Fungi and Fungus-like Organisms in a Temperate Deciduous Forest Canopy

Der Fakultät für Biowissenschaften, Pharmazie und Psychologie

der Universität Leipzig

eingereichte

KUMULATIVE DISSERTATION

zur Erlangung des akademischen Grades

Doctor rerum naturalium
(*Dr. rer. nat.*)

vorgelegt von

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geboren am 05. Mai 1975 in Malsch, Karlsruhe

Preface and acknowledgements

This dissertation is of cumulative type and consists of five papers dealing with canopy research at the Leipzig Canopy Crane (LAK) research facility. The papers have been published in or accepted by both national and international journals. Two contributions from newsletters are also included.

Four of the five peer-reviewed papers and one short article deal with the investigation of diversity and ecology of wood decay fungi and fungus-like organisms. The remaining two contributions about tree frogs (*Hyla arborea*) on trees in up to 30 metres in height exemplify the importance of incidental observations during the fieldwork. As cryptogams are not considered in the articles, their contents will not be discussed further. The papers are listed in consequential order in the second part of the thesis.

The overview of this PhD thesis consists of a review of the publications. A compact description of the methods applied in the field of the Leipzig crane site and in the laboratory is given as well as a spanning discussion of the main results of this work.

Studying treetops of the world's forests and the life inside is a comparatively new area of environmental science. As mycology is still linked poorly with canopy research, a brief summary of past and present scientific activities in forest canopies follows this preface, hoping that it will help mycologists and other groups interested in environmental science getting familiar with foggers, climbing gear, and canopy cranes.

To reduce the gap of scientific knowledge concerning fungi in tree crowns, the studies within this PhD thesis have been designed as a starting point for the first long-term investigations to assess the diversity and ecology of fungi and fungal organisms in the canopy of a floodplain forest. Studies about leaf-inhabiting endophytic fungi are currently performed at the Leipzig crane site and a molecular characterisation of lignicolous fungi is planned for the future. The aims of the present work were (i) to create a species list of lignicolous fungi, slime molds and myxomycete-like organisms occuring in the canopy, (ii) to analyse beta diversity, and (iii) to critically comment on the influence of ecological factors on the species composition of these organisms in tree crowns.

With respect to research about wood decay fungi, all field and laboratory work (e.g. sampling, microscopy, identification of fungi) as well as data interpretation, statistics, and paper writing have been done by myself with initial help from colleagues and my supervisors Prof. Dr. W. Morawetz and Dr. P. Otto.

Ophir Tal was entirely responsible for gathering, processing, and interpreting meteorological and small-scale climatic data.

The study of slime molds and myxomycete-like organisms was done in cooperation with Prof. Dr. M. Schnittler from the Botanical Institute at the Ernst Moritz Arndt University in Greifswald, Germany. I was responsible for the field work and for applying multivariate analyses to the data. Cultivation and identification of the organisms, additional statistical evaluations, and most of the paper writing was conducted in Greifswald.

As this work will be published solely under my name, it is my duty and pleasure to mention those persons and institutions who contributed most to the successful completion of my PhD thesis.

Wilfried Morawetz, head of the Department of Systematic Botany and Botanical Garden, was the person who initiated the LAK Project in 2001 and agreed to launch mycological studies one year later. From the beginning on I have been fully integrated into his 'canopy team'. As the Leipzig Canopy Crane is an object of high public interest, he mentioned my work in many interviews, and seeing myself regularly in newspapers and even in national telecasts greatly helped maintaining my motivation when times were hard and difficult. I am grateful to his lasting promotion of this work.

Peter Otto also agreed to be a supervisor of my doctoral thesis. He formulated the first proposal for this topic which has been a sound fundament to start working with canopy fungi.

Peter J. Horchler, the former coordinator of the LAK Project, played an important role as he introduced me to multivariate statistics and provided many informations, thoughts, and data of other studies within the crane project. Until he left the LAK it was a pleasure to share the workroom with him.

Without naming every single colleague and person of the department, I can say that I enjoyed an open-hearted, friendly, and very helpful atmosphere every day during my PhD thesis.

Financial support for my studies has been kindly provided through projects UFZ-16/2000 and UFZ-04/2004 from the UFZ Centre for Environmental Research Leipzig - Halle in the Helmholtz-Association (UFZ) and from the Friends of the Botanical Garden Leipzig.

I am deeply indebted to my girlfriend, my longtime companion, and mother of our son Jacob, Carmen Schmitt. With her patience and thoughtfulness for the many nights and leisure-times that I spent for my research, she accounted like no other person for my work. I also thank my parents for bringing me up the way they did and for providing everlasting support.

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A short introduction of canopy research

As there exist a number of comprehensive synopses of canopy research (Lowman & Nadkarni 1995; Stork, Adis & Didham 1997; Linsenmair *et al.* 2001; Mitchell, Secoy & Jackson 2002; Basset *et al.* 2003; and Lowman & Rinker 2004), as well as free online material (`http://www.stri.org/english/research/facilities/terrestrial/cranes/canopy_crane_network.php`) the following introduction to canopy science will be comparatively short. Although research in the treetops is of great public interest with impressiv documentaries in television (e.g. `http://www.zdf.de/ZDFde/inhalt/19/0,1872,2150003,00.html` or `http://www.bbc.co.uk/sn/tvradio/programmes/horizon/madagascar.shtml`) and full of emotional sensations with many books and articles broaching the issue of canopy science in a more popular way (e.g. Mitchell 1989; Lowman 1999; Hallé 2001; Nadkarni 2004; and `http://www.heraldtribune.com/apps/pbcs.dll/article?AID=/20050731/COLUMNIST18/507310439`), I will restrict the following section mostly to scientific facts.

It is nearly impossible to define an exact starting point for canopy research because the hidden life in the treetops attracted naturalists such as Alexander von Humboldt for a long time. One of the first successful attempts to explore the rainforest roof was made in 1929 during an Oxford University expedition to Moraballi Creek in British Guiana. With an enormous assortment of military equipment such as rocket-firing machines, line-throwing guns or rope ladders, and the help of many natives, the explorers managed to reach several crowns without felling the trees and to install simple, temporary platforms (Mitchell 1989, pp. 23-25).

Apart from this rare example, serious investigations of forest canopies started in the second half of the 20^{th} century not until new methods of reaching the treetops were successfully established. With permanent platforms or towers it was then possible to conduct longer or even permanent studies in tree crowns. The most famous canopy project at that time were certainly the studies on the steel tower in Mpanga Forest in Uganda. Built by the East African Virus Research Institute, it followed the trends of studying mosquitoes and other tropical biting insects since the secret of yellow fever cycle was disclosed in the mid 20^{th} century by Jorge Boshell and others (e.g. Bugher *et al.* 1944; Galindo & Trapido 1955). The studies of Corbet, Haddow and others (Corbet; Haddow & Corbet; Dirmhirn, all 1961) revolutionized the perception of ecological processes and abiotic parameters high above the forest floor.

Almost two decades later canopy scientists used further technologies adapted to biological research in tropical forests and launched the next generation of canopy science. One certainly could cite the initial works of Perry (1978), Erwin & Scott (1980) and Erwin (1982) as milestones in canopy research. For the first time, Donald Perry used climbing gear that was slightly modified from alpine techniques to meet the demands

of tropical forest canopies. He and his colleagues built cobweb-like nettings high above the ground on which they managed to move inside the canopy up and down, and from treetop to treetop. Thus they could assess and demonstrate the separation of organisms (e.g. moths and bees) and dynamics (e.g. flowering and pollination) systematically from the forest floor to the upper canopy (e.g. Bawa *et al.* 1985). The vertical stratification of tropical forests is generally accepted in tropical biology nowadays (e.g. De Vries *et al.* 1997; Schulze *et al.* 2001), but recent studies such as that of gliding ants in tropical forests (Yanoviak *et al.* 2005) demonstrate that many more unexpected phenomena in the canopy still await the impartial scientist.

Unlike Donald Perry, Terry Erwin and Joachim Adis (Erwin & Scott 1980; Erwin 1982; Adis *et al.* 1984) studied the canopy fauna from the forest floor. They used motor-driven 'foggers' to blast insecticides up into the tree crowns and collected the downfalling arthropods for identification. With their results and estimations of arthropod communities and species diversity in forest canopies (Erwin 1988), they expanded tropical biology and the discussions of global biodiversity to a great extent (e.g. Hawksworth *et al.* 1995; Ødegaard 2000; Ødegaard *et al.* 2000) and even encouraged the 'skeptical environmentalist', Bjørn Lomborg, to critically debate on "how many species are there" (Lomborg 2001, pp. 249-257). The method of fogging trees is widely used with several modifications in canopy research these days (e.g. Henry & de Paula 2004; Schonberg *et al.* 2004; Floren & Linsenmair 2005; Novotny & Basset 2005; Battirola *et al.* 2005) and is an effective tool to consistently bringing to light new arthropod species, genera and even families and orders. This is not surprising as many organisms are predicted to be canopy specialists that, if ever, are rarely seen at ground level (Ozanne *et al.* 2003).

The first installation of a construction tower crane for canopy research in a tropical forest in Panama in 1990 (Parker *et al.* 1992; Smith *et al.* 1993) marked the establishment of the perhaps most effective method to study forest canopies (Körner pers. comm.). Given that the crane is installed and that it is supplied with stable electricity, scientists, operating from a gondola, can virtually reach every location in the three-dimensional catchment area of the crane's jib whenever it is required. The longer such a crane is operating, the cheaper are its maintainance expenses. Furthermore it moves almost soundlessly and apart from cutting a small gap to erect the crane, damage to the investigation site can be reduced to a very minimum. If the crane is mounted on a railroad track (Kirmse *et al.* 2003; Morawetz & Horchler 2004; Unterseher *et al.* 2004; 2005; Unterseher & Tal in press), larger areas and more trees can be studied which increases the amount of useful data (Körner *et al.* 2005). The construction crane as a research tool was so successful that other cranes quickly followed that of the Smithsonian Tropical Research Institute in Panama and are now operating in a variety of both temperate and tropical forests (Mitchell *et al.* 2002; Basset *et al.* 2004).

As I elaborated on above, the focus on canopy science lay in the tropics from the beginning on, and still does. Considering the number of tower cranes as a research tool, canopy studies in temperate forests are gaining equal priority. This is justified as patterns and processes of temperate forest canopies are far beyond our understanding (Körner *et al.* 2005) and the investigation of organismical diversity seems to be as valuable as in the tropics (e.g. Schmidt *et al.* 2003; Unterseher *et al.* 2005; Arndt 2005; Unterseher & Tal in press; Schnittler *et al.* in press).

Studying arthropod communities in treetops was very popular *ab initio* in canopy research, since arthropod diversity is huge and promised to be still higher as canopies could be included into the investigations. In the last few years, several books and book chapters about arthropods in forest canopies have been published encompassing dozens of papers and hundreds of references on this massive topic (Stork, Adis & Didham 1997; Basset *et al.* 2003; Erwin 2004; Lowman & Rinker 2004).

Herbivory in forest canopies is closely linked with arthropods since insects play the most important role in leaf-damaging. As its comprehensive study additionally requires analyses of plant-specific processes (e.g. photosynthesis, nutrient contents, and defensive mechanisms of plants), it is mostly treated separately from entomological studies (Lowman 1995; Rinker & Lowman 2004, Shaw 2005).

A third area of canopy science with an increasing mass of publications is the field of remote sensing and the investigation of abiotic patterns in and between tree crowns such as forest structure, light regimes, temperature, or humidity. With modern laser devices (Lefsky *et al.* 1999; 2002), with the combination of canopy cranes and manual perpendicular measuring (Unterseher & Tal in press), or with data loggers recording small-scale climatic data, canopy models can be computed and provide important information to assess the history and dynamics of an investigation site (Ishii *et al.* 2004; Nadkarni *et al.* 2004), or the dispersion and diversity of organisms in the canopy (McCune *et al.* 2000; Shaw 2004; Unterseher *et al.* 2005; Unterseher & Tal in press).

The amount of studies and papers dealing with wood decay, leaf-parasitic, endophytic, or epiphyllous fungi, with lichens or other small organisms such as myxomycetes or nematodes still is evanescent but as the implementation of molecular techniques into ecological sciences is enhanced, these organisms probably are the forthcoming protagonists of canopy research.

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Overview of the PhD thesis

Introduction

The common theme of the studies has been the investigation of biodiversity and ecology of fungi and fungus-like organisms in the canopy of a riparian forest in Leipzig, Germany. The results of the first intensive surveys of fungal biodiversity on small twigs within a temperate forest canopy were published in or accepted by three of the most important international journals of mycology. Four further articles are also included as they introduce to the studies of wood decay fungi or highlight important byproducts of this work. All papers demonstrate the challenging complexity of organismical life in tree crowns in a temperate mixed deciduous forest.

Forest canopies, defined as the aggregate of all tree crowns in the forest, including fruits, foliage, twigs, fine branches, and both vascular and cryptogamic epiphytes, are amongst the most dynamic and diverse natural environments on earth. They are unique and irreplaceable habitats for a vast number of organisms. Forest canopies support about 40% of extant species on earth, of which 10% are predicted to be canopy specialists (Ozanne *et al.* 2003). Additionally, they provide a range of goods important to human social and economic well-beeing.

"Serious" work and long-term studies at this challenging frontier, which constitutes the important interface between terrestrial life – biodiversity – and the atmosphere, only began some 25 years ago but has already changed largely our understanding of key ecosystem processes. It is mostly due to the scientific activities of ecologists, botanists, entomologists or climatologists in forest canopies and of organisations such as the Global Canopy Programme (GCP), the International Canopy Network (ICAN), and the International Canopy Crane Network (ICCN) that these habitats are now recognised as a very important and interesting but seriously threatened part of every forest ecosystem. From the scientific community and from the public as well as from politics, it is nowadays accepted that forest canopies possess unique structural, climatological, floristical and faunistical peculiarities that cannot be found on the forest floor (Pennisi 2005).

Scientific motivation

Despite some more than 20 years of intensive canopy research which doubtlessly revolutionised the perception of forest ecosystems (e.g. Erwin 1982; Morawetz 1998; Ozanne *et al.* 2003; Körner *et al.* 2005), studies on the diversity and ecological impacts of microorganisms, and especially of fungi in forest canopies above 10 m in height, have been largely disregarded (exceptions are e.g. Lodge & Cantrell 1995; McCune *et al.* 2000; Keller 2004; Keller *et al.* 2004). Even in the current benchmark of canopy research, the recent edition of *Forest Canopies* (Lowman & Rinker 2004), only nine pages, less than 2% of the whole book, mention decomposing processes (Fonte & Schowalter 2004). When taking into account the exceeding diversity of fungi and extraordinary importance of fungal activities in forest ecosystems, this amount of infor-

mation surely does not reflect natural conditions.

Additionally, studies concerning fungi on dry, weathered wood, a substrate that is naturally occurring most frequently in tree crowns, have concentrated mostly on tropical forests, on the understorey or over short periods of time. (e.g. Boddy 1992; Hedger *et al.* 1993; Nuñez & Ryvarden 1993; Lodge & Cantrell 1995; Otto & Glowka 1998). Apart from corticioid species of Polyporales, Hymenochaetales and Russulales, pyrenomycete fungi are frequent inhabitants of decayed wood in dry habitats. They are able to continue growth under arid conditions or to survive long periods of drought (e.g. Ingold 1954; Munk 1957; Nuñez 1996). Different groups of the Helotiales also tolerate conditions, that occur regularly in forest canopies (Sherwood 1981; Baral *et al.* 2003). H.O. Baral appraises the *Orbilia*-related groups ("Orbiliomycetes") as predominantly xerotolerant that mainly occur on wood that is still attached to standing trees without contact to the ground (Baral *et al.* 2003).

In the 1980s already, a series of studies was published by Boddy and 'co-workers', focussing on the development and ecology of fungal communities on dead attached branches in the understorey. However, many studies were limited to single branches or to early stages of fungal succession (Boddy & Rayner 1982, 1983, 1984; Chapela & Boddy 1988a, b, c; Griffith & Boddy 1988, 1989, 1991), most probable because of the limited possibilities of canopy access at that time.

In the last three decades, great efforts have been made to optimise equipment and techniques for safe and earnest canopy research as can be learned from the introduction to canopy science at the beginning of this dissertation. In 2001 a construction tower crane for observation purposes was installed in a species-rich riparian forest stand in the city region of Leipzig, Germany (Morawetz & Horchler 2002; Morawetz & Horchler 2004). The use of the crane enables precise and continuous observations and measurements in the three dimensional canopy space. The crane is mobile on a 120 metre-long railway track and brings 1.6 ha of forest within reach. Scientists using a remote control to move the crane and standing in a gondola, can raise themselves above the forest then lower the gondola precisely to the location of interest in the canopy. The tips of small distal branches, which were previously inaccessible, and therefore scarcely investigated in terms of fungal diversity, were now easily reachable. First ecological-faunistical studies within the interdisciplinary Leipzig Canopy Crane (LAK) Project, such as of arthropod diversity, herbivory or of the behaviour of bats, provided us with additional arguments to focus our mycological interests on the canopy of this temperate forest as an habitat of eminently high biological activity and diversity.

Progression

The new challenge to operate in a three-dimensional space forced us to apply new procedures of collecting fungi. Methods described in previous studies concerning the diversity of lignicolous fungi (e.g. Boddy & Rayner 1984; Chapela & Boddy 1988a; Lindblad 1997; Hong *et al.* 1999) could not be used, as sampling in these studies was restricted to fallen logs or hanging twigs from the understorey.

Collecting dead branches from living trees between 10 and 30 m in height took place in the years 2002 to 2004 and was limited to spring and autumn but also occurred during summer and winter in times when favourable weather conditions supported fungal development. Six native and three introduced tree species were selected to obtain a comprehensive amount of different substrates: *Fraxinus excelsior*, *Quercus robur*, *Tilia cordata*, *Acer pseudoplatanus*, *Carpinus betulus*, *Cerasus avium*, *Populus* x *canadensis*, *Quercus rubra*, and *Robinia pseudacacia*. The accessibility of a broad range of different tree species enhanced the value of the studies since substrate specificity, a feature of many wood decay fungi, could now be analysed to a great extent. Field data included information on stratum (sub, middle, top canopy), height above ground, tree species and individual number, substratum features (white or brown rot, stage of decay), diameter of branches, coverage with epiphytic algae, lichens, and occurrence of old fruit bodies, location of fructifications on the branch (upper side, lower side), and exposure to sun (estimated as exposed, [more than 50% direct sunlight], semi exposed [10 to 50%], and shaded [less than 10% direct sunlight]).

Since the studies were limited by the identification of fruitbody-forming species only – including anamorphic pyrenomycetes (mostly Coelomycetes) – the cultivation of the samples for a certain time was considered necessary to enlarge the number of identifiable fungi. Please refer to Unterseher *et al.* (2005) in part 2 of the thesis (section 2.2) for a detailed description of the laboratory methods.

The first step of the studies about the biodiversity of wood decay fungi in that particular canopy consisted in the investigation of species richness. A definite species list of wood decay fungi from the canopy with 118 different species (in 77 genera) depicted the broad spectrum of fungi occurring in tree crowns for the first time in this study (Unterseher *et al.* 2005). Corticioid fungi (e.g. Corticiaceae, Stereaceae, Hymenochaetaceae) were the most abundant group of species, which share similar morphologies and ecological requirements, with 37 species; pyrenomycetes, a second ecological group, were present with 18 species. Both groups clearly outnumbered other divisions of macrofungi. Agaric fungi (Agaricales and Cortinariales) were scarce. Taxa with minute sessile basidiomes, such as *Resupinatus*, dominated the fungal composition of these orders, whereas the observation of agarics with larger sporomes was scanty. This is a feature that is different from patterns of occurrence of wood decay fungi on the forest floor, where exposed "mushrooms" clearly are more diverse.

The number of rarely recorded species (singletons and doubletons) was eminently high – 61% – despite enormous sampling efforts. Interestingly, the mystery of rare species appears regularly in various studies of organismical biodiversity; for instance when studying arthropod diversity in the Tropics (Novotný & Basset 2000 and makes statistical analysis and interpretation of the data difficult (Colwell & Coddington 1995). Among our records, there was a considerable number of fungi that can be considered as rare or seldom recorded (e.g. *Patellaria atrata* or *Hyphodontia microspora*). The latter species was found only twice in Germany so far and is considered to be very uncommon worldwide (Dämmrich, pers. comm.).

Without doubt the detected richness of 118 fungal species is preliminary. One can clearly see that all species-accumulation curves shown in Unterseher *et al.* (2005) continue to rise almost linearly, which means that many more samples have to be collected before species saturation can be approached and a serious number of total species richness in that particular canopy can be given. Since many fungi form cryptic species or species complexes with populations being physiological and genetically, but not morphologically, different (for 'Corticiaceae' see e.g. Hallenberg & Parmasto [1998] and Nilsson *et al.* [2003] for *Hyphoderma setigerum*; Hallenberg, Larsson & Larsson [1994] for *Hyphoderma praetermissum* and Chamuris [1991] and Hallenberg & Larsson [1992] both for *Peniophora cinerea*), the identification of fungi restricted to morphological-chemical characters only allows to make limited predictions of the effective diversity of biological species of a study site (Hawksworth 2001).

After the circumstantial investigation of the most basic component of biodiversity – the α-diversity or species richness – the second task was to observe the next level of biodiversity, the distribution of wood decay fungi in the three-dimensional space on different tree species, in different canopy layers, in different moisture and temperate regimes, and on different substrate types.

In the articles of Unterseher *et al.* (2005) and Unterseher & Tal (in press) ecological patterns of the organisms were evaluated using multivariate statistics such as non-metrical multidimensional scaling (NMS), Cluster Analysis (both in McCune & Mefford 1999 and McCune & Grace 2002), and Correspondence Analysis (Gauch 1982 and Ter Braak & Šmilauer 2002) and by calculating indicator values (Colwell & Coddington 1995 and Colwell 2004).

Communities of wood decay fungi showed distinct variations both in species richness and composition with respect to the tree species, height in the canopy, stage of decay, and branch diameter. Pyrenomycetes and their anamorphs dominated the mycobiota on thin, exposed twigs at great heights, indicating their ability to overcome extended periods of drought and high levels of solar irradiance. Some taxa of Tremellales (*Exidia*

spp.), Orbiliales (*Hyalorbilia inflatula*, *Orbilia* spp.) or Agaricales (*Episphaeria fraxinicola*, *Cyphellopsis anomala*, *Lachnella* spp.) also exhibit features that enabled them to develop in lesser protected habitats in tree crowns.

The highest species richness and the highest density of fruit bodies was observed on *Tilia cordata*. Dead branches of *Acer pseudoplatanus* turned out to be the least populated habitats in the canopy. Fungal indicator species could be significantly assigned to six of the nine investigated tree species as there was virtually no overlapping in the species composition of fungi on the different tree species (Unterseher *et al.* 2005).

In the paper "Influence of small-scale conditions on the diversity of wood decay fungi in a temperate, mixed deciduous forest canopy" (Unterseher & Tal in press), climatic and structural peculiarities of the ecosystem compartment 'forest canopy' are described and their effect on the ecology of canopy fungi are discussed. Given that the upper canopy is widely composed of young, thin twigs and exposed to high illumination levels, to strong winds, and heavy rainfall, fungi living in this particular forest area need adequate adaptations to the extreme weather conditions and the limited substrate availability. Contrarily, inner and lower canopy layers are formed by a broad range of thin twigs and thick branches with a patchwork of sunny and shady places that provide many different ecological niches for wood decay fungi, especially for species with small fruit bodies and limited mycelium vagility. With respect to temperature and relative humidity, marked differences existed between forest floor and upper canopy layers that persisted on smaller scales and on different aspects of single branches (north, south, east, west). As it was shown in the article of section 2.3, the climatic and structural features in the canopy are an important factor determining the spatio-temporal patterns of distribution of lignicolous fungi.

In the short article from the ICAN newsletter *What's up?* finally, *one* particular example of hundreds or thousands of potentially different small-scale habitats in *one* canopy is given (section 2.5). The description of a tiny fragment of a decayed branch from a cherry tree (*Prunus cerasus*) makes us realise that it is almost impossible to reveal every single pattern of organismical behaviour in environmental sciences and that reductions should be achieved to a certain extent in ecological studies (Popper 1974, p. 23 in this thesis). Nevertheless, the attentive monitoring of organismical occurrence in the tree crowns is of great value for a better comprehension of ecosystematic patterns and processes, although they often cannot be quantified at first, such as the detection of tree frogs (*Hyla arborea*) in window traps of entomologists and sitting on leaves of *Acer pseudoplatanus* in 25 m in height. (Schmidt *et al.* 2003a, b, section 2.6 and 2.7).

The same holds true for the study of MMLO – slime molds and myxomycete-like organisms (Schnittler *et al.*, section 2.4). As a byproduct of the work on lignicolous fungi, sporocarps of slime molds were frequently noted in the field. During the cultivation of

twigs in the laboratory many phaneroplasmodia and sporocarps of myxomycetes emerged rapidly on the branches after a few days of storage. This indicated that the canopy might be an ideal habitat for slime molds and leaded to a research project comparable to that of lignicolous fungi.

So far, most studies of MMLO focused on myxomycetes from temperate zones and targeted habitats on the forest floor. However, also aerial plant parts can be inhabited by these organisms. This applies especially for Neotropical forests, where they often occur in greater diversity than on ground substrates (Schnittler & Stephenson 2000 and Schnittler *et al.* 2002). The canopy as a myxomycete habitat was first investigated by Snell & Keller (2003) and Keller *et al.* (2004) in broadleaved deciduous forests of the Appalachians using single rope techniques, and focusing on bark-inhabiting species. With the use of the Leipzig Canopy Crane it was now possible for the first time to investigate small twigs from the canopy at up to 30 m height for the occurrence of MMLO.

