial biomass and degradation rate (Gessner and Chauvet 1994, Kominkova et al. 2000, Newell et al. 2000). The water chemistry can also have a regulatory effect on the microbes (Suberkropp and Chauvet 1995, Gulis and Suberkropp 2003a, Gulis and Suberkropp 2003c). This was confirmed by ANOVA in Paper V, although water chemistry was a weaker regulatory factor than substrate quality in multivariate analyses. Also, in a multivariate analysis, there were relationships between fungal biomass and total nitrogen concentration and between bacterial abundance and total phosphorus (Paper V).

Function of microbial decomposers

Extracellular enzyme production

The production of extracellular enzymes by bacteria and fungi was studied in Paper III. Activity of seven extracellular enzymes was followed in micro-

cosms with sterilized *Phragmites* leaves inoculated with either bacteria, fungi or both together (a similar experimental set-up was also used in Papers I, II and IV, see Methods section for an overview). Unsterilized leaves were also included to follow a natural microbial community. The enzymes studied were primarily associated with the degradation of different carbon fractions: cellulose and hemicellulose (β -glucosidase, β -xylosidase and cellobiohydrolase), lignin (phenol oxidase), and chitin (β -glucosaminidase). Enzymes involved in nutrient uptake (leucine-aminopeptidase, β -glucosaminidase and phosphatase) were also monitored. Bacteria and fungi differed remarkably in their production of extracellular enzymes. Fungal contribution widely exceeded bacterial with respect to all enzymes except leucine-aminopeptidase, which was produced in almost equal amounts by bacteria (*Figure 4*).

Bacteria did not contribute to the production of phenol oxidase and cellobiohydrolase, since for these enzymes there was no significant difference in activity between the bacteria-only treatment and the sterile control. However, except for these two enzymes, the biomass specific activity was higher for bacteria. Thus, the higher enzyme activity associated with fungi seemed to be related to the higher biomass of fungi compared to bacteria (Table 1). Reduced fungal growth in presence of bacteria is therefore the most probable cause for the generally lower enzymatic activity in F+B as compared to the fungi-only treatment. The difference in biomass specific activity was most pronounced for the enzymes associated with nutrient assimilation (phosphatase and leucine-aminopeptidase). The reasons are probably stoichiometric differences between the organisms. Bacterial cells are known to be rich in phosphorus and nitrogen (Vrede et al. 2002, Makino et al. 2003) while these elements generally have lower concentrations in fungal tissue (Cromack and Caldwell 1992).

The results in Paper III hence suggest that fungi contribute most to the enzyme production through their higher biomass. In addition, bacteria seem to benefit from the enzymatic capacity of fungi, in particular when it comes to enzymes involved in degrading plant polymers (lignin, cellulose and hemicellulose), the most refractory parts of plant tissue, which make up a considerable part of *Phragmites* (Farmer and Morrison 1964). Thus, bacteria are able to assimilate partly degraded organic molecules released by fungi (Sala and Güde 2004), and this is supported by the high biomass-specific activity in bacteria for polysaccharide-degrading enzymes. Additionally, the positive effect of fungi on bacteria may partly be due to increased surface area for bacteria provided by fungal hyphae (Suberkropp and Klug 1980).

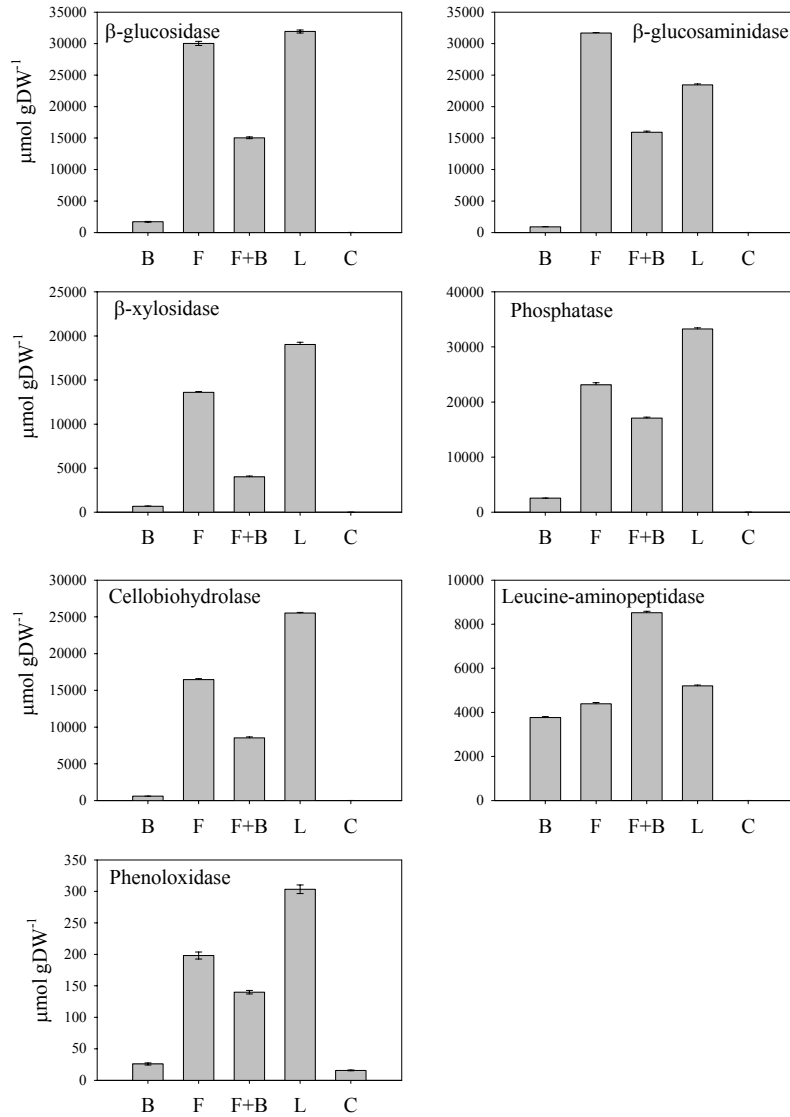


Figure 4. Production of extracellular enzymes by different microbial communities. B = Bacteria, F = Fungi, F+B = Fungi+bacteria, L = Leaves with a natural microbial community, C = Control. Error bars are 95% confidence intervals.

Table 1. Bacterial and fungal biomass and specific enzyme activities (expressed per g of microbial carbon) after 61 days of incubation of *Phragmites* leaves. Biomass values are means (n=4) with standard deviation in brackets. Details and an extended version of this table are presented as Table 2 in Paper III.

	Treatment B	Treatment F
Microbial biomass (mg C gDW⁻¹)		
Bacterial biomass	0.99 (0.37)	0
Fungal biomass	0	66.0 (30.35)
Biomass specific enzyme activity (mmol gC⁻¹h⁻¹)		
β-Glucosidase	0.91	0.51
β-Xylosidase	0.49	0.25
Cellobiohydrolase	0*	0.26
Glucosaminidase	0.81	0.48
Phenol oxidase	0*	0.003
Phosphatase	1.50	0.31
Leucine-aminopeptidase	2.30	0.003

*These activities were not significantly different from the activity in the sterile control.

Decomposition products

Due to their different enzymatic capacities, bacteria and fungi are anticipated to contribute to a different extent to decomposition, and also to utilize different fractions of the organic matter. This presumption is strongly supported by the results presented in this thesis. A carbon budget for decomposition of *Phragmites* culms was constructed in Paper I, while the quality of the dissolved organic carbon was examined in Paper IV. Similar experimental setups were used in these papers. In Paper I, the carbon metabolism was remarkably similar in treatments inoculated with different organisms, regardless of great differences in microbial biomass development. The decomposition of the refractory culms was slow, and hence the mass loss in all treatments was merely around 5% during the 79 days of experiment. Still, similarities regarding the fate of decomposition products were found between Papers I and IV. In both experiments, DOC contents were lowest in treatments dominated by bacteria, while controls and fungal treatments had higher levels of DOC.