From the samples of fungal studies, one branch was picked out at random and two 5-cm long pieces were removed from its ends. Moist chamber cultures for cultivating MMLO were prepared by placing small pieces of air-dried, decorticated wood from the 5-cm long twig in a plastic Petri dish upon a disk of filter paper. As the methods of cultivating MMLO and adjacent statistical procedures are mentioned in detail in the paper, please refer to corresponding article in this thesis (section 2.4).

Several results of myxomycete studies differ from the findings of Unterseher *et al.* (2005) and Unterseher & Tal (in press). In the study of MMLO on dead decorticated twigs from the canopy 37 different taxa were isolated. Estimations of species richness showed that this particular habitat was investigated sufficiently to recover a majority of the likely species – 42 to 45 – depending on the estimators used. This was clearly not the case with wood decay fungi. It is also worthwile to compare the substrate specificity of MMLO with that of lignicolous fungi. Whereas wood-dwelling species showed distinct adaptations to their host trees no clear preferences for certain tree species were found for MMLO. Instead, they responded to the mostly plant-independant parameters stage of decay, water holding capacity, and pH value. The only exception, the observed specificity of *Stemonitis pallida* for *Quercus robur* was due to the more acidic, heavily decayed branches from oak trees. Therefore, decaying wood as a substrate seems to be much more uniform among tree species for superficially living organisms like MMLO than for wood decay fungi.

Conclusion

Considering that wood decay fungi and fungus-like organisms in the canopy are an inconspicuous but important component of the biota of forest ecosystems, that are also associated with other organisms such as canopy arthropods, investigation of the diver-

sity and ecological patterns of fungi in the canopy may be crucial to the understanding of organismical interactions and their distribution between canopy and soil (wood endophytes start growing on attached branches and, if branches drop, most likely complete life-cycles on the ground). The varying microclimatic conditions caused by the structural complexity of the forest canopy, together with the broad range of available substrates, lead to the suggestion that the diversity of fungi and fungus-like organisms is high in the canopy, and that the ecological phenomena are highly variable and provide a rich source for further investigations.

The amount of studies and papers that deal with wood decay, leaf-parasitic, endophytic, or epiphyllous fungi, with lichens or other small organisms such as myxomycetes or nematodes in forest canopies is still evanescent. As the implementation of molecular techniques into ecological sciences is enhanced, these organisms probably are the forthcoming protagonists of canopy research. However, recent studies such as that of gliding ants in tropical forests (Yanoviak *et al.* 2005) demonstrate that many more unexpected phenomena in the canopy still await the impartial scientist.

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A successful reduction is, perhaps, the most successful form conceivable of all scientific explanations, since it achieves what Meyerson . . . stressed: an identification of the unknown with the known.

. . . we should, nevertheless, on methodological grounds, continue to attempt reductions. The reason is that we can learn an immense amount even from unsuccessful or incomplete attempts at reduction, and that problems left open in this way belong to the most valuable intellectual possessions of science: I suggest that a greater emphasis upon what are often regarded as our scientific failures (or, in other words, upon the great open problems of science) can do us a lot of good.

Before we can even attempt a reduction, we need as great and as detailed a knowledge as possible of whatever it may be that we are trying to reduce. Thus before we can attempt a reduction, we need to work on the level of the thing to be reduced (that is, the level of 'wholes').

——— Karl R. Popper (1974)[1]

[1]Scientific Reduction and the Essential Incompleteness of All Science. In F. J. Ayala & T. Dobzhansky (Eds.), *Studies in the Philosophy of Biology: Reduction and Related Problems.* (pp. 259–283) London Macmillan.

Articles

Studies of the diversity of lignicolous fungi in the canopy of a floodplain forest in Leipzig, Saxony

Martin Unterseher, Peter Otto & Wilfried Morawetz

Boletus **26 (2)**, 117–126, (2003).

Studies of the diversity of lignicolous fungi in the canopy of a floodplain forest in Leipzig, Saxony

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In May 2002 a study was launched within the project 'Leipzig-Canopy-Crane' to investigate the diversity of lignicolous fungi in the canopy of a floodplain forest. Using a construction crane dead wood has been collected at different heights. The focus lay mainly on the tree species *Quercus robur*, *Fraxinus excelsior* and *Tilia cordata*. The collected branches were stored in high humidity for 2 weeks and were screened regularly for the occurrence of fructifications. 85 species from 62 genera could be determined so far (Asco- and Basidiomycetes incl. Fungi imperfecti). This indicates that fungi play an important role as destructive agents and perthophytes in the ecosystem compartment 'canopy'. The high frequency of species with adaptions to aridity was obvious, e.g. the ability to continue fruitbody development after desiccation. It is noteworthy, that a few agaric fungi with comparatively delicate fruitbodies were found in heights up to 25 metres, e.g. *Mycena galericulata* and *Gymnopilus hybridus*. Probably, a typical vertical pattern of species richness has been observed. With 24 species the upper canopy showed the lowest diversity, 58 were detected from the middle canopy and 31 from the lower. In the top region of crowns only 4 genera (*Cryptosphaeria*, *Diatrypella*, *Nitschkia*, and *Peniophora*) dominated the fungal composition with approx. 60% of all records. With increasing species diversity towards the lower heights the abundance of species decreased. The systematic-taxonomic composition of the mycota within the different strata varied clearly. The investigated trees are distinctively colonised by fungi. For instance dead wood of *F. excelsior* showed the lowest diversity with 13 species, 21 different fungi colonised dead hanging twigs and branches of *Q. robur* and the highest number with 37 species was found on *T. cordata*. Surely, the continuation of the diversity study will reveal more than 100 teleomorphic lignicolous fungal species. From the canopy a characteristic for Germany rarely recorded discomycete, *Patellaria atrata*, is described.

THE LEIPZIG CANOPY CRANE PROJECT

An interdisciplinary project was launched in the north-west of Leipzig (nature reserve ' NSG Burgaue') in June 2001 to investigate the ecosystem 'floodplain forest' with particular interests in the forest canopy. Within the Leipzig Canopy Crane Project (LAK), mainly financed and conducted by the University of Leipzig, the Centre for Environmental Research Leipzig-Halle (UFZ) and the City of Leipzig, spatio-temporal patterns of biodiversity and ecological interactions are studied (Morawetz & Horchler 2002). A construction tower crane, mobile on a railroad track provide easy access to the forest canopy that normally can be hardly reached (Fig. 1). Standing in a gondola, the scientist is able to study the upper tree layers in an area of about 1.6 ha for many years comparatively trouble-free (Fig. 2). The investigation site possesses a high diversity of wooden plants (14 tree species) which doubtlessly affects the species

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diversity of other organisms such as birds, small mammals or arthropods in a positive way. Surely the mycoflora also benefits thereby.

Measurements of light intensity in vertical transects with PAR-sensors confirmed the inhomogeneity of this canopy that can be divided into different compartments. (Horchler, pers. comm.). First ecological-faunistical studies, such as of herbivory or of the behaviour of bats provided us with additional arguments to focus our mycological interests on the canopy of this temperate forest as an habitat of eminently high biological activity and diversity.

Fig. 1: Areal view of the investigation site in the Leipzig floodplain forest.

LIGNICOLOUS FUNGI IN THE CANOPY OF THE LEIPZIG FLOODPLAIN FOREST

Introduction

As the special importance of fungi as saprobes of leaf-litter or lying deadwood and as partners of mycorrhizae is known for a long time and intensively studied since decades, little is known about the role of fungi in the upper layers of forests. Very few studies of diversity and substrate specificity of wood decay fungi in the canopy were published which moreover concentrated mostly on tropical forests and on the understorey or were conducted over short periods of time. (e.g. Boddy 1992, Hedger *et al.* 1993, Nuñez 1996, Otto & Glowka 1998).

Fig. 2: Many locations in the plot can be visited and studied nearly undisturbed per gondola.

Apart from poroid and corticioid fungi (especially Poriales, Hymenochaetales, and Stereales), Pyrenomycetes are known as wood dwellers of exposed, dry habitats. Different groups of the inoperculate cup-fungi (Leotiales *s.l.*) also prefer such substrates. Sherwood (1981) for instance reported a high diversity of these fungi on dry, weathered wood and bark. H.O. Baral appraises the *Orbilia*-related groups ("Orbiliomycetes") as predominantly xerotolerant that mainly occur on wood that is still attached to standing trees without contact to the ground (Baral *et al.* 2003).

Despite such reports the assumption is widespread that investigating non-lichenized fungi is only promising in humid habitats. This is surely a fundamental reason why fungi play a minor role

or are not considered at all in the canopy projects in tropical forests (Australia, Malaysia, Panama) as well as in temperate zones (Japan, USA, Switzerland) (Mitchell *et al.* 2002).

The main aims of the mycological studies in Leipzig are (1) to investigate the diversity of lignicolous fungi, and (2) to analyse their ecological needs and their communities on decayed branches between 10 m and 34 m in height. First results of our studies, that have begun in May 2002, will be described in this paper. Another subproject will be the investigation of slime molds (Myxomycetes). It will be conducted in cooperation with Prof. Dr. M. Schnittler (University of Greifswald, Germany). Furthermore, studies of leaf-endophytic, parasitic and epifoliar fungi are planned as from 2004.

Methods

Dead wood of 30 individual trees was collected mostly in autumn 2002 and spring 2003. Sampling focussed on the most dominant tree species at the crane site, *Fraxinus excelsior*, *Quercus robur*, and *Tilia cordata*. Six individuals each of the three tree species with a large amount of dead wood were chosen for sampling (it is planned to sample ten trees each). Further 12 trees, randomly selected, belonged to *Acer pseudoplatanus*, *Carpinus betulus*, *Cerasus avium*, *Populus* x *canadensis*, *Quercus rubra*, *Robinia pseudacacia*, and *Ulmus carpinifolia*. Dependant on the amount of substrate, 50-cm to 1-m long pieces of dead twigs and branches were collected at as many locations as possible in the tree crowns. At a consequence several metres of dead wood per tree, with a maximal diameter of 6 cm were scanned for the occurrence of fruit bodies. Fruit bodies on larger branches were removed with a knife. We attempted to collect the same amount of wood in every canopy layer (upper canopy [26-34 m], middle canopy [18-26 m], lower canopy [10-18 m]). Because of the generally bad accessibility of lower strata as branches blocked the way from above, this was not always possible. Environmental parameters recorded in the field were height above ground, canopy layer (upper, middle, lower canopy), tree species, substrate characteristics (stage of decay, diameter, coverage with algae, other fruit bodies, or lichens), the location of the fruit body (upperside, underside of branch) and exposition to sun and wind (estimated as exposed, half-shaded and shaded).

Firstly, the branches were screened for the occurrence of fruit bodies with a dissecting microscope in the laboratory. Afterwards they were washed under flowing water, to reduce superficially adhering diaspores. The samples were stored under high humidity in open plastic boxes for two weeks to allow development of sporomes, basidiomes and ascomes from mycelia previously established in the wood and further growth of fruiting initials. Once a day the samples were sprayed intensively with water to maintain rather high water content of the wood and high air humidity. The samples were inspected every three to four days. All teleomorphic species were recorded, anamorphs were only considered if they grew in deeper layers of bark or wood (fungi imperfecti with pycnidia ['Sphaeropsidales'], acervuli ['Melanconiales'] or immersed sporodochia [Moniliales pp.]). Imperfect fungi with rapidly developing, mostly superficial mycelia were deliberately excluded because they could have occurred as secondary colonisers and probably do not belong to typical wood inhabiting species of the canopy.

First results

Eighty-five wood-dwelling, fungal species (Asco- and Basidiomycetes incl. Fungi imperfecti) from 62 genera could be identified. As expected, the amount of fungi with xeroresistant or xerotolerant fruit bodies was very high (e.g. *Exidia*, *Nitschkia*, *Orbilia*, *Schizophyllum*). They are capable to continue growth after rewetting. In the case of *Peniophora* or *Vuilleminia* this can be within one day and is easily visible because of a characteristic light reflection on the fruit body's surface. Some species with very small fruitings (e.g. *Episphaeria*, *Lachnella*, *Orbilia*, and *Unguicularia*) developed after few days under humid conditions. Up to now, a low number of imperfect fungi could be determined to genus or species level: (*Exosporium tiliae* (Link) Link, *Fusarium* sp., *Flagellospora curvula* Ingold, *Rabenhorstia* cf. *tiliae* (Fr.) Fr., *Stegonsporium acerinum* Peck, *Trichoderma* sp., and *Tubercularia vulgaris* Tode).

Agaric fungi were almost completely absent. *Mycena galericulata* (Scop.: Fr.) S.F. Gray (on *Q. robur*), *Gymnopilus hybridus* (Fr.: Fr.) Singer, *Plu-*

teus atricapillus (Batsch) Fayod (both on *T. cordata*), and *Pleurotus cornucopiae* (Paulet ex Pers.) Rolland (on *F. excelsior*) were only found once between 20 and 25 m in height. They developed in shaded places after extensive rainfall and in high relative humidity on thick branches with more than 6 cm diam. The tiny and delicate fruit bodies of *Pleurotellus chioneus* (Pers.: Fr.) Kühn. and *Resupinatus trichotis* (Pers.) Singer emerged only in well protected locations like clefts in the wood or under partly detached bark.

About 43% of all fungi belonged to the corticioid fungi (mostly Corticiaceae and Peniophoraceae), ca. 14% to the Diatrypaceae, the third most abundant family were the Nitschkiaceae with ca. 5.5% (systematic arrangement after Hawksworth *et al.* 1995). 40 fungal species, that is almost one half of all fungi recorded at the investigation plot, could be recorded only once. Some frequently or even often found species are considered to be rare in Germany such as *Episphaeria fraxinicola* (Berk. & Br.) Donk, *Lachnella villosa* (Pers.: Fr.) Gill., *Patellaria atrata* (Hedw.) Fr. (see below) or *Nitschkia cupularis* (Pers.) P. Karst. (compare Krieglsteiner 1991, 1993).

At a first glance on the diversity of true slime molds, Prof. Dr. M. Schnittler could preliminary identify 15 species. Abundant were for instance *Stemonitis fusca* Roth and *Arcyria cinerea* (Bull.) Pers.

Comparing the sampling heights of abundant fungal species, different preferences are clearly visible (Fig. 3). The ranges of sampling heights of *Nitschkia cupularis* (Pers.: Fr.) P. Karst. and *Colpoma quercinum* (Pers.) Wallr. are clearly diverging. *N. cupularis* was recorded solely in heights greater than 20 m (mean 26.3, median 25.5) (mean substrate diameter 2.5 cm). The gregarious growing perithecia were found mostly in small interstices of bark. *C. quercinum* on the other hand, was found only below 22 m in height (mean 15.7, median 13). The species settled only on thin twigs. (mean diameter 0.9 cm).

Twenty-four fungal species could be identified on decayed branches from the upper canopy. The middle layer exhibited by far the largest diversity with 58 species, 31 were found in the lower canopy. The four most abundant genera in the upper canopy were *Cryptosphaeria* (15.2% of all records), *Diatrypella* (7.6%), *Nitschkia* (17.7%), and *Peniophora* (17.7%). Findings of these taxa accounted for nearly 60% of all records in this stratum. Their abundance was considerably lower in the middle canopy with ca. 30%. The strong decline was mainly due to the lower abundance of Pyrenomycetes (*Cryptosphaeria* 6.3%, *Diatrypella* 4.2%, *Nitschkia* 3%). *Nitschkia* disappeared completely in the lower canopy, the frequency of *Cryptosphaeria* and *Diatrypella* declined to ca. 1% and 4.9% respectively (abundance of the four genera only 23.6%). As the occurrence of Pyrenomycetes decreased drastically with decreasing height, the relative abundance of *Peniophora* remained almost constant. (upper canopy 17.7%, middle canopy 17.4%, lower canopy 18.4%).

Regarding the changes in species composition, one example will be given at least. The species composition of the genus *Peniophora* varied greatly within the canopy strata. Only two and three species could be recorded in the lower and upper canopy respectively (*P. cinerea* [Pers.: Fr.] Cooke, *P. rufomarginata* [Pers.] Litsch., upper canopy additionally with *P. quercina* [Pers.: Fr.] Cooke). In the middle layer five species were found (additionally *P. laeta* [Fr.] Donk and *P. lycii* [Pers.] Höhn. & Litsch.).

The fungal colonisation of dead wood from the main tree species *Fraxinus excelsior*, *Quercus robur*, and *Tilia cordata* differed strongly. With comparable amounts of substrate from each tree species, *F. excelsior* showed the lowest diversity with 13 fungal species, followed by *Q. robur* (21) and *T. cordata* (37) (teleomorphs only).

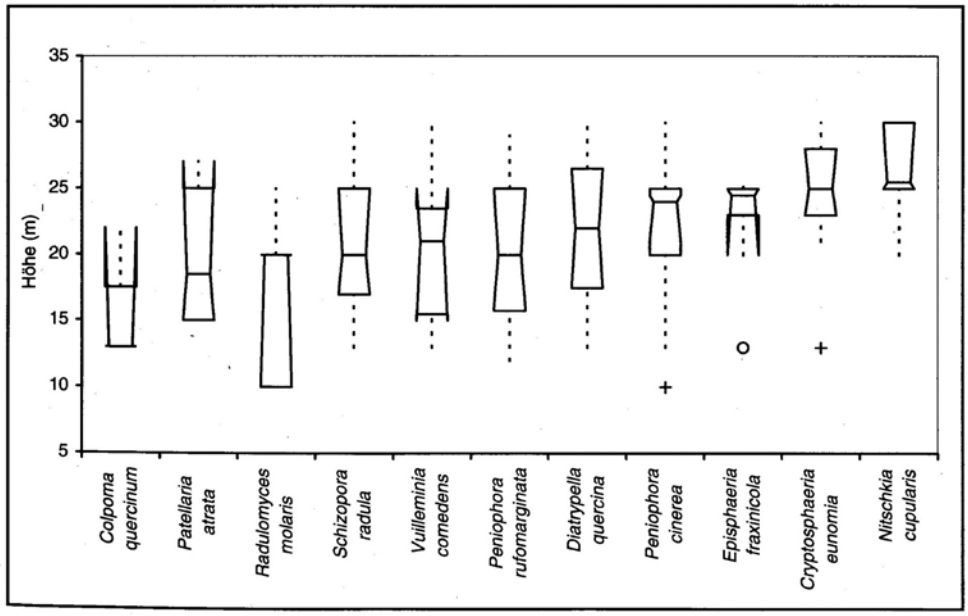

Fig. 3: The range of sampling heights of abundant species from the investigation site as Box-Whisker plots.

Discussion

The number of 85 lignicolous fungi and 15 slime molds has to be considered as preliminary. This is due to the consequent circumstances: (1) As the identification of the fungi was done only morphologically, many samples could not be determined at all because of too poorly developed fruit bodies. (2) More trees will be included into the study. (3) Many species of Pyrenomycetes and of Leotiales possess tiny and short-living fruit bodies that are easily overlooked (especially in desiccated conditions). (4) The fructifications of numerous fungi occur only sporadically, which requires longer investiation periods.

The canopy of the Leipzig crane site seems to be a suitable habitat for slime molds, as a change between arid and humid weather conditions are involved in the sporulation processes. These organisms are able to endure long periods of drought and frost through the development of lasting stages (spores, microcysts). Plasmodia were visible on nearly every single branch hence making the investigation of slime molds certainly promising.

To completing their life cycles from spore germination to the development of fruit bodies and new spores, fungi living in the tree tops have to be adapted to the partly very adverse climatic conditions (e.g. strong solar irradiance, high temperatures on the branches' surface, long periods of aridity). Structural-morphological and physiological accomodations of the fungi will be pointed out briefly.

Every fungal species with a comparably slow development of fruit bodies over weeks to months must possess the ability to stand desiccation without damage. This counts mostly for fungi that established in the canopy successfully. After rewetting, growth or spore dispersal can continue (xerotolerant or xeroresistant species in the sense of Bewley 1979). Pyrenomycetes are characteristic representatives of this type. Cyphelloid fungi on the other hand take an exceptional position. The rapidly developing, cup-shaped fruit bodies of *Episphaeria*- or *Lachnella*-species for instance are capable to overcome aridity by closing the 'cups' to tiny globes. In such fragile desiccated conditions, the hymenium is protected by the hairy subiculum against mechanical forces. Moistened with water, the fruit bodies spread again quickly and often continue spore dispersal.

Species with effuse-growing fruit bodies such as the cortidioid fungi *Peniophora*, *Hyphoderma*, *Hyphodontia*, or *Vuilleminia* grow positively geotropic, which means that they fructificate on the

underside of horizontally hanging branches. This seems to be an advantage in sunny and dry habitats against fungi growing away from the substrate (negatively geotropic) like many Agaricales. Growing on the underside means to escape harmful ultra-violet radiation and extra-high temperatures. Furthermore the availability of water is notably greater there, e.g. by downflowing rainwater.

The decrease of species richness in the top canopy can be explained by the deterioration of hygric and thermic conditions which become more extreme and uniform. Additional arguments for the decrease of diversity are the reduction of substrate and therewith the restriction of ecological niches. The highest range of different substrates and habitats can be found in middle canopy layers, which also exhibit the most diverse mycota. Here, exposed and shaded areas occur close to eachother; thin, recently decayed twigs co-exist with thick branches in later stages of decay. Many lignicolous fungi seem to respond to the diameter of the substrate as it was mentioned earlier by Helfer & Schmid (1999). Our preliminary results additionally correlate with faunistical reports which also display the central canopy as the most diverse habitat concerning species richness and substrate type.

This study of diversity and substrate specificity of wood decay fungi revealed strong differences between tree species. Species-specific structures of tree crowns as well as morphological and biochemical properties of the wood (incl. phloem fibres and bark) surely account for the differing numbers of fungal species. Wood of *T. cordata* was colonised by the largest number of fungal species. This seems plausible as it is poor in growth-restricting metabolites. Because of its low density, it possesses a good hygroscopicity which most probably facilitates fungal establishment. Insects, which play an important role in the dispersal and establishent of xylotrophic fungal species (Dix & Webster 1995) easily penetrates the soft wood of linden trees.

Quercus robur and *Fraxinus excelsior* possess very hard wood that is rich in tanning agents, which could be restrictive to the colonisation of fungi. The large species richness on *Q. robur* can be explained by a high structural complexity of its tree crowns. Measurements of light intensity (PAR) demonstrated more heterogenous light patterns than in *F. excelsior* crowns (Horchler, pers. comm.). The variability of small-scale habitats therefore increases resulting in more possibilites for niche partitioning among the fungal organisms.

PATELLARIA ATRATA (HEDW.) FR. - A CHARACTERISTIC CUP-FUNGI ON WOOD OF STANDING TREES

The first description of this species was made by J. Hedwig (1787-89), E. M. Fries (1822) placed it in the genus *Patellaria* (lat. *patella*: cup, bowl; *atra*: black). From today's systematical point of view, the genus is eponymous for family and order (Patellariaceae, Patellariales) and belongs to the bitunicate discomycetes. Confusions during identification are mostly due to species of the genus *Patellariopsis* and with lichens of the Lecanoraceae, who produce black-bordered apothecia. A unique morphological-chemical feature of *Patellaria atrata* are the bitunicate asci with an apical apparatus showing no amyloid reaction (*Patellariopsis* with unitunicate asci and an amyloid apex).

Fig. 4: Apothecia of *P. atrata* between phloem fibres of *T. cordata*. scale bar (left hand side): 1mm.

Locality and sampling description

Saxony, MTB 4639/24, Leipzig, north-western floodplain forest, eastern border of nature reserve "Burgaue", LAK-plot, 102 m above sea level, X. 2002 - IV. 2003, leg. M. Unterseher, det. P. Otto & M. Unterseher (voucher specimen in the herbarium of the University of Leipzig [LZ]).

P. atrata was found eight times at four different trees of *Tilia cordata*. Prefered substrate were free phloem fibres, in three cases the apothecia emerged on the naked wood, too. The decayed twigs, between 1 und 2,5 cm in diameter, without visible coverage of cryptogamic epiphytes were classified as strongly decayed (white rot, ca. 1/2 of the diameter clearly decayed). The sampling height was between 11 and 28 m, six sample points were shaded, two were located in the upper, strongly exposed canopy. Several times, the species was found in close association to *Rabenhorstia* cf. *tiliae* (Fungi imperfecti), which is the anamorph of *Hercospora*. *Patellaria* and *Rabenhorstia* apparently have similar ecological requirements and probably compete against each other.

The crane site is characterised as a former oak and elm rich floodplain forest (*Querco-Ulmetum minoris* Issler 1924, = *Fraxino-Ulmetum* [R.Tx.1952] Oberd. 1953). Due to the lack of regular innundations for the last ca. 70 years, succession has tended towards a forest rich in *Acer pseudoplatanus* L. and *Fraxinus excelsior* L. The species *A. pseudoplatanus* and *A. platanoides* L. already are the most dominant tree species in the understorey and sub canopy, indicating the atypical hydrological conditions of this lowland forest.

Description of fruitbodies

Dry apothecia 0.3 to 1.3 mm in diam., fragile, fresh up to ca. 1.6 mm and relatively soft, young apothecia with well developed rim, even to slightly convex, underneath bald and weakly shining, developing sessile on or between phloem fibres, mostly gregarious, up to 20 fruit bodies per cm^2 (compare Fig. 4). Asci with eight spores, bitunicate, slightly clavate, ca. 115-125-(130) x 14-16-(20) μm, apically with distinct wall, porus not clearly visible, apex inamyloid; spores oblique biseriate, *Pars sporifera* 3/4 to almost the entire length of ascus (Fig. 5). Ascospores distinct clavate, slightly to distinctly flexuose, ripe with eight to eleven cross-septae, colourless, without granular content, (29)-34-40-(45) x (5,5)-7,1-8,0-(9,5) μm (Fig. 6, middle); unripe spores with granulae and guttulae, septae emerging simultaneously (Fig. 6 left); aberrant and malformed spores partly occurring, here dispersal of plasm and development of septae and walls very irregular (Fig. 6 right). Paraphyses numerous, slender from the middle on mostly multiple branched, up to 2 μm in diam., apically club-shaped, up to 4 μm wide and through extra cellular, ± crystalline exudate olive-green to olive-brown, in Melzer's reagent partial, reddish discolouration of cell content. The mentioned features mostly agree with comments in literature (e.g. Dennis 1978, p. 479f., Ellis & Ellis 1985, p. 12).

Fig. 5: Ascus of *P. atrata* in 5% KOH. scale bar 15μm.

Annotations to distribution and abundance

Patellaria atrata is not mentioned often in literature. Dennis (1978) for instance described the species as rare for Great Britain. In the 'atlas of distribution' from Krieglsteiner (1993), *P. atrata* (as *Lecanidion atratum*) is displayed with findings in 13 MTB (occurrences in Schleswig-Holstein,

Lower Saxony, Rhineland-Palatinate, Bavaria und Baden-Württemberg).

Fig. 6: Spores of *P. atrata*. Unripe spores in 5% KOH, ripe spores in H_2O + Melzer, malformed spores in H_2O + Melzer (from left to right, scale bar left 8 μm, middle and right 10 μm).

On the evidence of H.O. Baral the species is frequent on dead standing wood. From recent times the following findings are known (vouchers in LZ): (1) Saxony, MTB 4639/2, City of Schkeuditz, ca. 300 m NO Domholzschänke, on clearly decayed wood of a bench, 29. IX. und 02. X. 2003, leg. J. Wesenberg, det. P. Otto. (2) Thuringia, MTB 4932, City of Erfurt, Vieselbach, Hasenberg, ca. 1.5 m in height, inside a hollow branch of *Malus domestica*, leg. et det. P. Otto (on the evidence of Dr. G. Hirsch [Jena] it is about the first finding of *P. atrata* in Thuringia).

ACKNOWLEDGEMENTS

We cordially thank Mr. H.O. Baral (Tübingen) for the identification of inoperculate cup-fungi and Mr. F. Dämmrich (Limbach-Oberfrohna) for the help with corticioid fungi. Thanks also go to Mr. Baral, Dr. G. Hirsch (Jena) and P. Horchler (Leipzig) as they kindly provided informations on ecological-chorological data and on canopy research.

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Species richness and substrate specificity of lignicolous fungi in the canopy of a temperate, mixed deciduous forest

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Mycological Progress **4**, 117–132, (2005).

Species richness and substrate specificity of lignicolous fungi in the canopy of a temperate, mixed deciduous forest

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In the more than twenty years in which long-term canopy research has been conducted, mycology has been largely disregarded. Our studies using a construction crane to gain access to the canopy of a forest in Leipzig, Germany, are the first long term investigations assessing the diversity and ecology of wood decaying fungi in a canopy. Thirty-seven individuals of nine different tree species with a large amount of dead wood were selected. Sampling focussed on the four most prominent tree species *Acer pseudoplatanus*, *Fraxinus excelsior*, *Quercus robur* and *Tilia cordata*. In the years 2002 and 2003 dead wood was collected in different canopy strata. Dead branches were removed and stored for two weeks in open boxes with high humidity to allow growth of fructifications in the laboratory. One hundred eighteen different taxa were identified (one hundred eight species, seventy-seven genera). Corticioid fungi (e.g., Corticiaceae, Stereaceae, Hymenochaetaceae) dominated the fungal composition with thirty-seven species, pyrenomycetes were present with eighteen species. Agaric fungi (Agaricales and Cortinariales) were scarce. Species with minute basidiomes dominated the fungal composition of this systematic group. Agarics with larger sporomes were found only once and were restricted to strongly decayed branches in shaded canopy areas. Concerning species richness and fungal composition the four tree species mentioned above differed remarkably. As expected, many fungi that grew on bark or slightly decayed wood showed a distinct host and substratum specificity. It is noteworthy that fungi which are purportedly to be non-specific were found on single tree species only.

INTRODUCTION

More than twenty years ago, studies on the diversity of forest canopies revealed a large quantity of organisms dwelling in the tree tops (Sutton *et al.* 1983, Erwin 1982, Erwin & Scott 1980). Many of these organisms are predicted to be canopy specialists (Ozanne *et al.* 2003). This implies that forest canopies house a large portion of worldwide species diversity (Ozanne *et al.* 2003, Hawksworth *et al.* 1995, Lowman & Moffett 1993, Erwin 1988, 1982). Since the first approaches to study life in tree crowns by rope techniques (Perry 1978) or fogging (Erwin 1982, Erwin & Scott 1980), the scientific community has seen a rapid development of different canopy research fields (Mitchell, Secoy & Jackson 2002, Nadkarni 2002, Morawetz 1998, Lowman & Moffet 1993).

A new era of canopy research was launched in 1990 when the Smithsonian Institute established a construction crane for observation purposes in a panama forest (Wright 2002). For the first time it was possible to easily gain access to the upper forest regions and to study the canopy of a particular site over many years. In consequence, 10 further canopy crane projects have been launched in the last decade. One of them is the Leipzig Canopy Crane Project (LAK) (Morawetz & Horchler 2004) of which this mycological study is part.

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The importance of fungi on forest soils as saprobionts of leaf litter and woody debris and as partners of mycorrhizae is well-known and still a matter of intense research. Studies about diversity and ecological impacts of fungi in forest canopies however are very rare even though intense canopy research has been conducted for more than two decades. Two years ago, mycological research played no significant role in the canopy projects worldwide (Mitchell, Secoy & Jackson 2002).

Differences in biotic and abiotic factors like solar radiation (eg. photosynthetic active radiation [PAR]) (Horchler 2004, Anhuf & Rollenbeck 2001), the quantity of available water (Bellot, Avila & Rodrigo 1999), diurnal and annual gradients in temperature, and the quality and amount of different substrates over time and space, result in distinct mesoclimatic conditions from the forest floor to the canopy. This most probably affects the richness and species composition of lignicolous fungi in the two habitats (e.g. Hallenberg & Parmasto 1998, Lodge & Cantrell 1995).

Dead, hanging branches are naturally occuring, essential parts of nearly every tree crown (e.g. Boddy & Rayner 1983, Butin & Kowalski 1983). In the canopy decayed wood dessicates faster than at ground level and may provide niches for xerotolerant and xeroresistant fungi (for definition of xerotolerance and xeroresistance, see Bewley 1979). The few studies concerning fungi on dry, weathered wood have concentrated mostly on tropical forests, on the understorey or over short periods of time. (e.g. Otto & Glowka 1998, Lodge & Cantrell 1995, Hedger, Lewis & Gitay 1993, Nuñez & Ryvarden 1993, Boddy 1992). Apart from corticioid species of Polyporales, Hymenochaetales and Russulales, pyrenomycete fungi are frequent inhabitants of decayed wood in arid habitats. They are able to continue growth under arid conditions or to survive long periods of drought. (e.g. Nuñez 1996, Munk 1957, Ingold 1954). Different groups of the Helotiales also tolerate such conditions (Baral, Baral & Marson 2003, Sherwood 1981). Tejera & Rodrguez-Armas (1999) studied the diversity of Aphyllophorales in desert-arid-semiarid areas of the Canary Islands. Their preliminary results showed a comprehensive species richness with 18 new species to the particular islands and four new to the 'canarian fungal checklist'. In the 1980s a series of studies was published by Boddy and 'coworkers', focussing on the development and ecology of fungal communities on dead attached branches in the understorey. However, many studies were limited to single branches or to early stages of fungal succession (Boddy & Rayner 1984, 1983, 1982, Chapela & Boddy 1988a, b, c, Griffith & Boddy 1991, 1989, 1988).

To reduce the gap of scientific knowledge concerning fungi in tree crowns, our investigations, started in may 2002, have been designed as the first long term investigations to assess the diversity and ecology of wood-decaying fungi in the canopy. The aims of the present study are (i) to create a species list of lignicolous fungi occuring in the canopy, (ii) to analyse beta diversity and (iii) to comment on the influence of ecological factors on species composition in tree crowns.

Fig. 1: The construction tower crane of the Leipzig Canopy Project (LAK). The small gondola permits easy access to different levels of the canopy.

MATERIAL AND METHODS

Canopy access

The interdisciplinary long-term project LAK started in 2001 and is conducted by the University of Leipzig, financed by the UFZ Centre for Environmental Research Leipzig-Halle and supported by the City of Leipzig. With a construction tower crane (Liebherr 71 EC, height of tower 40 m, jib length 45 m, max. sampling height ca. 33 m), mobile on a 120 metre-long railway track, 1.6 ha of forest can be explored (Fig. 1). Scientists using a remote control to move the crane and standing in a gondola, can raise themselves above the forest then lower the gondola precisely to a location of interest in the canopy. The tips of small distal branches, which were previously inaccessible, are easily reachable (Fig. 2).

Fig. 2: Definition of an appropriate sample size. A scientist collecting twigs inside an imaginary cube with a side length of about 3 metres.

Investigation plot

The investigation plot is situated at the margin of a former oak and elm rich floodplain forest (*Querco-Ulmetum minoris* Issler 1924, = *Fraxino-Ulmetum* [R.Tx.1952] Oberd. 1953). Due to the lack of regular innundations for the last ca. seventy years, succession has tended toward a forest rich in *Acer pseudoplatanus* L. and *Fraxinus excelsior* L. The species *A. pseudoplatanus* and *A. platanoides* L. already are the most dominant tree species in the understorey and sub canopy, indicating the atypical hydrological conditions of this lowland forest. The investigation plot comprises seventeen tree species.

Sampling design

The new challenge to operate in a three-dimensional space forced us to apply new methods of collecting fungi. Methods described in previous studies concerning the diversity of lignicolous fungi (e.g. Hong, Klinka & Song 1999, Lindblad 1997, Chapela & Boddy 1988a, Boddy & Rayner 1984) could not be used, because sampling was restricted to fallen logs or hanging twigs in the understorey.

Especially because of the limited opportunity to use the crane for mycological studies it was not possible to investigate all tree individuals occuring in the crane site. The following tree species were selected: *Fraxinus excelsior*, *Quercus robur* L., *Tilia cordata* Mill., *Acer pseudoplatanus*, *Carpinus betulus* L., and *Cerasus avium* (L.) Moench as typical and rather abundant species for floodplain or mixed deciduous forests, additionally *Populus* x *canadensis* Moench, *Quercus rubra* L., and *Robinia pseudacacia* L. as often cultivated species. For selecting individuals of these species the following two criteria were used: (i) tree height at least 25 m and (ii) comparatively large amount of dead wood in different canopy strata. Due to the fact that only few trees of the crane site fulfilled these criteria and further locations in the plot were occupied by other scientists a stochastical choice of individuals was not possible and seemed not to be useful. Either all or many relevant trees of the above mentioned species were sampled to obtain comprehensive data on fungal diversity in the canopy (Fig. 3). Table 1 gives an overview of sampling design.

Sampling took place in the years 2002 and 2003 and was limited mostly to spring (march, april, may) and fall (september, october, november) but also occured during summer and winter.

Table 1: Overview of sampling design and amount of sampled wood.

Tree species	No. of sampled trees	No. of total samples			Total length of sampled twigs [m]
		subcanopy	middle canopy	top canopy	
Acer pseudoplatanus	7	6	6	8	45
Carpinus betulus	2	3	4	4	20
Cerasus avium	2	2	1	1	ND
Fraxinus excelsior	8	4	9	12	28
Populus x *canadensis*	1	1	2	1	ND
Quercus robur	5	6	6	9	23
Quercus rubra	1	2	1	1	ND
Robinia pseudacacia	2	2	2	3	ND
Tilia cordata	9	11	10	7	26
total	37	37	41	39	more than 150

Dead twigs were collected at nine or more different locations in each tree crown resulting in a total number of 703 collections. It was intended that the same amount of wood in three different vertical zones (sub canopy [10-17 m], middle canopy [17-24 m], top canopy [24-31 m]) be collected. Often, however, this was not possible because of a generally bad accessibility of the sub canopy (branches blocking the access from above).

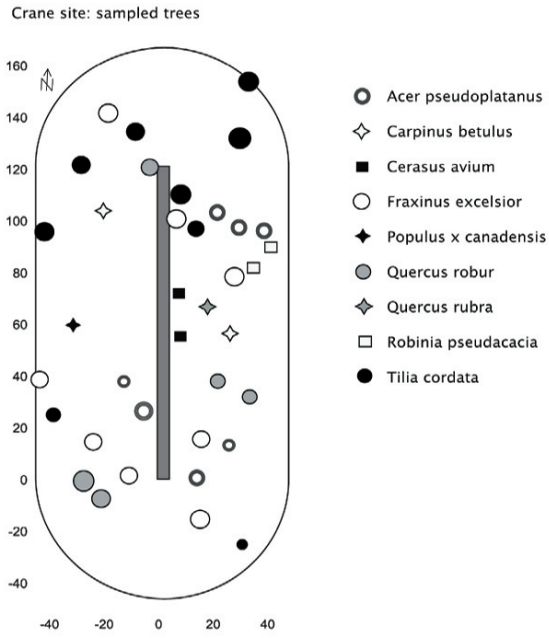

Fig. 3: Distribution of sampled trees at the canopy crane site. The long grey bar marks the 120 metres long railway track on which the tower crane can be moved. The black line encircles the area reachable by crane.

Removed twigs, including short bifurcations, were treated only as partial samples because it turned out that this amount of substratum was unsuitable for analyses due to a large amount of variance in twig length. This resulted in selective very low fungal species numbers and therefore unbalanced datasets. Therefore sample size was defined as the amount of twigs collected in an imaginary cube around the gondola with a side length of 3 m (Fig. 2). This resulted in a better comparability of total samples. to analyse substrate specificity, a further aggregation of total samples to sample groups was carried out for characterising upper and lower canopy or tree species.

Additional field data included information on stratum (sub, middle, top canopy), height above ground level, tree species and individual number, substratum characters (kind and stage of decay), diameter of branches, coverage with epiphytic algae, lichens and occurrence of old ascomes, basidiomes or sporomes, location of fructifications on the branch (upper side, lower side) and exposure to sun (estimated as exposed [more than 50% direct sunlight], semi exposed [10 to 50%] and shaded [less than 10% direct sunlight]). Studies on the succession and ecology of 'canopy fungi' based on these data will be treated in a separate publication.

Several methods for cultivating fungi on natural woody substrates in the laboratory were tested. The following seemed to be suitable to initiate or promote fruitbody development and to simulate conditions in tree crowns during humid weather periods. Samples were put separately in tap water for one day to allow soaking of the wooden tis-

sues. Afterwards they were washed under flowing water, to reduce superficially adhering diaspores. The samples were stored under high humidity in open plastic boxes for two weeks to allow development of sporomes, basidiomes and ascomes from mycelia previously established in the wood and further growth of fruiting initials. Once a day the samples were sprayed intensively with water to maintain rather high water content of the wood and high air humidity. Using this method the wooden surface could also dry up. The samples were inspected every three to four days for the occurrence of fructifications. All teleomorphic species were recorded, anamorphs were only considered if they grew in deeper layers of bark or wood (fungi imperfecti with pycnidia ['Sphaeropsidales'], acervuli ['Melanconiales'] or immersed sporodochia [Moniliales pp.]). Imperfect fungi with rapidly developing, mostly superficial mycelia were deliberately excluded because they could have occurred as secondary colonisers and probably do not belong to typical wood inhabiting species of the canopy. The collected fungi are stored in the Herbarium LZ, University of Leipzig.

Stages of wood decay

Previous studies were used as a guideline to define states of wood-decay (Lumley, Gignac & Currah 2001, Winterhoff 2001, Lindblad 1997): State 0: living but obviously weak, bark intact without fissures, wood unchanged. State 1: dead, bark cracked, slightly decayed, wood mostly unchanged. State 2: bark clearly to heavily decayed, often covered with algae, often present as small patches, wood superficially decayed, heartwood mostly unchanged. State 3: decay of sapwood advanced to about half of the branch's diameter, wooden structure mostly destroyed, easily removable with a knife. State 4: branches mostly decorticated, wooden tissue spongy, heartwood often clearly decayed, resulting in conspicious reduction of weight. following this classification, the state of decay directly near the sporomes was noted as proposed by Høiland & Bendiksen (1996).

Statistical analysis

To analyse species diversity and tree specifity, presence-absence data were used. Analysis of tree specificity was done using the four most abundant canopy tree species in the plot, *A. pseudoplatanus*, *F. excelsior*, *Q. robur* and *T. cordata* and the most abundant fungi with three or more counts per tree. The species composition was analysed by two common ordination methods, correspondence analysis (CA) (Gauch 1982), and nonmetrical multidimensional scaling (NMS) using a Sørensen similarity matrix (McCune & Grace 2002). the CA was performed using the software 'Canoco 4.5 for Windows' (Ter Braak & Šmilauer 1998), the NMS using 'PC-Ord' (McCune & Mefford 1999). Substrate specificity could be assessed by the results of the CA. Additionally we analysed specificity by calculating indicator values using the free software 'Indval 2.0' (Dufrêne & Legendre 1997). Significance levels of the indicator values were calculated applying a Monte-Carlo permutation procedure. Estimations of species richness were performed using the free software 'EstimateS 6 beta' (Colwell 2000). Selected software options of all methods are given in the captions of figures and tables.

Nomenclature and systematical arrangement

The 'Dictionary of the Fungi', 9th edition (Kirk, Cannon, David & Stalpers 2001) was used as a guideline to species and authorities names.

RESULTS

Species richness

One hundred eighteen different taxa were determined at species or generic level (Tab. 2). With a total sample number of 128 imaginary cubes (see Fig. 2), 50 species were singletons, another 22 were doubletons. Approximately 10% of all samples could not be identified or were placed in larger groups or orders. They are not included in the species list. Members of the corticioid Russulales were present with 37 species (29.7% of the total observed species richness), 18 pyrenomycete species were recorded. They belong to the orders Diaporthales, Xylariales, Dothideales, Pyrenulales and Sordariales. Sixteen mitosporic species (incl. Coelomycetes) were identified. Agaric fungi were scarce. Except *Gymnopilus hybridus* (Bull.) Maire, *Pluteus cervinus* P. Kumm and *Mycena galericulata* (Scop.) Schaeff., which were found once,

only species with minute basidiomes were present: *Pleurotellus chioneus* (Pers.) Kühner, *Resupinatus applicatus* (Batsch) Gray, *R. trichotis* (Pers.) Singer, *Episphaeria fraxinicola* (Berk. & Broome) Donk, *Cyphellopsis anomala* (Pers.) Donk, *Crepidotus subtilis* P.D. Orton and *Lachnella* spp.

Table 2: All fungi identified to species or generic level are listed in alphabetical order. Abbreviation of species (***) that are presented in the CA-diagrams (Figs. 5, 6), their host trees (*) and the number of counts (**) are also shown. *: Ap=*Acer pseudoplatanus*, Cb=*Carpinus betulus*, Ca=*Cerasus avium*, Fe=*Fraxinus excelsior*, Pc=*Populus* x *canadensis*, Qr=*Quercus robur*, Qru=*Quercus rubra*, Rp=*Robinia pseudacacia*, Tc=*Tilia cordata*. **: Number of counts based on 128 samples (sample size was imaginary cube).

Fungal Species	Tree Species *	Counts **	Abbr***
Ascomycetes			
Diaporthales			
Diaporthe oncostoma (Duby) Fuckel	Rp	3	ND
Melanconium atrum Link	Cb	2	ND
Valsa ambiens (Pers.) Fr.	Pc	2	ND
Dothideales			
Karschia lignyota (Fr.) Sacc.	Qr	1	ND
Teichospora obducens (Schumach.) Fuckel	Fe	1	ND
Helotiales			
Ascocoryne cylichnium (Tul.) Korf	Tc	2	ND
Hyalinia rosella (Quél.) Boud.	Qr	1	ND
Hyalorbilia inflatula (P. Karst.) Baral & G. Marson	Qr	1	ND
Mollisia cinerea (Batsch) P. Karst.	Ca	2	ND
Mollisia melaleuca (Fr.) Sacc	Cb	1	ND
Mollisia sp.	Ca	1	ND
Orbilia cf. *coccinella* (Sommerf.) P. Karst.	Cb, Qr, Tc	7	orbicocc
Orbilia crystallina (Quél.) Baral	Tc	1	ND
Orbilia euonymi Velen.	Qr	1	ND
Orbilia sarraziniana Boud.	Cb	1	ND
Hypocreales			
Hypocrea rufa (Pers.) Fr.	Ap, Fe, Qr, Tc	9	hyporufa
Hypocrea sp.	Tc	1	ND
Nectria cinnabarina (Tode) Fr.	Qr	1	ND
Patellariales			
Patellaria atrata Cooke	Tc	5	pateatra
Pleosporales			
Fenestella vestita (Fr.) Sacc.	Ap	1	ND
Melanomma pulvis-pyrius (Pers.) Fuckel	Pc	1	ND
Pleomassaria carpini (Fuckel) Sacc.	Cb	2	ND
Pyrenulales			
Massaria anomia (Schwein.) Petr.	Rp	4	ND
Massaria pupula (Fr.) Tul. & C. Tul.	Ap	4	ND
Rhytismatales			
Colpoma quercinum (Pers.) Wallr.	Qr	3	ND
Sordariales			
Coniochaeta pulveracea (Ehrh.) Munk	Tc	3	ND
Coniochaeta sp.	Tc	1	ND

Table 2: continued

Fungal Species	Tree Species *	Counts **	Abbr***
Coronophora gregaria (Lib.) Fuckel	Ca	1	ND
Lasiosphaeria ovina (Pers.) Pat.	Tc	2	ND
Lasiosphaeria sp.	Cb, Qr	1	ND
Nitschkia cupularis (Pers.) P. Karst.	Fe	17	nitscupu
Nitschkia sp.	Ap	1	ND
Xylariales			
Cryptosphaeria eunomia (Fr.) Fuckel	Fe	22	crypeuno
Diatrypella quercina (Pers.) Cooke	Qr, Qru	13	diatquer
Eutypa maura (Fr.) Sacc.	Ap	16	eutymaur
Eutypa sp.	Rp	1	ND
Basidiomycetes			
Agaricales			
Crepidotus sp.	Fe	1	ND
Crepidotus subtilis P.D. Orton	Fe	1	ND
Cyphellopsis anomala (Pers.) Donk	Ap, Pc, Tc	4	cyphanom
Episphaeria fraxinicola (Berk. & Broome) Donk	Fe	12	episfrax
Gymnopilus penetrans (Fr.) Murrill	Tc	2	ND
Lachnella filicina (P. Karst.) W.B. Cooke	Ap, Pc, Tc	4	lachfili
Lachnella sp.	Ap, Fe, Tc	4	lach_sp
Lachnella villosa (Pers.) Gillet	Fe	2	ND
Mycena galericulata (Scop.) Gray	Qr	1	ND
Pleurotellus chioneus (Pers.) Kühner	Ca, Tc	4	ND
Pleurotus cornucopiae (Paulet) Rolland	Fe	1	ND
Pluteus cervinus P. Kumm.	Tc	1	ND
Resupinatus applicatus (Batsch) Gray	Cb, Tc	2	ND
Resupinatus trichotis (Pers.) Singer	Cb, Qr	2	ND
Unguicularia cf. *millepunctata* (Lib.) Dennis	Qr, Tc	4	ungumill
Auriculariales / Tremellales			
Auricularia auricula-judae (Fr.) J. Schröt.	Ap, Pc, Rp, Tc	5	auriauri
Basidiodendron eyrei (Wakef.) Luck-Allen	Tc	1	ND
Exidia cartilaginea S. Lundell & Neuhoff	Tc	3	ND
Exidia glandulosa (Bull.) Fr.	Ap, Qr, Qru, Tc	4	ND
Exidia thuretiana (Lév.) & Fr.	Tc	7	exithur
Exidia villosa Neuhoff	Tc	1	ND
Sebacina calcea (Pers.) Bres.	Qru	1	ND
Dacrymycetales			
Dacrymyces cf. *lacrymalis* (Pers.) Sommerf.	Fe	1	ND
Dacrymyces stillatus Nees	Ca, Fe, Qr, Rp, Tc	9	dacrstil
Hymenochaetales			
Hyphodontia microspora J. Erikss. & Hjortstam	Tc	2	ND
Hyphodontia nespori (Bres.) J. Erikss. & Hjortstam	Qr	2	ND
Hyphodontia sambuci (Pers.) J. Erikss.	Ap, Fe	3	ND
Phellinus contiguus (Pers.) Pat.	Qr	5	phelcont
Phellinus sp.	Ca, Qr, Rp, Tc	8	phell_sp
Schizopora radula (Pers.) Hallenb.	Cb, Qr, Qru, Tc	13	schiradu
Polyporales			
Brevicellicium sp.	Cb	1	ND
Byssomerulius corium (Pers.) Parmasto	Tc	2	ND
Cerrena unicolor (Bull.) Murrill	Ap	2	ND