Paper IV also presents evidence for differences between bacterial and fungal utilization of DOC fractions (*Figure 5*). A treatment with both bacteria and fungi is excluded from the figure, since fungi were suppressed by bacteria to such an extent that the result was similar to the treatment with only bacteria. Bacteria utilized DOC composed of low-molecular-weight (LMW) compounds effectively, as shown in other studies (Amon et al. 2001, Benner 2003). Also medium-molecular-weight (MMW) DOC was exploited to some extent, while DOC consisting of compounds with high molecular weight (HMW) accumulated in bacterial treatments. The increase of HMW

DOC was possibly due to excretion of exopolymers, i.e. polysaccharides produced by bacteria attached to surfaces (Sutherland 1999).

Fungi on the other hand diminished the concentration of HMW DOC, while MMW DOC was highly enriched in the fungal treatment. This pattern was probably caused by enzymatic attack by fungi on the large lignified particles, hence decreasing these and meanwhile releasing intermediate decomposition products in form of medium-sized aliphatic (non-aromatic) compounds and humic substances. LMW DOC remained in the fungal treatment at a similar level as in the control, which was somewhat surprising. However, as discussed previously, fungi are rather inefficient in their substrate assimilation (Sinsabaugh and Findlay 1995, Baldy and Gessner 1997).

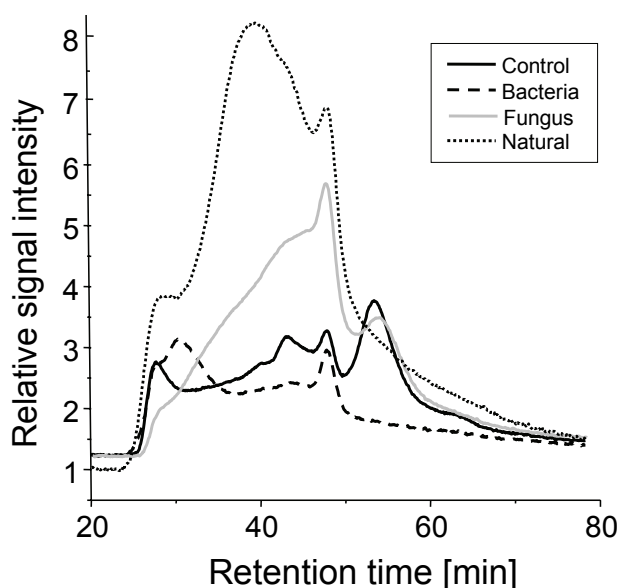


Figure 5. Size-exclusion chromatograms of total DOC released from *Phragmites* leaves incubated with different microbial communities as well as from a sterile control. Small molecules have a longer retention time. Thus, the peak at about 30 minutes represents HMW compounds, the peak at 55 minutes corresponds to LMW compounds and the large peak in between (37–48 min) represents MMW compounds.

Conclusions and perspectives

In conclusion, I present evidence for strong and in general antagonistic interactions between decomposer bacteria and fungi on aquatic detritus. The underlying reason for this negative relationship seems to be competition, but rather interference competition involving excretion of allelochemicals than simple exploitation competition (Lockwood 1992, Wicklow 1992). The ecological interactions influenced the growth and hence also the biomass development of the microbes, which affected enzyme activity as well as assimilation of dissolved organic matter. Therefore, I suggest that ecological interactions between bacteria and fungi influence degradation of plant litter in aquatic systems.

Future research within this field could preferably aim at verifying the role of ecological interactions between microbial decomposers in natural habitats. In connection, the importance of various potentially limiting elements for the outcome of interactions would require assessment. Also, research concerning the production and significance of allelochemicals in saprotrophic microbes is needed. Questions remain about the triggering of allelochemical production, and neither the specificity of allelochemicals for target organisms nor how the production is distributed among taxa is clear. Some of the results in this thesis suggest the ecological interactions between bacteria and fungi to be particularly important during colonization of new substrata, and hence I recommend the regulatory power of interactions during the colonization phase as well as throughout decomposition to be further elucidated.

På ren svenska (Summary in Swedish)

Vattenväxter och deras nedbrytning

Små och grunda sjöar utgör den vanligaste sjötypen i världen. Dessa sjöar har ofta ett betydande inslag av vass och andra emergenta vattenväxter, d.v.s. sådana växter som når över vattenytan. När de bryts ner frigörs mycket stora mängder kol och näringsämnen, vilket kan ha stor betydelse för övriga organismer i sjön. Nedbrytningen av denna typ av växter sker dock väldigt långsamt, eftersom de innehåller strukturbildande ämnen som ger växten stadga nog att stå emot vind och vågor. Därför är nedbrytningen av emergenta vattenväxter en näst intill kontinuerlig process, som erbjuder sjöar en mer stabil ämnesomsättning.

Mikroorganismer står för nedbrytningen

Mikroorganismer står för merparten av nedbrytningen i naturen. De viktigaste nedbrytarna är mikrosvampar och bakterier, och även om ganska få studier hittills gjorts på vattenväxter verkar svamparna bidra mest till nedbrytningen. Detta beror förmodligen till stor del på svamparnas större förmåga att producera vissa enzymer. Både svampar och bakterier utsöndrar s.k. exoenzymer, vilka verkar utanför organismen, där de bryter ner stora molekyler till mindre som sedan kan tas upp genom organismens cellmembran. Det är sedan länge känt att terrestra svampar är överlägsna bakterierna när det gäller svårnedbrytbara material, som t.ex. trä. På senare år har det dock framkommit att även akvatiska svampar producerar kraftfulla enzymer. Förmågan att producera enzymer är starkt knuten till nedbrytningen, eftersom olika molekyler angrips av olika enzymer, vilket också innebär att olika nedbrytningsprodukter bildas.

Bakterier och svampar interagerar med varandra

Eftersom båda grupperna fungerar som nedbrytare, och dessutom lever tätt tillsammans, är det inte speciellt förvånande att bakterier och svampar interagerar med varandra. Interaktioner mellan organismer kan vara av flera slag. Antagonism (negativ påverkan) grundar sig ofta i konkurrens om någon resurs som båda parter behöver. Synergism (positiv påverkan) kan ha sin grund i att den ena parten producerar ett ämne som har en positiv effekt på t.ex. tillväxten hos den andra parten. Interaktioner mellan organismer kan vara mycket kraftfulla, och ibland t.o.m. avgörande för deras fortsatta exi-

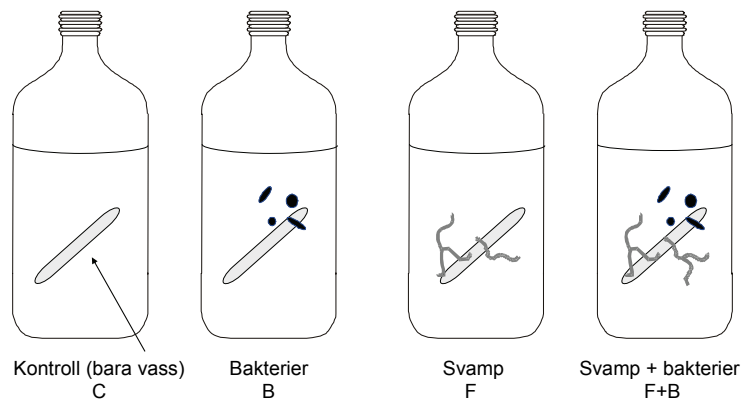
stens. Eftersom bakterier och svampar har olika betydelse för nedbrytningen är det viktigt att klargöra hur deras inbördes interaktioner påverkar dem och deras funktioner som nedbrytare.

Syfte med avhandlingen

Jag har studerat svampar (kallas i denna avhandling F, efter engelskans fungi) och bakterier (kallas B) på vattenväxter under nedbrytning, för att ta reda på följande:

- Vilken kapacitet att producera enzymer har bakterier respektive svampar?
- Vilka nedbrytningsprodukter bildas av respektive grupp?
- Vilken typ av interaktioner förekommer mellan dessa organismer?
- Är interaktionerna mellan bakterier och svampar så starka att de påverkar enzymproduktion och därmed nedbrytningen?