Table 2: continued

Fungal Species	Tree Species *	Counts **	Abbr***
Lopharia spadicea (Pers.) Boidin	Tc	1	ND
Coriolopsis gallica (Fr.) Ryvarden	Ap	1	ND
Cylindrobasidium laeve (Pers.) Chamuris	Cb	1	ND
Daedaleopsis confragosa (Bolton) J. Schröt.	Ca	2	ND
Galzinia incrustans (Höhn. & Litsch.) Parmasto	Cb	1	ND
Hapalopilus rutilans (Pers.) P. Karst.	Qru, Tc	2	ND
Hyphoderma medioburiense (Burt) Donk	Tc	1	ND
Hyphoderma mutatum (Peck) Donk	Tc	1	ND
Hyphoderma praetermissum (P. Karst.) J. Erikss. & Å. Strid	Qr, Rp	2	ND
Hyphoderma radula (Fr.) Donk	Cb, Ca, Qru Tc	4	ND
Hyphoderma setigerum (Fr.) Donk	Ca, Tc	3	hyphseti
Hypochnicium eichleri (Bres.) J. Erikss. & Ryvarden	Qr	1	ND
Hypochnicium polonensis(Bres.) Å. Strid	Tc	1	ND
Hypochnicium vellereum (Ellis & Cragin) Parmasto	Cb	1	ND
Laetiporus sulphureus (Bull.) Murrill	Qr	1	ND
Merulius tremellosus Schrad.	Tc	1	ND
Oligoporus subcaesius (A. David) Ryvarden & Gilb.	Fe	2	ND
Phlebia cf. *centrifuga* P. Karst.	Tc	1	ND
Phlebia radiata Fr.	Qr	1	ND
Polyporus ciliatus (P. Karst.) Sacc.	Qr, Tc	2	ND
Radulomyces confluens (Fr.) M.P. Christ.	Cb, Fe, Pc, Rp, Tc	8	raduconf
Radulomyces cf. *hiemalis* (Laurila) Parmasto	Tc	1	ND
Radulomyces molaris (Chaillet) M.P. Christ.	Cb, Ca, Qr, Qru	9	ND
Trametes versicolor (L.) Lloyd	Qr	1	ND
Vuilleminia comedens (Nees) Maire	Qr	14	vuilcome
Russulales			
Peniophora cinerea (Pers.) Cooke	Ap, Ca, Fe, Qr, Qru, Tc	18	penicine
Peniophora incarnata (Pers.) P. Karst.	Cb	1	ND
Peniophora laeta (Fr.) Donk	Cb, Pc	7	ND
Peniophora lycii (Pers.) Höhn. & Litsch.	Ap, Fe	5	penilyci
Peniophora quercina (Fr.) Cooke	Qr	5	peniquer
Peniophora rufomarginata (Pers.) Bourdot & Galzin	Tc	19	penirufo
Peniophora violaceolivida (Sommerf.) Massee	Pc	2	ND
Stereum hirsutum (Willd.) Gray	Qr	2	ND
Stereum ochraceo-flavum (Schwein.) Fr.	Cb, Qr	2	ND
Stereum rameale (Schwein.) Burt	Cb, Qr	7	sterrame
Schizophyllales			
Schizophyllum commune Fr.	Ap, Qr, Tc	6	schicomm
Fungi imperfecti			
Camarosporium sp.	Rp	1	ND
Corniculariella spina (Berk. & Ravenel) DiCosmo	Fe	1	ND
Epicoccum nigrum Link	Ap	1	ND
Exosporium tiliae Link	Tc	5	exostili
cf. *Flagellospora curvula* Ingold	Qru	1	ND
Micropera sp.	Cb	1	ND
Phoma epicoccina Punith., M.C. Tulloch & C.M. Leach	Ap	1	ND
Phoma sp.	Ap	1	ND
Trichoderma sp.	Ap, Cb, Fe, Qr, Tc	5	ND
Tubercularia vulgaris Tode	Ap, Tc	6	tubevulg
Rabenhorstia tiliae (Fr.) Fr.	Tc	4	rabetili
Stegonsporium acerinum Corda	Ap	7	stegacer
Stegonsporium pyriforme (Hoffm.) Corda	Ap	8	stegpyri

The host trees are also listed in Tab. 2. The highest species richness was observed on lime trees (*T. cordata*) with 47 different species. Sycamore (*A. pseudoplatanus*) was colonised by 23 fungal species, ash (*F. excelsior*) by 19 and oak (*Q. robur*) by 34. Considering the different amounts of sampled wood, sycamore was least populated with a mean of about 0.5 species per metre or one species every 2.2 metres. The mean density of occurrence of teleomorphs on ash was one species every 1.4 metres or about 0.7 species per metre. The mean density on lime and oak trees was similar with about two species per metre. Fig. 4 shows original species accumulations (line with grey coloured circles) and species accumulations curves (line with black squares) for the four tree species (a-d) and for all existing data (e). After 100 samples each, the species number calculated by rarefaction was 23 on *A. pseudoplatanus*, 16 on *F. excelsior*, 25 on *Q. robur* and 40 on *T. cordata*.

Table 3: IndVal output showing substrate preferences. The values are the sums of occurrences of fungi per sample. Ranks and significance values are also displayed to allow definition of indicator species (written with bold). Program settings: 499 permutations, significance level: p=0.01, random number=5, no wheighting of species or samples. AcPs: *Acer pseudoplatanus*, CaBe: *Carpinus betulus*, FrEx: *Fraxinus excelsior*, QuRo: *Quercus robur*, TiCo: *Tilia cordata*, CeAv: *Cerasus avium*, PoCa: *Populus* x *canadensis*, QuRu: *Quercus rubra*, RoPs: *Robinia pseudacacia*. Sign.: **=significant as to define indicator species, NS=not significant, ??=undecided because of small number of samples.

Number of sampled trees	7	2	8	5	9	2	1	1	2		
Fungal Species	AcPs	CaBe	FrEx	QuRo	TiCo	CeAv	PoCa	QuRu	RoPs	Rank	Sign.
Eutypa maura	**16**	0	0	0	0	0	0	0	0	**1**	**
Stegonsporium pyriforme	**8**	0	0	0	0	0	0	0	0	**1**	**
Stegonsporium acerinum	7	0	0	0	0	0	0	0	0	6	??
Tubercularia vulgaris	5	0	0	0	1	0	0	0	0	17	NS
Massaria pupula	4	0	0	0	0	0	0	0	0	7	NS
Peniophora laeta	0	**6**	0	0	0	0	1	0	0	**4**	**
Schizopora radula	0	4	0	7	1	0	0	1	0	91	NS
Cryptosphaeria eunomia	0	0	**22**	0	0	0	0	0	0	**1**	**
Nitschkia cupularis	2	0	**15**	0	0	0	0	0	0	**1**	**
Episphaeria fraxinicola	0	0	**12**	0	0	0	0	0	0	**1**	**
Lachnella cf. *villosa*	0	0	3	0	0	0	0	0	0	147	NS
Lachnella sp.	1	0	2	0	1	0	0	0	0	415	NS
Vuilleminia comedens	0	0	0	**14**	0	0	0	0	0	**2**	**
Diatrypella quercina	0	0	0	11	0	0	0	2	0	11	??
Peniophora quercina	0	0	0	5	0	0	0	0	0	13	NS
Phellinus contiguus	0	0	0	5	0	0	0	0	0	12	NS
Stereum rameale	0	1	0	6	0	0	0	0	0	23	NS
Hypocrea rufa	1	0	1	6	1	0	0	0	0	55	NS
Colpoma quercinum	0	0	0	3	0	0	0	0	0	130	NS
Peniophora rufomarginata	0	0	0	0	**19**	0	0	0	0	**1**	**
Exosporium tiliae	0	0	0	0	5	0	0	0	0	23	NS
Patellaria atrata	0	0	0	0	5	0	0	0	0	23	NS
Exidia cartilaginea	0	0	0	0	4	0	0	0	0	157	NS
Rabenhorstia tilia	0	0	0	0	4	0	0	0	0	136	NS
Coniochaeta sp.	0	0	0	0	3	0	0	0	0	151	NS
Orbilia cf. *coccinella*	0	1	0	1	5	0	0	0	0	234	NS
Unguicullaria cf. *millepunctata*	0	0	0	1	3	0	0	0	0	241	NS
Schizophyllum commune	1	0	0	2	3	0	0	0	0	397	NS
Hyphoderma radula	0	1	0	0	0	2	0	1	0	7	??
Radulomyces molaris	0	2	0	4	0	2	0	1	0	33	NS
Hyphoderma setigerum	0	0	0	0	2	1	0	0	0	12	NS
Pleurotellus chioneus	0	0	0	0	3	1	0	0	0	14	NS
Peniophora lycii	1	0	2	0	0	1	1	0	0	224	NS
Phellinus sp.	0	0	0	5	1	1	0	0	1	208	NS
Merismodes anomalus	1	0	0	0	2	0	1	0	0	33	NS
Lachnella cf. *fillicana*	1	0	0	0	2	0	1	0	0	37	NS
Auricularia auricula-judae	1	0	0	0	2	0	1	0	1	151	NS
Peniophora cinerea	1	0	7	1	5	1	1	2	0	71	NS
Exidia glandulosa	1	0	0	1	4	0	0	1	0	63	NS
Dacrymyces stillatus	0	2	1	2	2	0	0	1	1	286	NS
Massaria anomia	0	0	0	0	0	0	0	0	**4**	**1**	**
Diaporthe oncostoma	0	0	0	0	0	0	0	0	**3**	**2**	**
Radulomyces confluens	0	2	1	0	1	0	1	0	3	41	NS

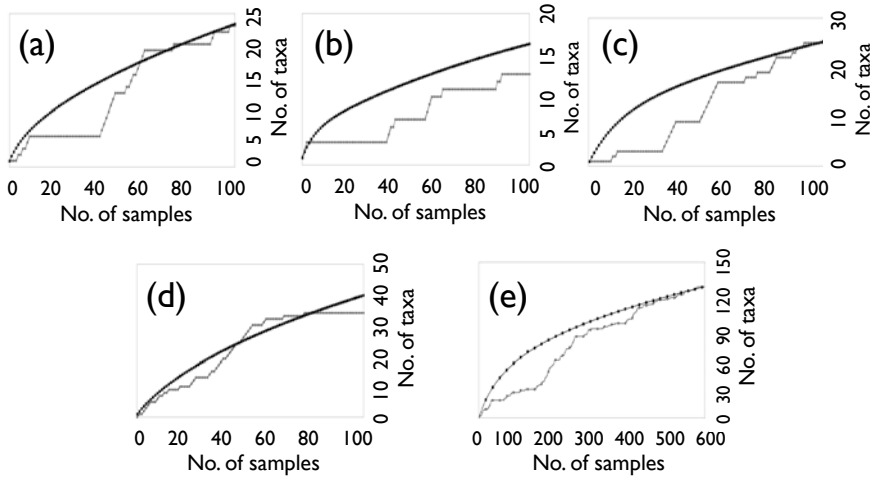

Fig. 4: Species-accumulation curves for *Acer pseudoplatanus* (a), *Fraxinus excelsior* (b), *Quercus robur* (c), *Tilia cordata* (d) and all existing data (e). Species richness of the four tree species is shown for the first 100 samples. The species-accumulation curves were calculated by a modified rarefaction analysis using the software 'EstimateS' and are shown in black lines with black squares. The non-modified, actually observed species richness is shown in grey circles.

Beta diversity

Regarding the fungal composition, the four tree species differ considerably (Figs. 5 and 6, Tab. 3). The ordination biplot diagrams (Figs. 5 and 6) display similarities and dissimilarities between fungi and tree species. The further two fungal species are apart, the less similar they are concerning their occurrence on different trees. The more distant two tree species are, the less similar they are concerning the composition of their mycota. Distinct groupings of samples and fungal species are apparent. In Fig. 5, axis 2 is plotted against axis 1. *Eutypa maura* (Fr.) Sacc., *Tubercularia vulgaris* Tode, *Stegonsporium acerinum* Corda and *Stegonsporium pyriforme* (Hoffm.) Corda are located clearly in the centroid of the examined individuals of sycamore (upper part of diagram). Individuals of oak group around *Peniophora quercina* (Pers.) Cooke, *Diatrypella quercina* (Pers.) Cooke, *Radulomyces molaris* (Chaillet) M. P. Christ, *Phellinus contiguus* (Pers.) Pat., *Stereum rameale* (Schwein.) Burt and *Vuilleminia comedens* (Nees) Maire respectively (lower left of diagram). In order to obtain a better resolution for fungal species clustering with *T. cordata*, axis 3 was plotted against axis 2 in Fig. 6.

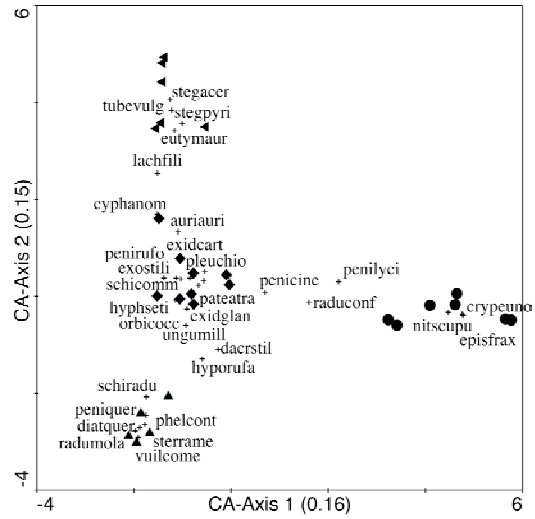

Fig. 5: Ordination biplot of a CA with axis 2 plotted against axis 1. Values in brackets are the percentage of total explained variation of species data (see Tab. 2) The data matrix contained presence-absence data of species with 3 or more counts per sample unit (tree individual). Only *Acer pseudoplatanus* (◀), *Fraxinus excelsior* (●), *Quercus robur* (▲) and *Tilia cordata* (◆) are considered.

In addition to the above mentioned groupings, it is apparent that *Patellaria atrata* Fr., *Exosporium tiliae* Link, *Exidia cartilaginea* S. Lundell & Neuhoff, *Peniophora rufomarginata* (Pers.) Bourdot & Galzin, *Pleurotellus chioneus* and *Hyphoderma setigerum* (Fr.) Donk also exhibit strong association to their hosts.

In contrast to this, other fungi lie between tree species like *Peniophora lycii* (Pers.) Höhn. & Litsch., *Peniophora cinerea* (Pers.) Cooke, *Lachnella filicina* (P. Karst.) W. B. Cooke, *Dacrymyces stillatus* Nees or *Radulomyces confluens* (Fr.) M. P. Christ. These fungi were found on different tree species and showed no substrate specificity. The arch effect, which occurrs often when using CA, was not obvious (for computation of CA by reciprocal averaging see Gauch [1982] or Ter Braak & Šmilauer [1998]). Analyses using NMS with 'PC-Ord' (McCune & Mefford 1999) resulted in similar diagrams (not shown). Additionally table 3 displays values and significances to define fungal species assemblages on each tree species. In consequence, indicator species can be named but is not done here.

Many fungal species were found fruiting on and in outer layers of the twig (bark, phloem fibres, sapwood) of one tree species exclusively. *Rabenhorstia tiliae* (Fr.) Fr., *Exosporium tiliae*, and *Peniophora rufomarginata* grew on *T. cordata*, *Cryptosphaeria eunomia* (Fr.) Fuckel, *Nitschkia cupularis* (Pers.) P. Karst. and *Episphaeria fraxinicola* on *F. excelsior*, *Diatrypella quercina*, *Peniophora quercina* and *Vuilleminia comedens* on *Q. robur*, *Peniophora laeta* (Fr.) Donk, *Pleomassaria carpini* (Fuckel) Sacc. on *C. betulus* and *Stegonsporium acerinum*, *S. pyriforme* and *Eutypa maura* occurred on twigs of *A. pseudoplatanus*.

DISCUSSION

Sampling and cultivation

As stated previously the number of examined individuals per tree species as well as amounts of sampled wood sometimes differed strongly. Nevertheless the gathered data on diversity and substratum preferences could be regarded as representative of the investigation plot and allowed for statistical analyses. Because of the multivariate nature of our data we decided to apply the multivariate statistics explained in the method section to extract main environmental gradients.

The storage of samples in open boxes and the temporary spraying with water prevented permanent moist conditions and minimized the occurrence of superficially fast growing imperfect fungi such as *Penicillium* Link, *Botrytis* P. Micheli ex Pers. or *Cladosporium* Link.

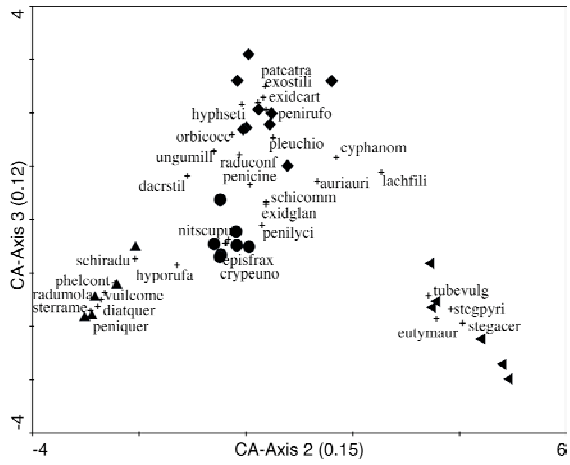

Fig. 6: Ordination biplot of a CA with axis 3 plotted against axis 2. Values in brackets are the percentage of total explained variation of species data (see Tab. 2) The data matrix contained presence-absence data of species with 3 or more counts per sample unit (tree individual). Only *Acer pseudoplatanus* (◀), *Fraxinus excelsior* (●), *Quercus robur* (▲) and *Tilia cordata* (◆) are considered. Program settings: CA, interspecies distance, Hill-scaling, no transformation, no weighting.

The only frequently found species of this group was *Trichoderma lignorum* (Tode) Harz. It appeared mostly on wood of *Q. robur* and grew on the surface of old basidiomes of *V. comedens* in more than 80% of cases. Few of these samples were stored for more than two weeks and occasionally the teleomorphic state *Hypocrea rufa* (Pers.) Fr. appeared between the *Trichoderma* mycelia. Our method of storing wood in high humidity after sampling seems appropriate to stimulate fructification especially if sampling occured during unfavourable conditions (drought, frost). Fruitbodies of *P. chioneus*, *R. applicatus*, *R. trichotis*, *E. fraxinicola*, *Orbilia* spp. and *Lachnella* spp. for instance often

were not present in the field but emerged within several days after keeping the samples in boxes at high humidity.

Many phaneroplasmodia and sporocarps of Myxomycetes emerged rapidly on the branches after a few days of storage in the laboratory. Together with the observation of many spororocarps in the field (eg. *Stemonitis* Gled., *Arcyria* Hill ex F.H. Wigg) this indicates that the canopy might be an ideal habitat for slime molds (Schnittler pers. comm. [a publication on this topic is in preparation]).

Species richness

Without doubt the detected richness of 118 fungal species is preliminary. One can clearly see that species-accumulation curves rise almost linearly and obviously more samples will have to be collected before species saturation can be approached and inferred (Fig. 4). About 10% of the collected material could not be identified at species or generic level because fructifications were in conditions lacking spores or other morphological features important for determination. With the identification of fungi restricted to morphological-chemical characters only data on the diversity of morphospecies were captured. We are aware of the fact that only the additional application of molecular methods allows us to define biological species and to estimate the effective species diversity of a study site (Hawksworth 2001, Küffer & Hallenberg 2000, Hallenberg & Larsson 1991, Hallenberg 1991). Isolating DNA samples from the species and analysing fungal DNA sequences was not possible within the framework of this research. To clarify the problem of defining biological species for wood inhabiting fungi a few examples are given for corticioid species found in the crane site. Following Nilsson *et al.* ([2003] for *Hyphoderma setigerum*), Hallenberg, Larsson & Larsson ([1994] for *Hyphoderma praetermissum* [P. Karst.] J. Erikss. & Å. Strid) and Chamuris (1991), Hallenberg & Larsson (1992) (both for *Peniophora cinerea*), many members of corticioid fungi form cryptic species or species complexes with populations being physiological and genetically different. Nilsson *et al.* hypothesise that due to high spore dispersal capacities of corticioid fungi, allopatric speciation probably played an important role in the diversification processes of this group. Chamuris supposed, that changes in host and substratum preferences may also be involved in the formation of European sibling species in the *P. cinerea* complex. Therefore, molecular analyses have to be done with the corticioid fungi we collected, to decide for instance if *P. cinerea* found on *F. excelsior* is a different biological species from that found on *T. cordata*. A similar taxonomical situation has to be assumed for other systematical groups that were typical for the investigated forest canopy such as pyrenomycete fungi. Aside from problems concerning the delimitation and recognition of fungal species there are additional difficulties in respect to their biology and ontogeny. Many fungi grow vegetatively most of the time and fructificate only sporadically or exist symptomless as endophytes in living or dead parts of a tree (Wilson 1995, 1993). Such fungi probably await death of the branch or suitable microclimatic conditions to expand into the wood (Boddy & Rayner 1983). The discovery of such species therefore may require several years of investigation and additional cultivation techniques. Many species of the pyrenomycetes, Coelomycetes or the Helotiales produce scattered, minute and short living fruitings. Especially cup fungi like *Orbilia* Fr. or *Mollisia* (Fr.) P. Karst., but also members of the Tremellales possess ascomes and basidiomes that are nearly invisible in dessicated conditions. Hence, such species are easily overlooked.

Fungal richness and composition on host trees

Our results show clearly that tree species differ with respect to their mycota. Lignicolous fungi that grow during initial stages of decay are often known to be highly specific to their hosts. This specificity is probably due to secondary compounds in bark and wood and to specific defense mechanisms that follow fungal infection (Pearce 1996). In our studies *T. cordata* possessed the richest mycota with 47 fungal species. This high diversity is probably due to the lack of phenolic compounds and the softness of the wood that facilitates the invasion of insects. Malloch & Blackwell (1992) speculated that insects most probably play an important role in the dispersal of fungal diaspores. Preliminary results of entomolo-

gical studies within the LAK project demonstrate a high diversity of insects on lime trees, especially xylotrophic beetles and mycetophagous flies (Schmidt, pers. comm.). This diversity seems to be positively correlated with the fungal richness and supports the idea that insects act as potent vectors of lignicolous fungi within the observed part of the forest.

Another probable reason for the high beta diversity and the differences in fungal richness on the tree species is the high structural complexity of the investigated part of the forest. PAR measurements in summer 2003 resulted in the division of canopy trees into three distinct vertical zones. Furthermore the conditions in ash crowns seemed to be more uniform than in oak crowns (Horchler 2004). The more heterogenous conditions with respect to solar radiation, and to a large extent, to temperature possibly result in the availability of more ecological niches in oak trees. Indeed, they are populated by a higher number of fungal species. Additionally, some of the oak trees accessible with the crane are more than 200 years old. They possess a large amount of dead branches as potential substrate for lignicolous fungi. Sycamore and ash are mostly younger than 100 years and enjoy sound health compared with oak and lime trees.

Canopy mycoflora

Species richness and composition in the canopy cannot be compared with that on the forest floor of the plot for the lack of comprehensive data (a comparative study is planned for the near future). However, there are some indications from the Leipzig crane site both from this study as well as from the literature that the fungal associations of the canopy strongly differ from those of the forest floor. Hallenberg & Parmasto (1998) mentioned that dead attached branches constitute a specific niche in nature for wood-inhabiting fungi. Such branches are often dry for long periods of time and fungal growth is limited to recurrent periods of humid weather. A characteristic flora of basidiomycetes of the orders Russulales, Polyporales and Hymenochaetales is found as primary occupiers in this habitat. This view is supported by our observation in which members of corticioid fungi (eg. Corticiaceae, Stereaceae, Hymenochaetaceae, Schizoporaceae) comprise about one third of the total species richness. Nuñez (1996) describes also several corticioid fungi growing frequently on dead hanging branches. Ingold (1954) mentioned pyrenomycete fungi as a group which is also able to outlast long periods of aridity. In our studies they were the second most abundant group in the canopy with 15% of total species richness. Baral, Baral & Marson (2003) and Sherwood (1981) mentioned that xerotolerant or xeroresistant taxa of the Helotiales are frequent. In some genera and families xerotolerant species even outnumber the intolerant (Baral, pers. comm.) These are important factors to explain the majority of ascomycetes in the species list (Table 2). The high number of heterobasidiomycetes can also be explained by the special climatic conditions that occur in the canopy. Draught can do no harm to species like *Exidia* spp. because the sporomes are able to desiccate in dry periods. This process is reversible, the fungi start growing again if conditions change to higher humidity.

Taking into account the origin of decay in living deciduous trees as proposed by Boddy & Rayner (1983) it becomes understandable why fungal communities on dead attached branches differ from that of dead wood lying on the forest floor. Chapela & Boddy (1988c) reported on the disappearence of early colonisers that emerged in branches still attached to the tree after falling to the ground. Boddy & Rayner (1984) stated that communities established on attached twigs can be regarded as the starting point for subsequent development on the woodland floor. In their review, Lodge & Cantrell (1995) cited the studies of Nuñez & Ryvarden (1992) and Ryvarden & Nuñez (1992), who investigated wood-decaying fungi from understory and canopy of a rain forest in Cameroon, Africa. They found that the extreme moisture and temperature regimes of the canopy are apparently more selective, resulting in a lower species richness and different species composition.