För att besvara frågorna genomfördes en rad experiment. Organismerna hämtades från vattenväxter i någon närliggande sjö, varefter kulturer bestående av antingen bakterier eller svampar togs fram. Dessa fick sedan växa antingen var för sig, d.v.s. svamp *eller* bakterier eller tillsammans (svamp *och* bakterier) i vattenfyllda flaskor, där vass användes som näringskälla, och en kontroll utan några organismer inkluderades. Försöksupställningen återges schematiskt i *Figur 6*.



Figur 6. Schematisk bild över den vanligaste försöksupställningen, med förkortningarna för de olika behandlingarna angivna.

Svampar och bakterier har olika funktion

Bakterierna tar upp små molekyler

Flera av experimenten visade att bakterierna främst tog upp de minsta och mest lättillgängliga molekylerna, eftersom förekomsten av dessa minskade snabbt i behandlingar där bakterier dominerade. Svamparna bröt i stället ner de större molekylerna, vilket förmodligen berodde på deras högre kapacitet att producera enzymer.

Svamparna producerar mer enzymer

Produktionen av sju olika enzymer mättes i ett av experimenten. Svamparna visade sig bidra avsevärt mer till produktionen av enzymer jämfört med bakterierna, vilket framgår av *Figur 4* tidigare i avhandlingen. I figuren framgår även att den behandling som inkluderade både svamp och bakterier (F+B) generellt hade lägre enzymproduktion än den med bara svamp, vilket kan tyckas underligt. Detta berodde på att svamparna, som ju stod för huvuddelen av enzymproduktionen, hade en lägre tillväxt när de var tillsammans med bakterier, och alltså producerade mindre mängder enzym. Orsaken till det var interaktioner mellan organismerna, och det ska vi gå in på nu.

Kemisk krigföring?

Resultaten visade att bakterierna hade en starkt negativ inverkan på svamparna i alla de olika experimenten. Responsen hos bakterierna däremot var mer varierande; svamparna hade en negativ, utebliven eller t.o.m. positiv effekt på bakterierna (*Figur 1*). Orsaken till antagonismen verkade huvudsakligen vara konkurrens. Det verkar dock inte röra sig om ren s.k. resurskonkurrens, utan snarare om en typ av konkurrens som involverar utsöndrande av hämmande signalsubstanser. Denna form av kemisk krigföring verkar användas av både svampar och bakterier. Den positiva effekten på bakterier som svampens närvaro ibland kunde ha berodde förmodligen på att bakterierna kunde dra fördel av enzymerna svampen utsöndrade. Den sammanlagda effekten på bakterierna berodde på hur stor denna fördel var i förhållande till svampens hämmande verkan.

Förutom experimenten genomförde jag också en fältstudie, där förekomsten av bakterier och svampar studerades i tio olika sjöar. De tre växtarterna vass, säv och gul näckros ingick i studien. Utbredningen av bakterier och svampar hade motsatta mönster på dessa växter, d.v.s. när det fanns höga halter av bakterier fanns det lite svamp och vice versa. Detta skulle kunna bero på interaktioner mellan mikroorganismerna, men det kan också komma sig av att bakterier och svampar föredrar olika växtarter.

Betydelse av resultaten – vad händer i naturen?

Jag har visat att bakterier och svampar som bryter ned vattenväxter skiljer sig åt på flera avgörande sätt. Svamparna visade sig ha en överlägsen förmåga att producera vissa enzymer, vilket gjorde att de kunde bryta ner de stora strukturbildande molekylerna i växterna, medan bakterierna främst tog upp de minsta och mest lättillgängliga molekylerna. Det förekom starka interaktioner mellan bakterierna och svamparna, och dessa var alltid negativa för svamparna medan deras effekt på bakterierna varierade.

Resultaten pekar på att interaktionerna var avgörande för den inbördes betydelsen av bakterier och svampar. Eftersom deras olika enzymatiska förmåga resulterar i så markant olika funktioner inom nedbrytningen, avslutar jag med att hävda att interaktionerna mellan bakterier och svampar skulle kunna ha stor betydelse för nedbrytningen av vattenväxter, och i ett större perspektiv även för näringsomsättningen i sjöar.

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