The almost complete lack of fungi with ephemeral fructifications in the canopy of our plot was apparent. Lodge & Cantrell (1995) think that fruiting of agaric fungi may be rare and confined to the wet season. In our study basidiomes of *P. cervinus*, *M. galericulata* and *G. hybridus* were found only once. They emerged exclusively in shaded areas after extensive rainfall and high relative humi-

dity on thick branches (Unterseher, Otto & Morawetz 2003). Other Agaricales were represented by *E. fraxinicola*, *C. subtilis*, *P. chioneus*, *Resupinatus* spp. and *Lachnella* spp. *E. fraxinicola* and *Lachnella* spp. belong to the cyphelloid basidiomycetes, whose minute, cup shaped basidiomes are plastic. Under humid conditions they emerge quickly on the upper side of branches. They take a spheroidal shape when their tissues dry up thus enclosing the hymenium. This probably results in a slower dessication of the inner fertile, damageable structures. *C. subtilis* and *P. chioneus* possess small basidiomes of about 1 cm diameter. They develop well protected in clefts of branches and under partly detached bark.

The great number of available environments and substrata in old growth, species rich, temperate deciduous forests like the study area in Leipzig most likely leads to high local diversity but also makes sufficient sampling difficult. With the use of construction cranes in long-term canopy projects it becomes easier to investigate fungal richness at all vertical levels of a forest. Considering the fact that fungi play a very important role in nutrient cycling on both the temporal and spatial scales, and that various associations with other organisms exist, more attention should be given to fungi in all canopy projects worldwide.

ACKNOWLEDGEMENTS

We thank the UFZ, Centre for Environmental Research Leipzig-Halle and the friends of the botanical garden Leipzig for financial support. Many thanks go to Mrs. Dr. H. Große-Brauckmann, Mr. F. Dämmrich and Mr. H.O. Baral for the determination of difficult taxa and many helpful comments. We also thank Mr. Dr. C. Dormann (UFZ) and Mr. P. Horchler (Univ. Leipzig) for a critical review of the manuscript and additional statistical support, C. Seele for providing structural data of the crane site, C. Schmidt for providing lists of xylotrophic beetles and mycetophageous flies and Prof. Harvey E. Ballard, University of Ohio and Shirley-Ann and Georg Rueschemeyer for improvement of the English style.

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Influence of small-scale conditions on the diversity of wood decay fungi in a temperate, mixed deciduous forest canopy

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Mycological Research, in press. Available online at http://www.sciencedirect.com/science/journal/09537562

Influence of small scale conditions on the diversity of wood decay fungi in a temperate, mixed deciduous forest canopy

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Studies on fungal richness and ecology have been largely disregarded since the first intensive efforts to investigate organismal diversity in forest canopies. We used the Leipzig Canopy Crane research facility to sample wood-decaying fungi in a mixed deciduous forest canopy 10-30 m in height. The structural complexity of the canopy was analysed using different methods, including meteorological measurements. With respect to temperature and relative humidity, marked differences existed between forest floor and upper canopy layers that persisted on smaller scales. Of the 118 taxa found in 128 sample units, pyrenomycetes and corticioid fungi outnumbered other groups of macrofungi. Fungal communities showed distinct variations both in species richness and composition with respect to substrate (tree species), height in the canopy, stage of decay, and branch diameter. Pyrenomycetes and their anamorphs dominated the mycobiota on thin, exposed twigs at great heights, indicating their ability to overcome extended periods of drought and high levels of solar irradiance. Other taxa of Tremellales (*Exidia* spp.), Orbiliales (*Hyalorbilia inflatula*, *Orbilia* spp.) or Agaricales (*Episphaeria fraxinicola*, *Cyphellopsis anomala*, *Lachnella* spp.) also exhibited features that enabled them to develop in lesser protected habitats within tree crowns.

INTRODUCTION

The life of wood-decay fungi in the canopy of a temperate, mixed deciduous forest 10-30 m in height is rarely considered. The upper canopy is widely composed of young twigs and exposed to high illumination levels, to strong winds, and heavy rainfall. Inner and lower canopy layers formed by a broad range of thin twigs and thick branches with a patchwork of sunny and shady places provide many different ecological niches for different organisms including fungi (Unterseher *et al.* 2005; Lodge & Cantrell 1995), arthropods (Basset *et al.* 2003; Novotny & Basset 2000; Corbet 1961) and various epiphytes, including lichenized fungi (Freiberg 2001; McCune *et al.* 2000).

There are many methods of assessing and defining the structural complexity of forest canopies, and many areas of uncertainty as to how it influences the occurrence and variation of organisms (Parker & Brown 2000). Parker & Brown mentioned that general predictions and averaging data should be omitted in favour of interpreting single measurements, and that information about variability (e.g. transition zones between the upper canopy and the understorey with great variability in light transmittance) should not be discarded. Instead such data should be used along with that on the ecology of the organisms. Differences in biotic and abiotic factors such as solar radiation (Anhuf & Rollenbeck 2001; Kuuluvainen & Pukkala 1989, 1987), quantity of available water (Bellot *et al.* 1999), diurnal and annual gradients in temperature, and the quality and amount

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of different substrates over time and space, most probably affect the richness and species composition of sessile organisms such as fungi (including lichens) on a vertical scale (e.g. Unterseher *et al.* 2005; McCune *et al.* 2000; Hallenberg & Parmasto 1998; Lodge & Cantrell 1995). Light is obviously a critical resource in the canopy, and in case of direct solar radiation, immediately influences the temperature on surfaces of branches (Théry 2001; Dirmhirn 1961; Haddow & Corbet 1961).

Despite more than 20 y of intensive canopy research (e.g. Ozanne *et al.* 2003; Morawetz 1998; Erwin 1982), studies on the diversity and ecological impacts of microorganisms, and especially of fungi, in forest canopies above 10 m in height are very rare (e.g. Unterseher *et al.* 2005; Keller *et al.* 2004; Keller 2004; McCune *et al.* 2000; Lodge & Cantrell 1995). In the recent edition of 'Forest Canopies', the current benchmark of canopy research (Lowman & Rinker 2004), nine pages, less than 2% of the whole book, mention fungal activity (Fonte & Schowalter 2004).

Decayed wood desiccates faster in the canopy than at ground level, and may provide different niches for fungi than on the forest floor. Unterseher *et al.* (2005) presented a species list of wood-decay fungi from the canopy of a temperate mixed deciduous forest with 118 different taxa, but only three agaric species with a prominent stipe (*Mycena galericulata*, *Pleurotus cornucopiae*, and *Pluteus cervinus*). The few studies concerning fungi on dry, weathered wood have concentrated mostly on tropical forests, on the understorey or over short periods of time (e.g. Keller 2004; Lodge & Cantrell 1995; Hedger *et al.* 1993; Boddy 1992; Sherwood 1981). Apart from corticioid species of Polyporales, Hymenochaetales and Russulales (Tejera & Rodriguez-Armas 1999), pyrenomyceteous fungi frequently colonize decayed wood in arid habitats. Some are able to continue growth under dry weather conditions for some time if they possess large, immersed stromata and also to survive in desiccated conditions, if drought persists (e.g. Nuñez 1996; Munk 1957; Ingold 1954). Different groups of the Auriculariales, Helotiales, Orbiliales and Tremellales, also tolerate such conditions (Sherwood 1981, Baral, pers. comm.). In the 1980s, a series of studies was published by Boddy and co-workers focussing on the development and ecology of fungal communities on dead, attached branches in the understorey of temperate, deciduous tree species. Although dead, hanging branches occur naturally and are essential parts of nearly every tree crown (e.g. Boddy & Rayner 1983; Butin & Kowalski 1983), most of their studies were limited to single branches or to early stages of fungal succession (Boddy & Rayner 1984, 1983, 1982; Chapela & Boddy 1988a-c; Griffith & Boddy 1991a-c, 1989, 1988).

The aims of the present study were to: (1) expand knowledge of the diversity of wood-decay fungi in forest canopies; (2) extract fundamental climatic patterns that help; and (3) assess fungal ecology in this habitat. This paper shows a mycological approach to describing the forest canopy of a temperate, mixed deciduous forest in Central Europe, and presents new data on the diversity and ecology of corticolous and lignicolous fungi in a still widely unexplored ecosystem compartment.

MATERIAL AND METHODS

Study site

The climate of the Leipzig city area (51°20'16" N, 12°22'26" E) is characterized as intermediate between maritime and continental (mean annual temperature 8.8 °C; mean annual precipitation 512 mm). The soils at the crane site are nutrient-rich loamy floodplain (alluvial) deposits. The investigation site is at the margin of a former oak and elmrich forest that is classified as typical floodplain forest of the upper alluvial zone (*Querco-Ulmetum minoris* Issler 1924, syn. *Fraxino-Ulmetum* (R.Tx.1952) Oberd. 1953). Due to river straightenings and canalization, as well as extensive brown coal mining since the early 20^{th} century, the ground water level in the Leipzig floodplain forests dropped significantly. Thus, the forest suffered a gradual but notable change in species composition, favouring sycamore (*Acer pseudoplatanus*) which today represents the most frequent tree species. The forest stand at the crane site is characterized by a fairly diverse composition of woody species (17 tree species and five shrub species with 1 cm diam at breast height inclu-

ding four introduced tree species [Morawetz & Horchler 2004]). The actual canopy is mainly formed by oak (*Quercus robur*) trees (older than 250 y, 7% canopy cover) and younger trees of ash (*Fraxinus excelsior*), sycamore, and lime (*Tilia cordata*) (younger than 130 y, 53%, 17% and 10% canopy cover respectively). A peculiarity of the stand is the large amount of dead wood which provides an important habitat for several rare and endangered organisms.

Canopy access

With a construction tower crane (Liebherr 71 EC, height of tower 40 m, jib length 45 m, max. sampling height ca 33 m), mobile on a 120 m long railway track, 1.6 ha of forest can be explored (Unterseher *et al.* 2005). Many more information on canopy research and methods of access is given in Lowman & Rinker (2004), Basset *et al.* (2004) and Mitchell *et al.* (2002).

Sampling design and microhabitat descriptions

The new challenge to operate in a three-dimensional space with a construction crane forced us to apply new methods of sampling for mycological studies. Unterseher *et al.* (2005) give a detailed description of the methods applied in the field. Voucher specimens from the study are stored in the collections of the University of Leipzig (LZ).

Meteorological measurements

Meteorological measurements were performed on three scales. (1) On the 10 m scale three Hobo® devices (ONS-H08032-08, www.synotech.de) measured temperature and relative humidity at 29 m, 19 m, and 6 m above ground in a least disturbed part of the investigation plot. (2) On the 1 m scale, temperature was measured at different locations in the canopy contrasting inner and outer canopy and sunlit and shaded areas. Four N-thermistors (ONS-27-9M1002-C3) were connected to a Hobo® data-logger (ONS-H08-008-04). The thermistors possessed black beads, 2 mm diam, simulating to some extent biological bodies. Air temperature and direct solar irradiation influenced the temperature measured by the thermistors. (3) On the 10 cm scale, temperature was measured at different aspects of branches (north, south, east, west) more than 25 m height above the ground. The thermistors were fixed to the branches without touching their surfaces. Similar data-loggers as on the 1 m scale were used. Data collecting began on March 2004 and is ongoing. Measured intervals were 10 min at the 10 m scale and 2.5-8 min at the 1 m and 10 cm scales. The exact positioning of the data-loggers in the plot is available on request to the corresponding author.

Data on fungal abundances

In a previous paper on wood-decay fungi from the Leipzig Canopy Crane Project, untransformed presence-absence data were used to perform statistical analyses (Unterseher *et al.* 2005). For this paper the data were transformed as follows.

Beals smoothing

Beals (1984) introduced the 'index of sociological favourability', designed to relieve the 'zero truncation problem' in sparse community matrices and replace presences/absences in a sample by a species matrix with probabilities of occurrence estimated on the basis of observed sample composition (Beals 1984). This matrix operation was termed 'Beals smoothing' in the software package PC-Ord for multivariate analysis of ecological data (McCune & Mefford 1999).

Quantitative abundances

The abundances of fungal fruit bodies were assigned to four estimated values: (1) rare, (2) scattered, (3) frequent, and (4) abundant. To overcome the problem of differing total branch lengths per sample unit, an easy transformation was applied: for every fungal species identified in a sample unit, the length of the branch on which the fungus was found was divided by total branch length of the sample unit. The resulting quotient was then multiplied with the estimated abundances (1-4). In the field, *Cryptosphaeria eunomia* for instance, was frequent to abundant with a mean abundance of 3.5. *Episphaeria fraxinicola* was rare with an estimated abundance value of 1. With the adjustment to total branch length, the abundance of *C. eunomia* remained at 3.5 whereas that of *E. fraxinicola* dropped to 0.3. The abundances obtained were compared to the conditions occurring in situ as far as possible. In the present example, a more

than ten times higher abundance of *C. eunomia* compared to that of *E. fraxinicola* was more realistic than a 3.5:1 relation prior to transformation.

The calculated values of species abundances performed poor by with nonmetrical multidimensional scaling (NMS) and Sørensen distances (see below), with low numbers of cumulative explained variance for the ordination axes compared to transformed presence-absence matrices by the Beals smoothing function of PC-Ord. Therefore, we decided to use only data transformed with Beals smoothing to display community relationships and environmental variables. Our choice agreed with results of Ewald (2002) and McCune (1994), as Beals smoothing enhanced the ability to see and interpret patterns of species richness in environmental space because it reduced the number of zero occurrences in the data set and improved the detection of compositional gradients.

The raw sample - species matrix contained 128 samples and 118 species (species list in Unterseher *et al.* 2005). To reduce noise from very infrequent species (i.e. singletons or doubletons), we decided to delete all species with fewer than three occurrences. Empty samples resulting from the removal of species were also deleted. In the new matrix 45 species and 119 samples remained. After Beals smoothing outliers were sought by examining a frequency distribution of average Sørensen distance between each sample/species and all other samples/species in species/sample space (McCune & Mefford 1999). Four samples and three species were scanned as weak to moderate outliers. We decided to keep the samples and especially the fungi because they represented important species to display host tree specificity. Another matrix contained samples and different environmental factors: tree species, height above ground, canopy layer, diameter of twigs and the occurrence of fruit bodies on the substrate (e.g. bark or bare wood).

Ordination

We performed NMS on the data with Sørensen distance and the 'slow and thorough' autopilot option in PC-Ord to ordinate species in sample space. The autopilot used the best of 40 runs with the real data along with 50 runs with randomized data for a Monte Carlo test of significance. Sørensen distances expresses community resemblance (McCune & Mefford 1999). The habitat variables height, substrate (bark) and stage of decay were superimposed as radiating vectors on the resulting ordination. Their relative strength and direction from the centroid indicated the correlation with the ordination (Fig. 1).

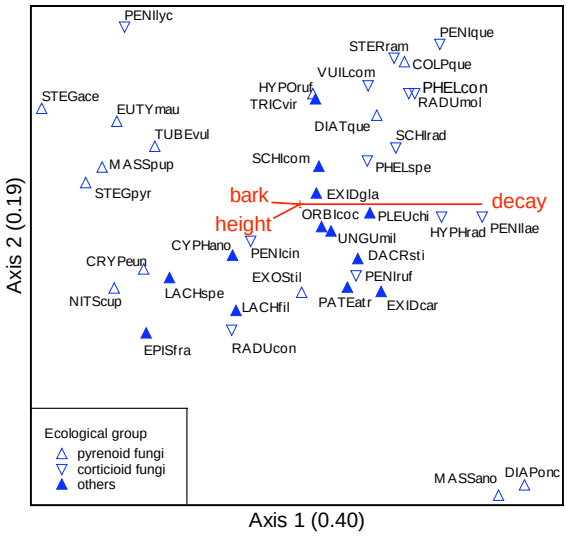

Fig. 1: Ordination of species in sample space with environmental variables overlaid as joint plot. Symbols indicate different groups of fungi (see Material and Methods). The lines radiating from the centroid indicate the relative strength and direction of correlation of variables with the ordination.

The ordination was rotated 25° to load the strongest environmental factor 'decay' on the most important axis. Host specificity of some abundant species was visualized using a simple scatterplot overlaid with the abundances of the species in sample space (Fig. 2). In this case the ordination with the calculated abundances (not shown) resulted in comparable patterns than the ordination after Beals smoothing. According to McCune and others, NMS is "the most generally effective ordination method for ecological community data" (McCune & Grace 2002; Clarke 1993).

Hierarchical clustering

We used cluster analysis in PC-Ord to detect interpretable patterns of species composition in the data set.

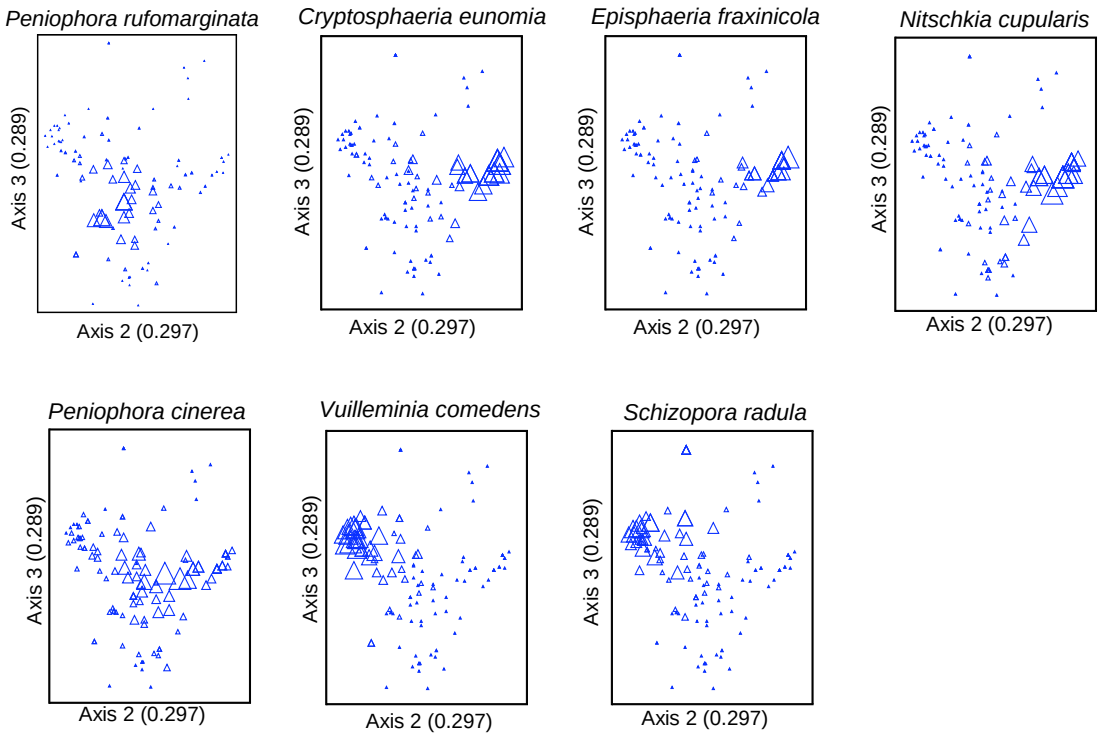

Fig. 2: Abundances of seven different fungal species. In each ordination the abundance is overlaid on an ordination of sample units. The size of the symbols in the graphs is proportional to the abundance of the fungi.

We applied a more rigid criterion for deleting rare species. Only those species with five or more occurrences were considered for analysis, since species with only a few occurrences provide little reliability in assigning them to groups (McCune *et al.* 2000). The resulting 27 species and 112 samples matrix was transformed with Beals smoothing function in PC-Ord. We used Ward's method of clustering with an Euclidian distance matrix after outlier analysis. Sørensen distance used for NMS is incompatible with Ward's method of clustering. The choice of distance measures however is of minor importance in the cluster analysis applied here. The dendrogram (Fig. 3) was scaled by Wishart's objective function converted to a percentage of information remaining (McCune 2002).

Grouping of species prior to analyses

Based on our knowledge and on comments in literature, we recognized two groups in all fungi. The first group (pyrenoid fungi) included all pyrenomycetes found in the canopy (e.g. Pleosporales, Pyrenulales, Sordariales, Xylariales) and their anamorphs that grew in deeper layers of bark or wood (mainly coelomycetes). They shared similar morphological features such as the blackish outer layer and the shape and size of spore producing organs (pycnidia, perithecia, or acervuli), that were often immersed partly or totally into the substrate and embedded in stromata. Most probably they also have comparable ecological needs. Group 2 (corticioid fungi) contained all corticioid fungi in the sense of Eriksson *et al.* (1973-87). The rest comprised fungi of different taxonomic groups. Most showed adaptions to drought and changed the shape of their fruit bodies on drying (plasticity), especially the perithecia of some pyrenomycetes (e.g. *Nitschkia cupularis*), fruit bodies of jelly fungi (*Auricularia auricula-judae* or *Exidia* spp.), cyphelloid agarics (*Episphaeria fraxinicola* or *Cyphellopsis anomala*), or discomycetes (*Mollisia* spp. or *Orbilia* spp.).

Table 1: Fungal species diversity. The overall species richness is displayed in the first line below the headings. Species diversity was also calculated for groups of sample units. Beta diversity was measured as the total number of species divided by the average number of species (McCune *et al.* 2000).

Group	Sample size	Av. spec. rich. (S.D.)	No. of spec.	β-div.
All	125	3.4 (1.9)	118	34.71
Corticioid fungi		1.2 (1.4)	40	33.33
Pyrenoid fungi		1.2 (1.0)	38	27.50
Tree species				
Acer	20	3 (1.4)	23	7.67
Fraxinus	24	3 (1.0)	19	6.33
Quercus	25	4.2 (2.2)	34	8.10
Tilia	29	3.5 (2.6)	47	13.43
Canopy layer				
Lower	36	3.3 (1.9)	63	19.09
Pyrenoid fungi		17		
Corticioid fungi		21		
Middle	49	3.3 (2.0)	72	21.82
Pyrenoid fungi		23		
Corticioid fungi		24		
Upper	40	3.3 (1.9)	55	16.67
Pyrenoid fungi		25		
Corticioid fungi		17		

RESULTS

Species diversity

Species richness was discussed in a broad sense by Unterseher *et al.* (2005), and a short summary with brief additions is given in Table 1. The average species number per sample unit was 3-4 with a standard deviation of 1.9. Overall beta diversity (species turnover rate) was very high at 34.7, but strongly decreased to 13.4 (*Tilia cordata*) and 8.3 (*Fraxinus excelsior*) when species richness on the four different host trees was calculated. This reflected the importance of substrate type for the occurrence of wood-decay fungi in the canopy. The high number of infrequently occurring species (72 fungi, 61%, were singletons or doubletons) also contributed to the unusually high beta diversities. Table 1 lists species numbers of the different morphological groups. With a comparable sample size, the amount of pyrenoid fungi increased from the lower to the upper canopy from 27% (17 species) to 45% (25) whereas the highest species number of corticioid fungi occurred in the lower and middle canopy with 33% compared to the upper canopy with 30% (17). The highest overall species number observed was in the middle canopy layers (Table 1).

Differences between habitats

The fungal community differed strongly between habitats (Figs 1-2). After rotation the first three axes in Fig. 1 chosen by the NMS autopilot option, PC-Ord explained 77% of the community variation.

In Fig. 1, the most important axis related to the stage of decay of sampled twigs. Tree specificity of fungi could be assessed clearly from the ordination. *Massaria anomia* (MASSano) and *Diaporthe oncostoma* (DIAPonc), were found only on *Robinia pseudacacia* and separated clearly from *Stegonsporium acerinum* (STEGace), *S. pyriforme* (STEGpyr), and *Eutypa maura* (EUTYmau), which were specific for *Acer pseudoplatanus*. In the field, the anamorph of *Nectria cinnabarina*, *Tubercularia vulgaris* (TUBEvul), was not restricted to sycamore but showed a strong association to weak, still living twigs. Fruit bodies of some species occurred only on bark such as conidiomata of *S. acerinum* and *S. pyriforme*, or ascomata of *Massaria pupula* (MASSpup). In contrast, *Peniophora laeta* (PENIlae), *Hyphoderma radula* (HYPHrad) and *Schizopora radula* (SCHIrad) were found on strongly decayed wood. Other traits were evident: *Episphaeria fraxinicola* (EPISfra), *Nitschkia cupularis* (NITScup) and *Cryptosphaeria eunomia* (CRYPeun) were found at greater heights and exclusively on *F. excelsior*. Several *Lachnella* species (LACHspe) also preferred twigs of ash in the higher canopy regions. Fungi with small fruit bodies, most of the pyrenoid fungi, coelomycetes, and all cyphelloids, dominated the left and the lower half of Fig. 1. However, most of the corticioid fungi with larger, expanded fruit bodies ordinated in the opposite direction, because they were found on thicker, stronger decayed branches in lower canopy areas.

Cluster analysis

The mycobiota was partitioned into several groups (Fig. 3).

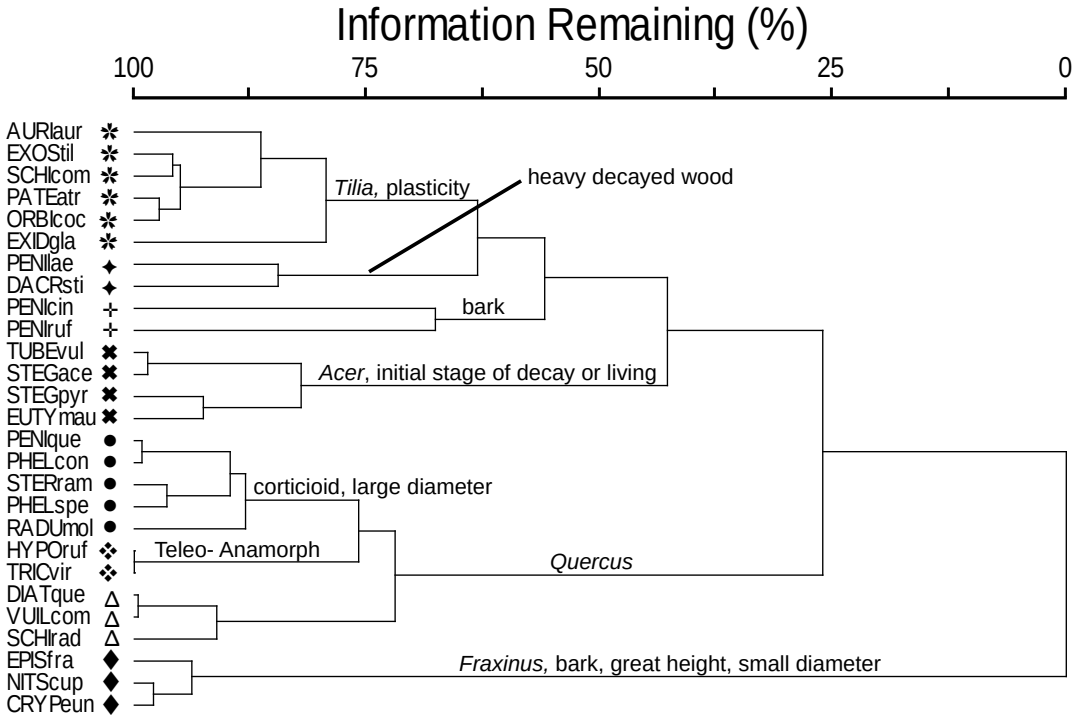

Fig. 3: Hierarchical dendrogram from cluster analysis. Species groups are indicated with different symbols.

Host-specific fungi of *Fraxinus*, *Quercus* and *Acer* were clearly separated, whereas the groupings of *Tilia*-specific fungi were less homogenous. *Peniophora rufomarginata* (PENIruf) for instance, a species specific to lime clustered with *P. cinerea* (PENIcin), an ubiquitous species, as did *P. laeta* (PENIlae) and *Dacrymyces stillatus* (DACRsti).

Microclimatic differences within the forest

Measurements of temperature and relative humidity revealed complex patterns in the canopy on all three scales (Figs 4-5). Significant differences were observed between 6 m and 29 m, with maximal values of 8 °C and 40% relative humidity. These gradients only existed during daylight from 7.00-20.00 h and disappeared at night. The increase of temperature at 29 m above ground during daytime was correlated with a decrease of relative humidity with about 7% for 1 °C (Pearson product moment $p < 0.001$, regression coefficient: 0.144). The total vertical difference in temperature was due to the crown layer (19-29 m) that explained 67% of the total variation in temperature, whereas the understorey and stemlayer explained 33% (Fig. 4, Mann-Whitney rank sum test $p < 0.001$, $n = 3336$ each). Comparable patterns existed for relative humidity (53% and 47% respectively). Saturation (100% relative humidity) was reached on 11 of 79 d at 6 m above ground, and on 7 d at 29 m above ground.

Differences of temperature within tree crowns (1 m scale) were also prominent and followed differences between sun and shade. In 30% of the days, differences in mean daytime temperature between the outer and inner tree crown exceeded 2 °C. Differences greater than 2 °C in the outer layer were observed in 20% of the days (outer minus inner crown), compared with 5% for the inner canopy layer (inner minus outer crown) (Mann-Whitney rank sum test $p < 0.001$). Mean differences of daytime and night temperature were significantly greater in outer than in inner canopy layers.

The mean differences of temperature around a branch (10 cm diam) are shown in Fig. 5. The gradients between exposed and shaded parts were clearly visible and correlated with sun movement.

Maximal differences rose up to 16 °C for north-south comparison and 11 °C for east-west comparison (values not accessible from Fig. 5).

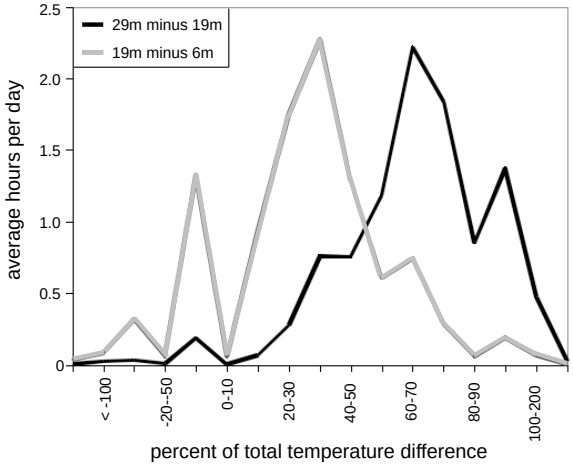

Fig. 4: Differences in temperature between 6 m and 29 m above ground divided into two seperated comparisons: The upper with the middle (black line) and the middle with the lower canopy (grey line). Negative values on the x axis indicate that temperatures measured at 6 m were higher than at 19 m and at 19 m higher than at 29 m respectively.

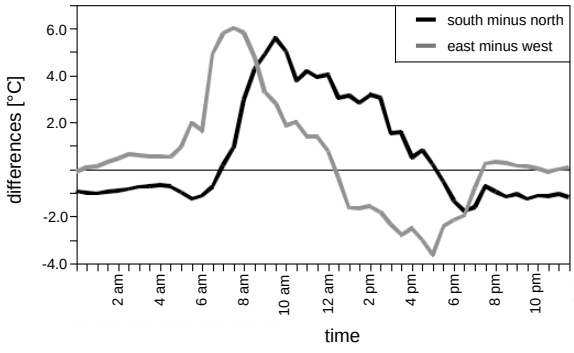

Fig. 5: Four sensors around a branch of *Tilia cordata* measured temperature in 29 m height at the four cardinal points. Differences between north and south (black line) and east and west (grey line) are shown as 30 min averages from 2 April 2004 till 19 May 2004. The black sensors with a diameter of 2 mm were fixed directly to the branch's surface and measured air temperature plus direct solar radiation.

DISCUSSION

Species richness

The distribution and diversity of wood-decay fungi in general is highly dependant on environmental factors such as exposure to sun and wind (temperature), availability of water, substrate type, diameter or kind and stage of decay (Unterseher *et al.* 2005; Pearce 2000; Helfer & Schmid 1990; Griffith & Boddy 1991a-c; Boddy 1983), and is highly variable in time and space (Frankland 1998; Lodge & Cantrell 1995). We agree with McCune *et al.* (2000) in saying that the canopy structure itself creates vertical gradients according to the unique canopy structure and climate of the study site, and with Parker & Brown (2000) that information about variability as well as the ecology of the organisms that are discussed in the context of canopy stratification should be used individually. Figure 6 shows the canopy surface of the Leipzig crane plot (Markus Rohrschneider, unpubl.). Its roughness and heterogeneity, with many gaps, small trees within clusters of taller ones, and large among small trees are clearly visible. The structural complexity continues under the canopy surface. We have shown that differences of temperature and relative humidity existed on all measured scales. Vertical gradients were observed from the generally warmer and drier tree tops to the understorey during the day, which disappeared at night. Gradients in temperature from outer to inner layers existed within tree crowns and were superimposed by effects of sun movement. On the smallest scale measured, gradients were maintained, and may or may not follow sun movement, depending on the spatial structure of twigs and branches. Despite the broad range of substrates sampled for this study, 700 collections in 128 different sample units on nine different tree species between 10-30 m in height in the years 2002-04, it was not possible to cover the full range of different habitats on decayed twigs and branches sufficiently. This is one reason why the list of 118 different taxa identified up to now must be considered preliminary (Unterseher *et al.* 2005).

Fungal compositions in the canopy

Nitschkia cupularis, *Cryptosphaeria eunomia*, and *Episphaeria fraxinicola*, were closely associated

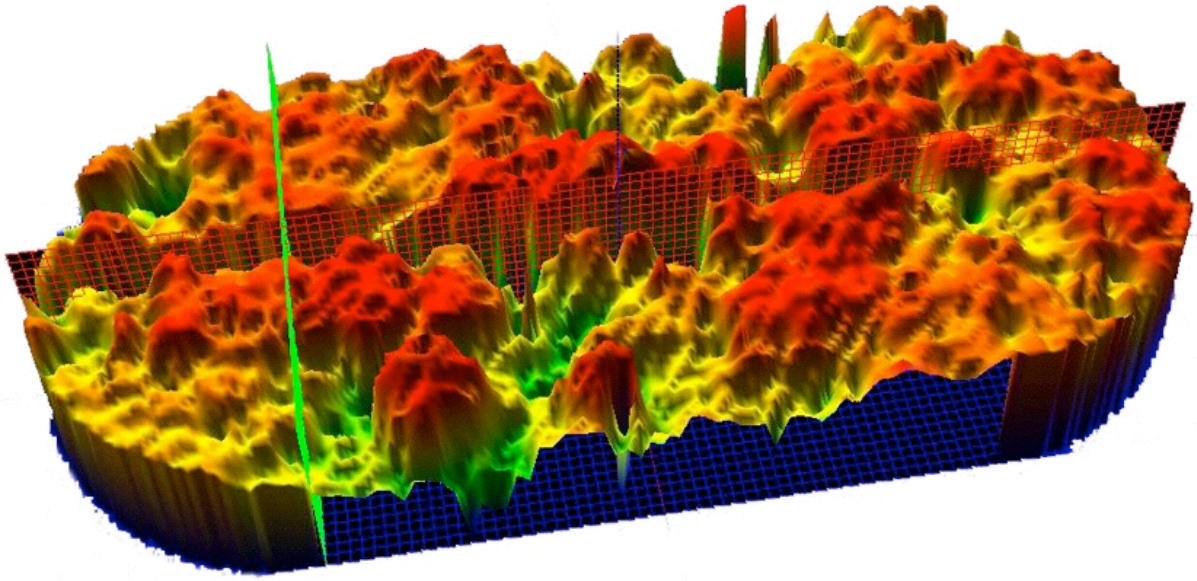

Fig. 6: Computer generated, 3-D canopy surface model of the Leipzig canopy crane study site based on 4500 single perpendicular measures. The railroad track on which the construction crane can be moved is visible as large gap from the left to the right. The study site measures 200 m from north to south (right to left) and 80 m from east to west.

with their host *Fraxinus excelsior*, and preferred thin twigs at greater height (Fig. 2, Unterseher *et al.* 2005). Additionally, *E. fraxinicola* occurred only on twigs were *C. eunomia* was also present. This agreed with sparse comments in literature, such as where *E. fraxinicola* grew on ash tree bark in close association with other pyrenomycetes (Dam & Dam-Elings 1991; Ellis & Ellis 1988; Moser 1983). *N. cupularis* was protected to a certain degree against the harsh environments of the upper canopy. Perithecia of the species were found only in bark fissures and under partly detached parts of branches. Their hard outer layer prevented inner spore-producing structures from drying out too rapidly. Additionally, many ascomata were aggregated densely together. If water was present it could be retained for several hours longer through capillary forces between the single perithecia (data not shown). This feature was common in the canopy of the study site.

Besides such traits, we observed collapsed perithecia of *N. cupularis*, of which many were still vital. This indicates that the species possess adaptations to xeroresistance in the sense of Bewley (1979). The height of fungal occurrence is connected with the tree species in this group because ashes were the most healthy and largest trees in the plot.

Fungi on *Quercus* could be separated into two groups (Fig. 2): *Hypocrea rufa* (HYPOruf) and *Trichoderma viride* (TRICvir) formed one group simply because *T. viride* is the anamorph of *H. rufa*. Stromata of *H. rufa* occurred exclusively together with its anamorph on the same branches. The remaining species were corticioid fungi found on branches with varying diameters. The only exception, the ascomycete *Diatrypella quercina* (DIATque), grouped closely with *Vuilleminia comedens* (VUILcom). Whenever *V. comedens* was sampled in the field, remnants of *D. quercina* were also visible on the branches as black lined circles. According to our data, we hypothesise the following interrelation: Stromata of *D. quercina* occur first, preparing the substrate for *V. comedens* by breaking through the bark's surface. In later stages of decay, *V. comedens* was overgrown by *Schizopora radula* (SCHIrad); compare the response of *S. radula* to decay in Fig. 1. Note that the position of *D. quercina* seems to be contrary to our hypothesis because it was associated with later stages

of decay, as was *S. radula*. *D. quercina* however, was the only fungus in this study that was indicated as 'present' if remnants or obviously dead fruit bodies occurred in the samples.

Nectria cinnabarina (anamorph *Tubercularia vulgaris*), *Stegonsporium acerinum*, *S. pyriforme*, and *Eutypa maura* were the dominant components on dead attached twigs and thin branches of *Acer pseudoplatanus*; for *Stegonsporium* see van Warmelo & Sutton (1980) and Sutton (1980). *Stegonsporium* and *Tubercularia* emerged on the bark's surface and occurred frequently on weak, still living branches. From initial stages of decay on, *E. maura* was present in the wooden tissue under fully intact bark. *E. maura* is a member of the Xylariales which are known to be common endophytic fungi in wooden tissues of trees (Worrall *et al.* 1997; Rogers 1979; Petrini *et al.* 1995). *E. maura* was not mentioned explicitly in these references, but the pattern of occurrence of the species made it most probable that it was already present as a dormant endophyte. As described by Worrall *et al.* (1997) for other Xylariales, *Eutypa* containing branches showed considerable weight loss. In our study the whole cross section of many branches was strongly and uniformly decayed, giving the wood an impression of white rot. Stromata of *E. maura* covered most of the branches' surface, probably making it impossible for saprophytic, secondary invaders to colonize the substrate. In the absence of *E. maura*, other species such as *Cerrena unicolor* (CERRuni), *Coriolopsis gallica* (CORIgal) or *Schizophyllum commune* (SCHIcom) were present. This uniformity of the fungal community on thin branches of sycamore mostly counted for its low diversity (Table 1).

The grouping of *Peniophora cinerea* and *P. rufomarginata* was unexpected, because *P. cinerea* was ubiquitous (Fig. 2), whereas *P. rufomarginata* occurred only on *Tilia cordata* (Eriksson *et al.* 1978; Fig. 2). However, *P. cinerea* was also found on lime trees and shared several habits with its relative. Their basidiomata, for instance, occurred exclusively on the surface of medium to strongly decayed branches and were not visible on the wooden surface of decorticated parts.

Fungi on *T. cordata* grouped less homogenously. *Exidia* species (EXID.) were found throughout all stages of decay, diameters, and different heights. The position of *P. laeta* among the *Tilia*-specific fungi could be explained by the occurrence of the species on heavily decayed wood, a feature shared with *Darcymyces stillatus*. *P. laeta* ordinated more on the right than *D. stillatus* in Fig. 1, because the effect of decay was superimposed by the effect of the host tree. Members of the topmost grouping on Fig. 3 all showed adaptions to drought. The basidiomes of the jelly fungi *Auricularia auricula-judae* (AURIaur) and *Exidia glandulosa* (EXIDgla) outlast longer periods of drought than other wood-decaying species (e.g. gilled fungi) because they store comparably large amounts of water. If arid conditions and evaporation of water from the fruit bodies continue, they can survive in a desiccated condition (xerotolerance in the sense of Bewley 1979) as do *Schizophyllum commune*, *Mollisia*, or *Orbilia* sp. (Ingold 1954; Baral, pers. comm.). Their tissues absorb water rapidly, and growth and spore discharge can continue a few minutes after rewetting (data not shown). Additional to the tough black cortical layers in the apothecia of *Patellaria atrata* (PATEatr) and the conidiomata of *Exosporium tiliae* (EXOStil), both possess large, septate spores (Ellis 1971; Unterseher *et al.* 2003) that provide a clear advantage over small ones in unstable environments (Huhndorf & Glawe 1990).

The fungi's ability to protect fertile structures from rapidly drying out, to develop spore producing organs inside and under the surface of substrates (pyrenomycetes and coelomycetes), and to tolerate desiccation together with a rapid uptake of water and rapid development of spore producing structures (e.g. *Orbilia*, *Lachnella*, *Episphaeria*, *Exidia*, *Auricularia*), made these species preferable inhabitants of dead wood still attached to the tree in the canopy. In a canopy, many species, such as pyrenomycetes, probably escape the problems of slow or limited growth. The retarded growth of pyrenomycetes in the canopy (more than 5 wk of spore development time for *Diaporthe oncostoma* [DIAPonc], pers. obs.) could also be an adaption to slow decaying processes in aerial habitats that provide stable niches (Stone *et al.* 1996).

Huhndorf & Glawe (1990) studied the development of pycnidia from ascospores of a *Fenestella* species, a genus also represented in our studies (*F. vestita*), and discussed the ability of *F. princeps*

ascospores to develop directly into pycnidia as an example of heterochronic evolution. This unusual mode of ascospore germination is present with some variations in several other pyrenomyceteous fungi, and may serve as a method for effective colonization of suitable substrates and a rapid spread to secondary colonization sites under arid conditions. In some cases, however, the canopy was not as dry as it seemed. On warm, sunny days the leaf layer slowed down the evaporation of water from deeper forest areas. This resulted in a higher humidity below the canopy surface for several hours each day, visible on steeper temperature gradients across the canopy compared to gradients of relative humidity. Additionally, microclimatic differences were compensated for during the nights at least in the periods studied (Figs 4-5). After rainfall, decayed branches acted as a sponge, absorbing downflowing water. If dead branches were still surrounded by intact pieces of bark, as was often the case on cherry or lime trees, water could be retained for many days. When the sun heated the substrate, warm and humid conditions inside the wood were created that most likely supported fungal growth even during long dry periods. Dead wood in the canopy exposed to rainfall would be more suitable for the apparently splash-dispersed, smaller and more delicate conidia produced in conidiomata of various species; this could be a potent argument to explain the comparably high abundance of this group in the canopy of the Leipzig forest.

CONCLUSION

Considering that wood-decay fungi in the canopy are a mostly inconspicuous but important component of the biota of forest ecosystems (Unterseher *et al.* 2005; Hallenberg & Parmasto 1998 and Stone *et al.* 1996) that are also associated with other organisms such as canopy arthropods (Malloch & Blackwell 1992), investigation of the diversity and ecological patterns of fungi in the canopy may be crucial to the understanding of foodwebs and their links between canopy and soil (wood endophytes start growing on attached branches and, if branches drop, most likely complete life-cycles on the ground). The varying microclimatic conditions caused by the structural complexity of the forest canopy, together with the broad range of available substrates, lead to the suggestion that the diversity of fungal organisms in the canopy is high, and that the ecological phenomena are highly variable and provide a rich source for further investigations.

ACKNOWLEDGEMENTS

We thank the UFZ - Centre for Environmental Research Leipzig-Halle (UFZ-16/2000, UFZ 04/2004) and the Minerva Foundation for financial support. Many thanks go to Wilfried Morawetz, Peter Otto, Hans Otto Baral, Sarah A. Corbet, Dan Eisikowitch, and two referees for helpful comments and discussions, Markus Rohrschneider for providing additional data on canopy structure, and Wolfgang Vocke of Synotech for technical support.

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Species richness and ecological characterization of myxomycetes and myxomycete-like organisms in the canopy of a temperate deciduous forest

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Mycologia, in press.

Species richness and ecological characterization of myxomycetes and myxomycete-like organisms in the canopy of a temperate deciduous forest

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The ecological community of myxomycetes and myxomycete-like organisms (MMLO) that occupies the outermost canopy of living deciduous trees was studied in a canopy crane plot of a riparian deciduous forest at Leipzig, Germany. A systematic survey carried out with a total of 146 moist chamber cultures resulted in 386 records of 37 taxa, with 32 myxomycetes, two myxobacteria, two protostelids and the fruitbody-forming ciliate *Sorogena stoianovitchae*, the latter recorded for the first time for Europe. With 94% of all cultures positive for MMLO, these organisms are consistently present in the investigated sections of white rotten twigs attached to living trees between 10 and 30 m above the ground. Our sampling recovered a majority of the likely species, with 37 out of the 42Ð45 predicted according to a species-accumulation curve and two other estimators of species richness. Non-metric multidimensional scaling revealed pH, water retention and stage of decay to be the environmental factors most important in determining species distribution. *Arcyria cinerea* and *Perichaena depressa*, the most common species occurred in 32% and 29% of all samples, respectively. Viewing the sampled twigs as habitat islands and a single spore as sufficient to establish a population, a simulation program assuming a random spore rain estimated an average of 0.4 and 0.35 spore hits per twig as necessary to explain the observed frequencies. This is matched by the potential productivity of the substrate. All fruit bodies from the cultured twigs would be able to create a spore rain of 86 (*A. cinerea*) or 40 (*P. depressa*) spore hits per twig when dispersed evenly over the plot. Measuring the terminal fall velocity of spores gave a figure of about five hours for a spore to fall down from the canopy (30 m) in still air; indicating a rather high dispersal ability for MMLO inhabiting the canopy.

INTRODUCTION

In tropical forests, the canopy stratum is considered to contain a large proportion of the total species diversity of the entire community (for arthropods refer to e.g. Ødegaard *et al.* 2000, Sutton *et al.* 1983, Erwin 1982, Erwin & Scott 1980), and many of the species present are predicted to be canopy specialists (Ozanne *et al.* 2003). Temperate forests are much poorer in insects, mammals, and epiphytic plants, thus shifting the focus of research away from these habitats. However, for spore-dispersed organisms, micro-scale habitats such as bark or small decayed twigs attached to living trees should represent suitable niches if they can be reached by the propagules of the organisms in question (Unterseher *et al.* 2005).

This study focuses on an ecological guild hereafter referred to as myxomycetes and myxomycetelike organisms (MMLO). At least six groups of

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organisms can be included, which are not always closely related according to recent eukaryote phylogenies (Baldauf 2003). Clearly distant from all of the eukaryote groups listed below are the prokaryotic myxobacteria (Reichenbach 1993) with 40-60 taxa. The eumycetozoans as defined by Olive (1975) include myxomycetes, protostelids and dictyostelids and are suggested to be monophyletic (Swanson *et al.* 2002, Fiore-Donno *et al.* 2005). The myxomycetes are the most species-rich group of eumycetozoans (ca. 800 species recognized, Lado 2001), with some of the protostelids as possible ancestors (37 described taxa, Spiegel 2003) and dictyostelids (ca. 100 taxa, Cavender 1990, Swanson *et al.* 1999) as a sister group. The few species of acrasids seem to be members of the Heterolobosa, a group phylogenetically distant to the eumycetozoans (Roger *et al.* 1996, Baldauf 2003). Finally, the ciliate genus *Sorogena* develops fruiting bodies strikingly similar to those found in myxomycetes (Bardele *et al.* 1991).

All six groups share a number of ecological traits like (i) living as predators of other microorganisms, (ii) starting their life cycle as unicellular microorganisms form spore-like propagules, (iii) later combining their biomass by aggregation of cells or exclusively nuclear divisions (plasmodia of most Eumycetozoans) to finally (iv) convert it to typically stalked fruit bodies which (v) develop within hours not out of a true growth process but be rearrangement of the available biomass to (vi) release air-borne propagules for long-distance dispersal.

Myxomycetes are the most conspicuous of the MMLO and inhabit various kinds of plant material like decaying wood and litter in most terrestrial habitats. So far, most studies of MMLO focused on myxomycetes from temperate zones and targeted habitats on the forest floor. However, also aerial plant parts can be inhabited by these organisms, as shown for Protostelids by several papers of Moore & Spiegel (2000 a, b) for both temperate and tropical zones.

Especially in Neotropical forests, aerial plant parts form suitable habitats for slime molds, where they often occur in greater diversity than on ground substrates (Schnittler *et al.* 2002, Schnittler & Stephenson 2000). Living inflorescences of herbaceous plants in Costa Rica and Ecuador were reported as a newly discovered microhabitat of myxomycetes (Schnittler & Stephenson 2002), and even covers of foliicolous liverworts on understory woody plants in tropical forests have a species-poor but common assemblage of mostly members of the Physarales (Schnittler 2001b).

The canopy as a myxomycete habitat was first investigated by Snell & Keller (2003) and Keller *et al.* (2004) in broadleaved deciduous forests of the Appalachians using the single rope technique; focusing on corticolous species inhabitating the tree trunks. With the use of the Leipzig Canopy Crane research facility (Morawetz & Horchler 2002, 2004; Unterseher *et al.* 2005) it was possible for the first time to investigate small twigs from the canopy in up to 30 m height for the occurrence of MMLO.

The aims of the present study are to create a preliminary species list of the MMLO occurring on decayed wood of twigs in the canopy and to assess the ecology of these organisms.

MATERIAL AND METHODS

Canopy access

With the construction tower crane used (Liebherr 71 EC, height of tower 40 m, jib length 45 m, maximum sampling height ca. 33 m, mobile on a 120 m long railway track), 1.6 ha of forest can be explored (Morawetz & Horchler 2004). Scientists collect from a gondola, using remote control to move the crane, and can raise themselves above the forest to move the gondola precisely down to a desired location in the canopy. This brings the outermost small twigs of a tree crown, which were previously inaccessible, within reach.

Study site

The climate of the Leipzig area (51°20'16"N, 12°22'26"E) is intermediate between maritime and continental (mean annual temperature 8.8 °C, mean annual precipitation 512 mm). The site is a floodplain oak-elm forest of the upper alluvial zone (classifying as Querco-Ulmetum minoris Issler 1924, = Fraxino-Ulmetum [R.Tx.1952] Oberd. 1953) on nutrient-rich loamy soils near the river Luppe. Due to river rectifications and canalization, as well as extensive brown coal mining ac-

tivities since the early 20^{th} century, the ground water level in the Leipzig floodplain forests dropped significantly. As a result, the forest suffered a gradual but notable change in species composition, favoring for example maple, which represents the most frequent tree species today. All woody species of the study site are identified, mapped, and their dbh has been measured (Morawetz & Horchler 2004), resulting in five species of larger shrubs (stem dbh exceeding 1 cm), 13 native and four introduced trees. The actual canopy is mainly formed by old *Quercus robur* trees (> 250 years, 7% canopy cover) and younger trees of *Fraxinus*, *Acer* and *Tilia* (< 130 years, 53%, 17% and 10% canopy cover, respectively). A peculiarity of the stand is the large amount of dead wood due to its status as nature reservation; no trees were cut during the last decades. Additionally, several of the old trees of *Quercus* and *Tilia* suffer heavily from the change in hydrological conditions in the soil.

Sampling

We collected 146 dead twigs between two and five cm diameter located haphazardly throughout the crowns (minimal distance between two samples: 3-5 m) of the eight most common tree species, namely *Acer pseudoplatanus* (n = 22), *Carpinus betulus* L. (n = 18), *Cerasus avium* (L.) Moench (n = 6), *Fraxinus excelsior* L. (n = 38), *Populus* x *canadensis* (Aiton) Sm. (n = 6), *Quercus robur* L. (n = 18), *Robinia pseudoacacia* L. (n = 5), *Tilia cordata* Mill. (n = 33). For selecting individuals, the following two criteria were applied: (i) tree height at least 25 m and (ii) comparatively large amounts of dead wood in different canopy strata, because samples were simultaneously used to study lignicolous fungi (Unterseher *et al.* 2005). From each twig, two 5-cm long pieces with a minimal distance of 25-30 cm in-between were removed (mostly from both ends), decorticated and chopped with a snap cut into pieces of 0.5-1 cm size which were used for moist chamber cultures.

For ecological analyses, several environmental parameters were recorded along with the sampling. These included canopy layer (sub canopy: 10-17 m, middle canopy: 17-24 m, top canopy: 24-31 m), exact height above ground, tree species and individual number, substrate characters (water holding capacity, kind and stage of decay), diameter of branches, pH, exposure to sunlight (estimated as exposed: more than 50% direct sunlight, semi-exposed: 10 to 50% and shaded: less than 10% direct sunlight). All dead twigs were assigned to four different stages of white rot decay (state 1: dead, but still not decayed wood, bark usually firmly attached, only the knife tip penetrates, state 2: slightly decayed, still solid wood, knife tip penetrates easily, state 3: moderately decayed wood, still in form but appearing soft, can be cut with a knife, state 4: strongly decayed and partly destroyed wood, soft consistency). Even at stage 4, the bark of the twigs was more or less intact, effectively retaining moisture in the woody inner part.

Moist chamber cultures

Between three and seven g of air-dried, decorticated wood from the 5-cm long sampled twig was placed in a plastic Petri dish 9 cm in diameter upon a disk of filter paper, covering the whole surface of the dish. To estimate the water holding capacity of the wood, dishes were weighed three times: empty, filled with dry wood, and soaked with water. Dishes were filled with distilled water adjusted to pH 7.0, allowed to soak for 24 hours, and excess water was thoroughly poured off. After this, pH was measured for three pieces of substrate, using a touch-down probe pHuture with an Orion 610 pH meter, and the third weighing was carried out. Using several soaked empty dishes lined only with filter paper as control, this allowed us to determine water holding capacity as the weight of water-soaked wood minus weight of the dry wood. Cultures were kept for two months and checked six times at days 4, 9, 15, 22, 37 and 50; on the last occasion the dishes were entirely dried out. The number of sporocarps appearing in a culture was counted (if less than 200) or estimated to obtain an abundance measure for subsequent statistical analyses.

Data analysis

Only records from cultures were analyzed, using one twig (equaling one culture) as a sample. A species accumulation curve was constructed according to the rarefaction formula with the programme EstimateS (Version 7, Colwell 2004), which gives also a number of estimators of spe-

cies richness. A hyperbolic regression according to the formula y = ax/(b+x), resulting in a curve shape coming very close to a broken-stick model (Magurran 2004, compare Schnittler 2001a) was applied to the data, with the parameter 'a' giving an estimate for the maximum number of species to be expected at this kind of substrate.

First, an ordination of species and samples in species' space was performed. The raw samples *vs.* species matrix used for the ordination analysis contained 134 samples (all cultures with at least one record that could be determined to species) and 37 taxa. To reduce noise from very infrequent species (i.e., single or double occurrences) we decided to delete all species recorded on fewer than three occasions prior to analysis, which resulted in a reduced matrix of 127 samples and 23 species. Multivariate analyses were performed as non-metric multidimensional scaling (NMS) with Sørensen distance and the 'slow and thorough' autopilot option in the programme PC-Ord (McCune & Mefford 1999) to ordinate species in sample space. The autopilot used the best of 40 runs with the real data along with 50 runs with randomized data for a Monte Carlo test of significance. Sørensen distances expressed community resemblance (McCune & Mefford 1999). The following environmental parameters were included: position in canopy (sub, middle, top), height above ground (m), tree species, diameter of twig (cm), pH (mean of three measurements), light exposure (1-3), stage of decay (1-4), and water holding capacity (ml per dry wood). In case of significant effects, the parameters were superimposed as radiating vectors on the resulting ordination. Their relative strength and direction from the centroid indicated the correlation with the ordination.

To decide, if empty samples characterize a combination of environmental parameters unsuitable for MMLO and their deletion would have an effect on the NMS, we performed a second NMS of all samples in sample space. We hypothesized that if the empty samples group together or are located far away from the majority of samples then removing them could have an effect on the ordination of species in sample space because they were characterized by a unique set of environmental parameters that affect the occurrence of MMLO negatively. Otherwise, if those samples can not be distinguished from the majority of samples, the lack of MMLO on this twigs occurred most probably by chance and their removal would not affect the first ordination. Additionally, a DCA (26 segments) with the same settings was carried out.

For statistical analyses of the data set obtained from moist chamber cultures, weighted abundances were calculated by dividing the absolute number of sporocarps recorded in a particular sample by the mean value for all cultures yielding this species (Schnittler 2001a). This measure was used since it equalizes the very different fructification numbers of the species (for a *Stemonitis*, 50 sporocarps were still a small fruiting colony, but for a *Perichaena* this would represent a rather large fruiting colony). However, weighted abundances performed poorly with NMS and Sørensen distances (maximum 30% of cumulative explained variance for the first three axes) compared to presence-absence matrices transformed by the Beals smoothing function (McCune 1994, 77% explained variance). We thus decided to use only data transformed with Beals smoothing to display community relationships and environmental variables. Our choice agreed with the results of Ewald (2002) as Beals smoothing enhanced the ability to see and interpret patterns of species richness in environmental space because it reduced the number of zero occurrences in the data set and improved the detection of compositional gradients.

The successional sequence of the more common species was calculated as the proportional increase in sporocarp numbers on each of the six control days. These proportions were weighted with the total sporocarp number a species produced in all cultures (thus the sum of all six increases is equal to one).

Spore productivity and dispersal

Potential spore productivity was calculated as following for some common myxomycete species: First, spore numbers per sporocarp were counted in a Abbe-Zeiss counting cell chamber by dissolving one entire sporocarp in 0.1 ml 30% alcohol (to counter the effects of spore hydrophobicity).This was carried out with 5 average-sized sporocarps, and for each sporocarp 32 fields of the cell chamber were counted. Second, spore productivity per culture was calculated by multiplying the mean

number of spores per sporocarp with the number of sporocarps recorded in a culture.

Spore diameter was measured under the light microscope with oil immersion via the ocular micrometer.

The terminal fall velocity of spores was measured in a glass cylinder 0.5 m tall and 11 mm inner diameter with openings on both sites, where in darkened room without any airflow (windows sealed) as few as possible spores were released from sporocarps by gentle touching them with a needle. Using a cold-light source (LED), the spore cloud was traced. The time required for a small spore cloud to pass a distance of 5 cm (*Stemonites fusca* var. *rufescens*) or 10 cm (*Perichaena depressa*) was used as estimate for the fall velocity. Only very small clouds in the central section of the glass cylinder were measured. The mean of 30 measurements per species was used as an estimate.

Following the assumption that MMLO can reach a decaying twig only via air-borne spores dispersed at random by wind (which leaves out animal vectors at this point), but one spore hit can establish a population, the minimum spore fallout necessary to explain the frequencies observed was calculated. To simulate this, we wrote a programme which sets up as many slots (defined by a range of numbers between 0 and 1) as we have samples (here: 146); with the first slot defined as the range 0 to 1/146, the second 1/146 to 2/146, and so on. We than simulated spore fall by generating random numbers between 0 and 1 and counted the number of slots hit at least once. This procedure stopped at the moment were as many slots had been filled as recorded positive for a certain species; and the number of repeats would give an estimate for the number of likely spore hits to explain the frequency of this species. Since this is a kind of Monte-Carlo procedure, we here present the mean of 1000 runs of the program.

RESULTS

From the 146 cultured samples of dead aerial wood, 137 (94%) were positive for MMLO (including unidentified myxomycete plasmodia), giving a total of 386 records (90 unidentified myxomycete plasmodia, 12 myxobacteria, 9 protostelids, 268 myxomycetes, and 7 records of *Sorogena*). Of these, 286 could be identified to species; representing 37 taxa in total (Tab. 1). Nine of these (and four additional taxa) were found as well in the field during sampling. Vouchers (189 specimens) of this survey are deposited at the Botanical State Collection, Munich (M); label information will be made available via internet, using the GBIF portal.

Species richness and development time

For all moist chamber cultures performed, a species accumulation curve was constructed (Fig. 1) using the 137 samples positive for MMLO. The number of species to be expected is 43.7 ± 0.2 according a hyperbolic curve fit, 42.3 ± 4.4 with the Chao 1 estimator, and 44.9 ± 2.7 with the Jacknife 1 estimator. The Shannon diversity value for the community is 2.90. All species recorded at least five times are arranged according to their successional sequence (Fig. 2).

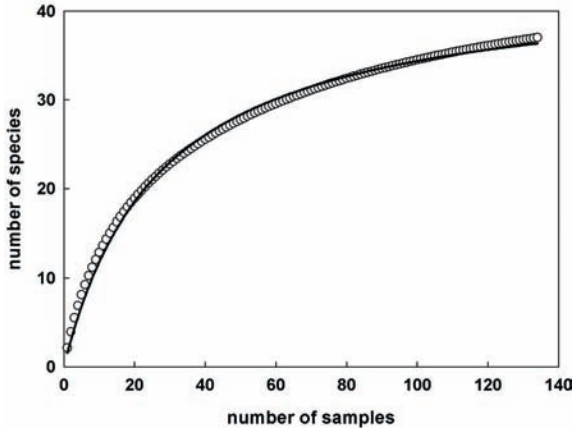

Fig. 1: Species accumulation curve for myxomycetes and myxomycete-like organisms from thin dead branches of the outer canopy, 146 twigs cultivated. The hyperbola shown represents the best fit according to the equation y = 43.7x / (27.1 + x), R = 0.998.

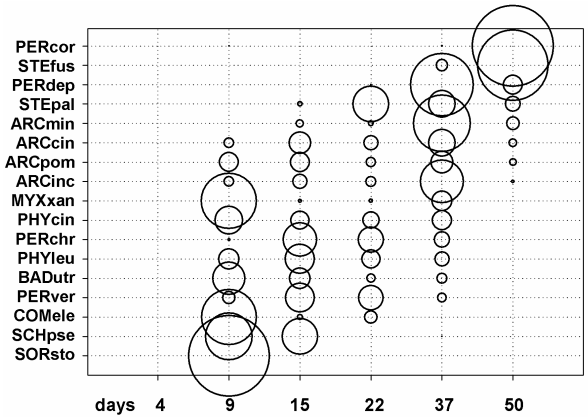

Fig. 2: Successional sequence of the more common MMLO in moist chamber cultures.

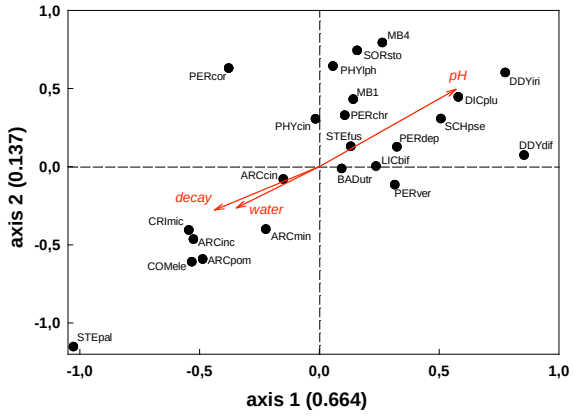

Fig. 3: Ordination of species in sample space with environmental variables overlaid as joint plot, using NMS.

Table 1: List of myxomycetes and myxomycete-like organisms found in the canopy of the study plot. Nomenclature refers to Lado (2001) for myxomycetes, Reichenbach (1993) for myxobacteria and Spiegel (2003) for protostelids. Species with a '?' could not be identified with certainty since they were represented by only scanty and/or mal developed specimens. For the 23 more common taxa, mean values for stage of decay and pH are given. Asterisks indicate species with a mean pH differing significantly (* $p < 0.05$, ** $p < 0.001$) from the mean of all samples (non-transformed pH values, Mann-Whitney Rank Sum Test).

species	abbr.[6]	records[7]	mean pH[8]	mean decay[9]
Myxobacteriales				
Mellitangium lichenicola Beebe 1941	MB1	-/3	6.02	2.0
Myxococcus xanthus s.l. (Thaxter 1892) McCurdy 1971	MB4	-/9	6.18	2.3
Protosteliales				
Ceratiomyxa fruticulosa (Mull.) T. Macbr.		1/1		
Schizoplasmodiopsis pseudoendospora Olive, Martin & Stoianovitch	SCHpse	-/9	6.45*	1.9
Myxomycetes				
Arcyria cinerea (Bull.) Pers.	ARCcin	-/47	5.77	2.5
Arcyria incarnata (Pers.) Pers.	ARCinc	2/10	5.55*	2.8
Arcyria insignis Kalchbr. & Cooke		-/2		
Arcyria minuta Buchet	ARCmin	-/9	5.22*	2.6
Arcyria pomiformis (Leers) Rostaf.	ARCpom	2/10	4.96**	3.1
Arcyodes incarnata (Alb. & Schwein.) Cooke		-/1		
Badhamia utricularis (Bull.) Berk.	BADutr	4/11	5.77	2.9
Badhamia affinis Rostaf.		1/-		
Badhamia panicea (Fr.) Rostaf.		4/-		
Badhamia populina Lister & G. Lister		1/-		
Comatricha elegans (Racib.) G. Lister	COMele	-/5	4.87*	3.0
Comatricha laxa Rostaf.		-/1		
Comatricha ? nigra (Pers. ex J.F. Gmel.) Schroet.		-/1		
Cribraria microcarpa (Schrad.) Pers.		-/1		

to be continued on the next page

Table 1: continued

species	abbr.[6]	records[7]	mean pH[8]	mean decay[9]
Myxomycetes				
Didymium anellus Morgan		-/1		
Didymium difforme (Pers.) S.F. Gray	DDYdif	-/3	6.58	1.8
Didymium iridis (Ditmar) Fr.	DDYiri	1/3	6.65	1.7
Dictydiaethalium plumbeum (Schum.) Rostaf.	DICplu	-/4	6.40	1.6
Echinostelium minutum de Bary		1/2		
Enerthenema papillatum (Pers.) Rostaf.		1/-		
Fuligo septica (L.) F.H. Wigg.		1/-		
Licea biforis Morgan	LICbif	-/3	6.50	2.2
Licea kleistobolus G.W. Martin		-/2		
Licea operculata (Wingate) G.W. Martin		-/1		
Perichaena chrysosperma (Currey) Lister	PERchr	-/18	6.17	2.5
Perichaena corticalis (Batsch) Rostaf.	PERcor	-/5	6.15	3.0
Perichaena depressa Libert	PERdep	-/42	6.22*	2.3
Perichaena vermicularis (Schwein.) Rostaf.	PERver	-/16	6.44*	2.3
Physarum cinereum (Batsch) Pers.	PHYcon	-/3	5.74	2.8
Physarum compressum Alb. & Schwein.		-/2		
Physarum decipiens M.A. Curtis		-/2		
Physarum didermoides (Pers.) Rostaf.		1/2		
Physarum leucophaeum Fr.	PHYlph	-/12	6.22	2.4
Physarum nutans Pers.		2/1		
Stemonitis axifera (Bull.) T. Macbr.		-/1		
Stemonitis fusca var. *rufescens* Roth	STEfus	1/19	6.12	2.5
Stemonitis pallida Wingate	STEpal	-/9	4.66**	3.2
Ciliata				
Sorogena stoianovitchae Bradbury & Olive	SORsto	-/7	6.57*	2.3

[6] Only for the more common species included in statistical analyses.
[7] Field collections / collections from moist chamber culture.
[8] Mean of three measurements, only for records from moist chamber cultures.
[9] Mean stage of decay according to a scale from 1 to 4.

Species preferences

All cultured samples of wood originated from dead twigs between 4.5 and 0.9 cm diameter (mean 2.1 ± 0.06 cm), collected between 10.0 and 31.5 m height (mean 22.1 ± 0.5 m), with a mean pH value of 5.80 ± 0.07 and a mean stage of decay of 2.53 ± 0.07. The mean pH values of the samples from the eight trees did not differ significantly from one another (one way ANOVA, pairwise multiple comparison, Holm-Sidak method, $p = 0.05$), except for the more acidic wood of *Quercus* (mean pH 4.67 ± 0.13, all combinations different), and the more basic wood of *Acer* (mean pH 6.58 ± 0.09, all combinations except for those with *Populus* different). The joint NMS plot with 0.1 of r-square cutoff displayed three of eight possible environmental factors, pH value, water retention and stage of decay (Fig. 3). The opposite direction of the vectors indicated that pH value was negatively correlated with stage of decay. Indeed, in the course of wood decay the pH seems to decrease from 6.30 ± 0.21 ($n = 8$) at stage 1 to 5.09 ± 0.21 ($n = 11$) at stage 4 (pH *vs* decay, Pearson's product moment: $r = -0.38$, $p < 0.01$), whereas water holding capacity increases from 1.45 ± 0.25 ml per g dry wood at stage 1 to 4.51 ± 0.27 at stage 4 (water holding capacity vs decay, Pearson's product moment: $r = -0.59$, $p < 0.01$). Other factors such as

height, canopy layer and exposure to light had no significant influence on the occurrence of MMLO. Preferences for pH vary among taxonomic groups of MMLO: from the more common species with a mean pH significantly different from the average of all cultivated substrates, most species of *Arcyria*, *Comatricha elegans* and *Stemonitis pallida* displayed a preference for more acidic substrates. However, species of *Perichaena* but also *Sorogena* and the protostelid *Schizoplasmodiopsis* inhabited more basic substrates (Tab. 1).

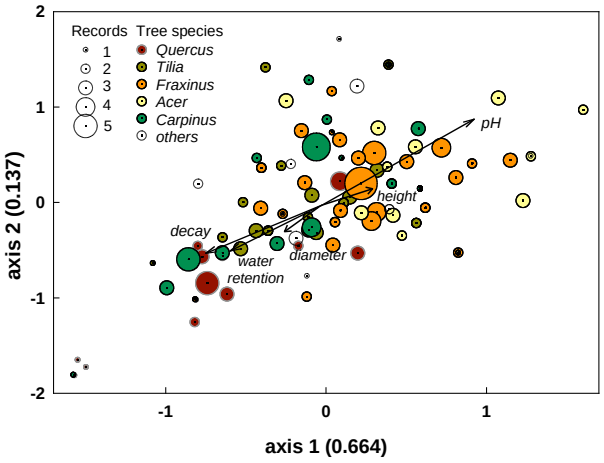

Fig. 4: NMS biplot of samples in species' space. Common tree species are indicated by colored circles. The size of the symbols is proportional to the number of records of the culture, their position is defined by the sample scores.

No clear host specificities of the organisms could be detected; the scores of the samples are rather randomly arranged in species' space (Fig. 4.). Even if the pH value tends to decrease, most substrata seem to become more suitable for MMLO in progressive stages of decays. This is underpinned by quite similar values for the mean number of records per sample as well as their Shannon diversity indices: (*Acer*: 1.59 records; $\acute{H} = 2.39$; *Carpinus*: 2.28; 2.58; *Fraxinus*: 2.29, 2.51; *Quercus*: 1.94; 1.95 and *Tilia*: 1.94, 2.07). From all of the common trees, only *Acer* seems to be a less suitable substrate; it has a lower average number of records per sample, and half of the 12 samples not yielding any fructification of MMLO came from this tree. If the common species of MMLO were analyzed separately for host preferences, only *Stemonitis pallida* exhibited a preference for wood of *Quercus* (not shown).

The analysis of samples according to environmental parameters revealed the samples negative for the occurrence of MMLO to be widely spaced over the plot (Fig. 5).

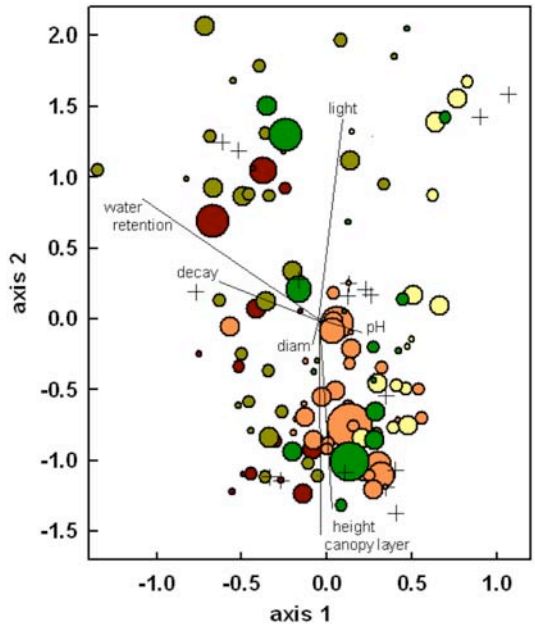

Fig. 5: NMS biplot of samples in environmental space. Common tree species are indicated by colored circles. The size of the symbols is proportional to the number of records of the culture, their position is defined by the sample scores. Crosshairs indicate samples with no or only rare species excluded from figures 3 and 4.

Interestingly, environmental parameters differed in their importance for the ordination of samples according to species (Fig. 4) and environmetal parameters (Fig. 5). Whereas pH values and the stage of decay explained less variation in samples, those factors were most important explaining variation in species' occurrence.

Spore productivity and dispersal

As calculated by the simulation program under the assumption that one spore can establish a population, for *Arcyria cinerea* (47 records) and *Perichaena depressa* (42 records) as the most common species, 57.9 ± 0.11 and 50.8 ± 0.10 spore

hits on the sampled 146 twigs, respectively, would be needed to explain the observed frequencies.

This translates to an average fallout of 0.4 and 0.35 spores per twig. If the two species are assumed to be heterothallic (two compatible spores are necessary to found a population, even-handed ratio of two mating types), these numbers increase to 200.7 ± 1.30 and 186.3 ± 1.31, respectively; or an average fallout of 1.4 and 1.3 spores per twig.

Spore numbers of 9.99 ± 0.49 x 10^5 spores per sporocarp (1599 spores from 32 fields of each 0.001 mm^3 volume counted) were calculated for *Arcyria cinerea*, but only 1.24 ± 0.07 x 10^5 spores per sporocarp for *Perichaena depressa* (796 spores from 32 fields of each 0.004 mm^3 volume counted). The total of 838 sporocarps obtained for *A. cinerea* in our cultures equals 8.37 x 10^8 spores (or an average of 17.8 million per occupied twig). For the *Perichaena* (3093 sporocarps obtained) the respective number is 3.85 x 10^8 spores (or an average of 9.2 million per occupied twig). As a random spore rain on the 1.6 ha crane plot, this amount of spores would result in 5.2 (*Arcyria*) and 2.4 (*Perichaena*) spores per cm^2, respectively.

Estimating the average upper surface of one of the sampled 5 cm long twig sections (mean diameter 2.1 cm) as 0.5*Π*2.1 cm*5 cm with 16.5 cm^2, the productivity of the twigs in culture would be sufficient for a spore fallout of 86 and 40 spores per occupied twig.

For two species, *Stemonitis fusca* var. *rufescens* and *Perichaena depressa*, the terminal fall velocity of spores was measured, resulting in 0.13 ± 0.028 cm / sec for the spores of the first species (diameter 7.52 ± 0.59 μm, 25 spores measured) and 0.19 ± 0.033 cm / sec for *Perichaena* (spores 11.2 ± 0.77 μm in diam.).

DISCUSSION

Studies of the diversity and ecological impacts of microorganisms, especially of fungal organisms, in forest canopies are quite rare (Lodge & Cantrell 1995, Keller *et al.* 2004, Snell & Keller 2003, Unterseher *et al.*, 2005, McCune *et al.* 2000). In the recent edition of 'Forest Canopies', a benchmark of canopy research (Lowman & Rinker 2004), only nine pages or less than 2% of the whole book mention facts relating to fungal activity in the forest roof (Fonte & Schowalter 2004).

Species richness and development time

Only one clearly delimited microhabitat was investigated in this study: wood of dead twigs attached to their still living parts, forming ïslandsïn the canopy. In spite the relative homogeneity of this substrate, a rather species-rich assemblage of MMLO was found. *Sorogena stoianovitchae* was recorded as new for Europe. The output of three statistical models to predict the total number of species varied between 42 and 45, compared with 37 species found in reality. Since singlets and doublets have a large influence on all three models, we thus conclude that our sampling is at least sufficient to recover all of the more common species.

However, such an estimate is only valid for those taxa that occur readily in the moist chamber method applied. The rather low overlap between myxomycete species found in the field and in cultures stems from the fact, that due to limited time on the crane no regular survey was carried out; we collected only those species forming fructifications conspicuous enough to be seen from some distance. Only 24% of all myxomycete taxa detected in moist chamber cultures were found as well in the field, but 44% of all species found in the field appeared also in the cultures. Except for dictyostelids and acrasids, four of the six groups of MMLO have been recorded. Since agar cultures have not been carried out in this study, dictyostelids were not recorded; and protostelids were certainly underrepresented.

Judging from development times recorded in this study, typical life cycles of canopy MMLO seem to require between one and five weeks, with a tendency that small and stalked, more simple fructifications develop faster than complex, sessile ones with durable peridia. *Sorogena* develops very rapidly, indicating that fructifications form as the result of an aggregation process within already existing but dormant ciliate populations. Among myxomycetes, most common species belong to the Trichales, members of which are characterized by phaneroplasmodia, and fruit late during the successional sequence. The same holds true for the aphaneroplasmodia of *Stemonitis*, which seem to

be able to live in rather dry wood and appear only if the cultures have almost dried out.

Species richness of lignicolous canopy myxomycetes (this study: 32 species from 146 cultures) seems to be comparable with that of corticolous canopy myxomycetes recorded by Snell & Keller (2003) from the Great Smoky Mountains (48 species from over 418 cultures).

Species preferences

In contrast to microhabitats of epiphytic organisms, the investigated small dead branches are sheltered by the almost intact bark which is likely to buffer the influence of many abiotic factors such as radiation or water regime. This may explain why only pH, water retention and stage of decay had a significant influence on the species composition (Fig. 4), although samples differed more strongly in respect to light, height and canopy position (Fig. 5). These three variables are correlated, with pH decreasing and water holding capacity increasing with the progression of decay. However, abiotic factors like light exposition were estimated at a rather rough scale, which might have been blurred its influence.

As indicated by the mostly insignificant differences in pH values between tree species, pH seems to be determined more by the assemblage of fungi, bacteria and MMLO causing twig decay than the tree species itself. Eventually, initial differences in pH among the woods of various tree species may be decreased with ongoing decay (Fig. 5). For this reason, it is not surprising that with one exception (*Stemonitis pallida*) all MMLO showed no clear association with any host tree. *Arcyria cinerea* and *Perichaena depressa*, for instance, occurred on all sampled tree species. As indicated by the position of samples (not shown), the apparent specificity of *S. pallida* for *Quercus robur* was due to the more acidic, heavily decayed branches from oak trees. Therefore, decaying wood as a substrate seems to be much more uniform among tree species than bark, where Härkönen *et al.* (2004) found clear host preferences of corticolous myxomycetes between seven investigated tree species in Chinese plantations. By decorticating the sampled wood, bark-inhabiting myxomycetes have been mostly excluded from the present survey. The low host specifity of lignicolous MMLO as "followers" of a fungal succession is in contrast to the much higher host specifities of the fungi themselves as recorded by Unterseher *et al.* (2005). These relations are reflected by the similar figures for productivities (average records per sample) and diversity (Shannon-index) of the main tree species. Furthermore, ordinations carried out separately for each of the four most common tree species (*Acer*, *Fraxinus*, *Quercus*, and *Tilia*, not shown) resulted in similar arrangements of the main environmental factors (pH, water retention, stage of decay, height).

Although MMLO were surprisingly common judged by the applied"blind" sampling; twelve samples had no MMLO, and further seven had only rare species. The exclusion of these samples from the NMS performed according to species scores seemed not to have altered significantly the picture (Fig. 3), since those samples are rather at random distributed when seen in sample space (Fig. 5). It thus seems that accessibility of the habitats is often more limiting for abundances of MMLO than the environmental conditions of the dead twigs investigated. This may be explained by the mostly intact bark of the dead twigs, which seem to hold water over long periods of time. After a period of rainfall, decayed branches seem to act as a sponge absorbing water flowing down, as indicated by their high average water holding capacity (2.79 ± 0.12 ml water per g dry wood, $n = 145$). If dead branches were still surrounded by fully intact pieces of bark as it was often the case, water could be retained for many days. When the sun heated the substrate over the day, conditions very similar to those in moist chamber cultures may develop. This may be the reason for the occurrence of *Arcyria insignis*, a species more common in the Tropics. On the other hand, in winter snow caps on branches could persist for several weeks, keeping humidity in the branches (personal observation). Except for cold spells were they survive as sclerotia, these conditions may support plasmodia almost the year around.

Spore productivity and dispersal

The uniformity of the substrate may be one reason for the unexpected high frequency of some myxomycetes in the decaying twigs. Since they are always attached to living parts of the tree, each

twig forms a "habitat island" of its own in the canopy since in temperate zones vegetative stages of lignicolous MMLO are hardly able to travel between dead twigs of a tree on different living branches. Excluding the (poorly known) activities of animals acting as vectors, a twig can be reached only by air-borne spores, and for non-heterothallic species one spore may be sufficient to establish a population.

The potential spore productivity seems to be sufficient to maintain the observed frequencies. For *Arcyria cinerea*, a minimum average spore fallout of 0.4 spores per occupied twig (or 1.4 in the case of heterothally) needed to explain the observed frequency. There are two underlying assumptions: (i) random dispersal of airborne spores and (ii) all twigs are suitable for growth of the organism. A targeted dispersal of spores (i.e. by insects carrying spores from twig to twig) would lower this estimate. In contrast, of only a fraction of twigs are suitable habitat, the estimate would be higher, since the probability to hit a pre-defined suite of twigs with a certain amount of random spore hits is always lower than for a fraction only. As calculated from our cultures, for *A. cinerea* the potential maximum productivity would create a spore rain equalling 86 spores per twig section (2 x 5 cm) if evenly dispersed. This figure is about 200 times larger than the estimate for minimum spore fallout. Even if the conditions in our cultures are hardly to be realized in nature, the amount of decayed canopy wood available in the plot is at least 1000 times larger than that used for our cultures.

As such, it seems quite realistic that all or most of the species detected in culture will fruit in the field as well, which is supported by the fact 24% of all species of MMLO detected in cultures were found fruiting in even without a systematic survey. All together, our estimates point towards a rather effective dispersal of airborne spores. This seems to be confirmed by the very slow fall of the spores. With the measured speed of ca. 0.16 cm / sec, a spore theoretically needs about 5 h to fall from 30 m height in the canopy to the ground, and even a very slight horizontal breeze of 0.1 m / sec would cause this spore to drift about 1.8 km away. A storm (100 km / h or about 28 m / sec) would result in a theoretical drift of about 500 km. These rough estimates (thermics are still not considered) would make it appear quite conceivable that spores can reach every point in the canopy over the duration of a growing season (six months).

In contrast to tropical regions with many species occurring almost exclusively in the canopy, most of the MMLO detected during this study may fruit as well on logs of the ground. Installing aerial spore traps in the canopy would be necessary to assess the real dispersal abilities of canopy MMLO. Using artificially introduced spores of taxa not occurring in a plot being studied as a tracer, it could be determined if the canopy populations function rather as a source or a sink compared to populations of the same species on ground. Mainly unexplored and not considered here is the possibility of spore dispersal via animal vectors, such as wood-inhabiting insects. Since these organisms are attracted by substrates of the same kind, abilities for MMLO to disperse successfully could be even higher than suggested by the data obtained in this study.

ACKNOWLEDGEMENTS

We are grateful for technical assistance provided by A. Lübke as well as for the help of several students with collecting and boxing specimens. Funding for the field component of this study was provided through projects UFZ-16/2000 and UFZ-04/2004 from the Centre for Environmental Research Leipzig-Halle in the Helmholtz Association, Germany. Additional funding for the lab component came from a grant of the US National Science Foundation project DEB-0316284 "PBI: Global Biodiversity of Eumycetozoans". For valable comments we wish to thank the associate editor and two unknown reviewers.

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Diversity of lignicolous fungi in the canopy of a deciduous forest in Leipzig, Germany

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What's up? The Newsletter of the International Canopy Network **10 (2)**, 4–5, (2004).

Diversity of lignicolous fungi in the canopy of a deciduous forest in Leipzig, Germany

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INTRODUCTION

Fungi are important parts of almost every ecosystem, especially of forest soils. However, ecological investigations have largely ignored them as important members of the canopy. The few studies that have been conducted are mostly shortterm projects, focusing on the understory or studies in tropical forests (e.g. Boddy 1992, Hedger *et al.* 1993, Nuñez 1996). To fill this gap, we started a long-term project on the diversity and ecology of wood-inhabiting fungi in the canopy of a mixed deciduous forest in Leipzig (Central-east Germany). The study is part of the Leipzig Canopy Crane Project (Morawetz & Horchler 2002).

As with poroid and corticioid fungi, Pyrenomycetes are well-known wood dwellers of dry, exposed habitats. Different systematic groups of Discomycetes (Leotiales s.l.) also prefer such conditions (Sherwood 1981). Our studies focus on diversity patterns, substrate preferences and community structures of lignicolous fungi on trees between heights of 10-34 m.

METHODS

Dead wood of 30 individual trees (mainly ash [*Fraxinus excelsior*], oak [*Quercus robur*] and lime [*Tilia cordata*]) was collected in autumn 2002 and spring 2003. Twigs and branches were collected with a maximal diameter of 6 cm and a maximum length of 1 m. We tried to get the same quantities from sub- (10-18 m), middle (18-26 m) and upper canopy (26-34 m). To allow fructification of established mycelia and further growth of fruit body initials, the samples were stored for two weeks in high humidity. Only teleomorphic species (fungi with meiotic spores) and anamorphs (fungi with asexually produced spores [conidia]) that grew in deeper layers of bark and wood were tallied.

RESULTS AND DISCUSSION

A total of 85 species of 62 genera were identified. As expected, many of the fungi had xerotolerant or xeroresistant fruiting bodies. Fruiting bodies of lignicolous agarics were almost completely absent in the canopy. A total of 40 species (47%) were singletons. Some frequently found species had been rarely recorded in Germany. Further studies will surely increase the number of species because: (a) many specimens could not be identified due to poor stages of development; (b) many species form tiny and short-lived fruiting bodies that are easily overlooked, and (c) many fungi fructificate only sporadically and under certain climatic conditions. We found 13 species on *F. excelsior*, 21 on *Q. robur*, and 37 on *T. cordata*. Possible reasons for this variability are different antimicrobial defences in the bark and wood of the trees (Pearce 1996) and different morphological-anatomical characteristics (lime wood is soft oak and ash wood compact and hard).

In the canopy, fungi must be adapted to the severe climatic conditions to successfully complete their life cycle. Such adaptations occur especially in species that were found mostly in the upper canopy. Species with slow fruiting body develop-

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ment (over a period of weeks or even months) must be able to dry out without damage or to prevent complete desiccation (Bewley 1979). Characteristic representatives are the Pyrenomycetes; the three most abundant pyrenoid species were represented with 40.5% in the upper canopy. Their abundance decreased to 13.5% in the middle and 6% in the lowest canopy stratum. In the upper canopy, xerotolerance seemed to be more important than the speed of development, whereas the slow growth rate of Pyrenomycetes is probably detrimental in lower and more humid areas that are less exposed to solar radiation.

Figure 1 shows how difficult the investigation of the ecology of lignicolous fungi in the canopy can be.

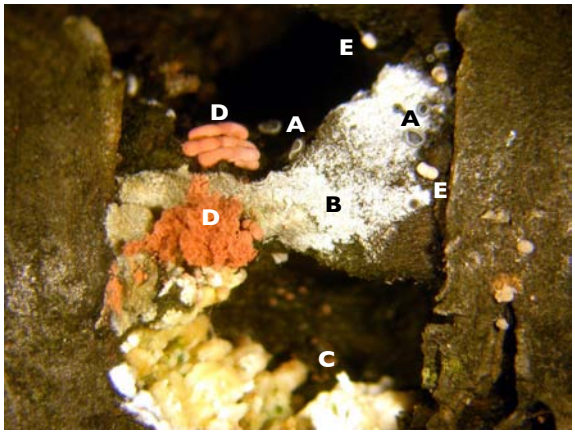

Fig. 1: Cryptogamic species in a micorenvironment of a *Cerasus avium* branch.

The image covers about 5 cm^2 of a weathered branch of a cherry tree (*Cerasus avium*). The bark on the left and on the right is still attached to the branch, and two cavities are present in the decorticated, heavily decayed area in the middle. Altogether, 5 different fungi and slime molds (Myxomycetes) can be identified: *Mollisia* sp. (A), an ascomycete, on *Hyphoderma setigerum* (B), a basidiomycete, and on wood deeper inside the gap. A second *Hyphoderma* species, *H. radula* (C) grows in close vicinity. The 2 slime mold species are *Arcyria incarnata* (D) and *Arcyria cinerea* (E) in the background.

The following overview of some strategies to survive in the canopy shows the diversity of possible interactions and adaptations.

- Fungi such as *Resupinatus trichotis* are facultative nematophages. They gain advantage over other fungi by using small invertebrates as optional food resources.
- Many genera (e.g. *Orbilia*, *Mollisia*, or *Episphaeria*) grow and fructificate on algae layers, old fruiting bodies of other fungi, or partly dried plasmodials of slime molds. In such organic matter, humidity prevails longer than on the surface of naked wood.
- Unlike agaric fungi whose fruit bodies grow upright (negative geotropism) and would rapidly desiccate in the windy and dry canopy very rapidly, fungi of the families Corticiaceae, Hymenochaetaceae, Stereaceae or Polyporaceae grow mostly underneath horizontal and oblique branches and are closely attached to the substrate (Fig. 2). Therefore they escape harmful UV radiation and rapid desiccation. They are able to use humidity efficiently.

Fig. 2: Fruit body of a corticioid fungi growing on the lower half of a hanging *Quercus robur* branch.

- Cyphelloid fungi, minute plate- or cup-shaped basidiomycetes are plastic. Under humid conditions, their fruit bodies emerge

quickly on the upper side of branches. However, they can survive arid periods by taking a spheroidal shape when their tissues dry up, thus enclosing the fertile, damageable structures of the hymenium and protecting them against complete desiccation.

The drastic decline of species richness from 58 in the middle canopy to 24 in the upper layer can be explained by more uniform and extreme thermal and hygric conditions. The greatest spectrum of microhabitats can be found in the middle canopy that also contains the most diverse mycota because (a) open sunny areas lie next to shaded zones and (b) thin twigs exist next to strong, thick branches with fissures and holes in the wood.

CONCLUSION

Our preliminary results showed that fungi are remarkably diverse in the upper regions of the forest, and that they may play an important role in the complex ecology of the canopy. In tropical forests, fungi probably increase overall plant diversity by causing heavy damage to hosts, which leads to rapid turnover rates. This cannot be explained solely by soils or direct effects of climates This mechanism might also exist as well in temperate forests. We conclude that mycological research should be an essential part of canopy projects in the future.

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Hyla, high!

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What's up? The Newsletter of the International Canopy Network **9 (2)**, 1, (2003).

Hyla, high!

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Fig. 1: *Hyla arborea* sitting on a leaf of a Sycamore crown at ca. 22 m height.

SHORT COMMUNICATION

Since the Leipzig Canopy Crane Project (see What's Up? Vol. 7 No. 3 Spring 2001) began in 2001, we have made some exciting observations that will contribute to our long-term interdisciplinary research projects (Morawetz & Horchler 2002).

After a strong decline of the amphibian fauna between 1950-1985, we are observing a slow but steady recovery of amphibian populations (Grosse 2001).

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This is due to improved water quality and controlled inundations of some forest areas.

We found snail species (*Arianta arbustorum* and *Cepea* sp.) foraging on mosses in the upper canopy. We observed Blue Tit birds (*Parus caeruleus*) seeking prey in flowers of the European Ash (*Fraxinus excelsior*) trees, hence acting as potential pollinators for this typically wind-pollinated tree species. Another 'unusual' potential pollinator is the squirrel (*Sciurus vulgaris*), which were observed licking nectar from flowers of the Norway Maple (*Acer platanoides*).

The most interesting discovery we have made is the first proof (in Germany) of the Greenback frog (*Hyla arborea* L.) in the forest canopy. Although its name indicates an arboreal lifestyle, it has never been collected at such a height. We detected the frogs during our regular inspection of traps installed in branches in the canopy to catch crawling arthropods. Four dead individuals were found in traps of two lime trees (*Tilia cordata*) on 5 June and 1 August 2002. The traps were located at 18.6 m, 22.4 m, 25.4 m, and 27.2 m above ground. The animals encountered were three juveniles (25 mm, 26 mm, and 28 mm long) and one adult (38 mm long). Two adult greenbacks have been observed at ca. 22 m height in the upper exterior part of a Sycamore (*Acer pseudoplatanus*) crown located at the edge of an old gap. One of the animals has been regularly observed sitting at the same place over a longer period (10 September to 25 October 2002) (Fig. 1).

Adhesive discs on their toes enable the frogs to climb up and sit in sunny hedges and shrubs at the edge of forests or near water during summer. Average sitting sites are 1-3 m above ground (Grosse 1998). Bioacoustic methods (Bitz *et al.* 1996) have documented that greenbacks are able to climb higher than that to reach the canopy. Until now, direct evidence was missing because the cryptic frogs elude direct observation beyond 2 m above the ground. It was supposed that mainly adult frogs climb up to the treetops (Bitz *et al.* 1996). However, half of the animals we found were juveniles. The total number of registrations is low; the phenomenon will be studied in more detail in the future.

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High above – sitting sites of the tree frog (*Hyla arborea* L.) in tree crowns of the Leipzig floodplain forest

Carsten Schmidt, Martin Unterseher & Wolf-Rüdiger Grosse

elaphe **11 (2)**, 43–45, (2003).

High above – sitting sites of the tree frog (*Hyla arborea* L.) in tree crowns of the Leipzig floodplain forest

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An interdisciplinary study to investigate the ecosystem 'forest' was launched in the nature reserve "Burgaue" in June 2001 (Morawetz & Horchler 2002). Spatio-temporal patterns of biodiversity and ecological interactions are studied within the Leipzig Canopy Crane Project (LAK) with a construction tower crane allowing access to the canopy region (Fig. 1). LAK is financed and conducted by the University of Leipzig, the Centre for Environmental Research Leipzig-Halle (UFZ) and the City of Leipzig.

Fig. 1: The canopy crane in the Leipzig floodplain forest.

To study the diversity of arthropods, 48 branch eclectors were installed on 12 individual trees (four each of *Quercus robur, Fraxinus excelsior*, and *Tilia cordata*). Four traps were mounted on every tree and remained there during the period 02/05/2002 – 06/11/2002. The intent has been to catch arthropods dwelling on branches. The eclectors were prepared with diethylenglycol and were located between 16.2 and 30.6 metres in height. Volatile attractants have not been used.

While emptying the traps four tree frogs (*Hyla arborea*) were found inside the eclectors on the 05/06/2002 and 01/08/2002. The traps were installed in heights of 18.6 m, 22.4 m, 25.4 m and 27.2 m. The frogs were about three one-year old animals (25 mm, 26 mm, 28 mm) and one two-year old female (38 mm). All measures were done after conservation in 80% ethanol. The age determination was carried out with sceletochronology of the right femur (Grosse 1999).

Two adults dwelling in about 22 m in height could be further observed. They were sitting on a *Acer pseudoplatanus* tree, in the outer, west-exposed canopy at the edge of an old tree-fall gap (Fig. 2). One of the animals remained constantly at the same locality for a longer period of time (10/09/02 – 25/10/02). Calls from the canopy could be heared repeatedly between August and the end of September.

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Fig. 2: *Hyla arborea* sitting on a leaf of *Acer pseudoplatanus* in about 22 m in height.

The tree frogs in the floodplain forest seem to recover step by step after a strong decline between 1950 and 1985 (Grosse 2001). This is due to an enhancement of the water quality in the region as well as the controled floodings in the north-western "Elster-Luppe" area. These conservation tasks resulted in the return of tree frogs evem towards the City of Leipzig (Grosse 2001).

Tree frogs prefer sitting in sunny hedges and shrubs on forest edges and in the vicinity of water. Sitting sites in one to three meters in height are mentioned in literature (Grosse 1998). It could be proved for a long time with bio-acoustic methods that tree frogs are able to clamber large heights, thanks to their adhering discs on the toes (Bitz *et al.* 1996). Up to now, direct evidence was missing since the animals are hardly to be seen above two metres in height. The recent findings document without doubt that tree frogs do climb trees and sojourn there.

So far, it was assumed that mostly adult frogs climb trees (Bitz *et al.* 1996, Grosse 1998). Our observations yielded the evidence that juveniles also dwell in the forest canopy. Yet, we have found more juveniles than adults in the trees. However, it has to be considered that the total number of individuals is very low and not sufficient enough to make unambiguous statements on the ecology of *Hyla arborea* in the canopy of the Leipzig floodplain forest.

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Summary

Summary

The present dissertation shows approaches to assess the biodiversity of wood decay fungi and fungus-like organisms such as slime molds (myxomycetes) and sporocarp-forming ciliates, which occur above ten metres in height on dead twigs and branches still attached to living trees. The use of a construction tower crane for research purposes enabled precise and continuous observations and measurements in the three dimensional canopy space of a temperate, mixed deciduous forest in Leipzig, Germany. The studies *in situ* were combined with cultivation techniques in the laboratory. The detailed disclosure of cryptogamic life in upper and outermost parts of tree crowns clearly expands the knowledge of biodiversity of fungi and fungus-like organisms on aerial substrates because comparable studies were previously restricted to the understorey and lower canopy. As mycology has been largely disregarded in the more than 20 years of intensive canopy research the present work also brings to light new aspects of canopy ecology.

The main objectives of the cumulative dissertation was to critically analyse the species richness, the host and substrate specificity, and ecological necessities of wood decay fungi and MMLO (myxomycetes and myxomycete-like organisms) in the canopy of the investigation site. Estimators of α-diversity come along with the species lists of wood decay fungi and MMLO. Ecological patterns (e.g. substrate specificity) of the organisms were evaluated using multivariate statistics such as non-metrical multidimensional scaling (NMS), cluster analysis, and Correspondence Analysis (CA) and by calculating indicator values.

The investigation site possesses a high diversity of wooden plants that doubtlessly affects the biodiversity of other organisms such as birds, small mammals or arthropods in a positive way. First ecological-faunistical studies, such as of herbivory or of the behaviour of bats provided us with additional arguments that the canopy of this temperate forest is a habitat of eminently high biological activity and diversity. Thus, the mycoflora surely benefits.

Sampling took place regularly in the years 2002 to 2004 – twice a week in spring and autumn and every two weeks during summer and winter. Six native and three introduced tree species were selected to collect dead branches that were attached to the living trees between 10 and 30 m in height: *Fraxinus excelsior*, *Quercus robur*, *Tilia cordata*, *Acer pseudoplatanus*, *Carpinus betulus*, *Prunus cerasus*, *Populus* x *canadensis*, *Quercus rubra*, and *Robinia pseudacacia*. Field data included information on stratum (sub, middle, top canopy), height above ground, tree species and individual number, substratum features (white or brown rot, stage of decay), diameter of branches, coverage with epiphytic algae, lichens, and occurrence of old fruit bodies, location of fructifications on the branch (upper side, lower side), and exposure to sun (estimated as exposed, semi exposed, and shaded).

As cultivation procedures are very important in mycological research in general and in these studies in particular, the methods are described at length. The following methods for cultivating fungi on natural woody substrates in the laboratory seemed to be suitable to initiate or promote fruitbody development and, most important, to simulate conditions in tree crowns during humid weather periods: Samples were put separately in tap water for one day to allow soaking of the wooden tissues. Afterwards they were washed under flowing water to reduce superficially adhering diaspores. The samples were stored under high humidity in open plastic boxes for two weeks to allow development of sporomes, basidiomes and ascomes from mycelia previously established in the wood, and further growth of fruiting initials. Once a day the samples were sprayed intensively with water to maintain rather high water content of the wood and high air humidity. Using this method the wooden surface could also dry up. The samples were inspected every three to four days for the occurrence of fructifications. All teleomorphic species were recorded, anamorphs were only considered if they grew in deeper layers of bark or wood. Imperfect fungi with rapidly developing, mostly superficial mycelia were deliberately excluded because they could have occurred as secondary colonisers and probably do not belong to typical wood inhabiting species of the canopy. Previous studies were used as a guideline to define stages of wood decay from stage 0 (living but obviously weak) to stage 4 (branches mostly decorticated, wooden tissue spongy).

A somewhat different protocol to observe slime mold diversity was used. From the samples of fungal studies, one branch was picked out at random and two 5-cm long pieces were removed from its ends. Apart from the environmental parameters mentioned above, the additional substrate characters water holding capacity and pH were measured. All dead twigs were assigned to four different stages of white rot decay comparable to the above mentioned (without stage 0). Even at the latest stage of decay, the bark of many twigs was more or less intact, retaining effectively moisture in the woody inner part.

Moist chamber cultures for cultivating slime molds and myxomycete-like organisms were prepared by placing pieces of air-dried, decorticated wood from the 5-cm long twig in a plastic Petri dish upon a disk of filter paper. Dishes were filled with distilled water allowed the wood to soak for 24 hours, and excess water was thoroughly poured off. Cultures were kept for two months (with closed lid) and checked six times at days 4, 9, 15, 22, 37 and 50. The number of sporocarps appearing in a culture and spore numbers per sporocarp were counted or estimated to obtain abundance measures for adjacent statistical analyses.

In the first paper, originally published in German in 2003, an introduction to the interdisciplinary LAK Project and the methods of collecting fungi in the tree tops is given. The diversity and ecological traits of the mycoflora in this particular canopy are touched

on for the first time in this dissertation. Additionally, the abundant fungus *Patellaria atrata* (Patellariales, Ascomycetes) that is rarely recorded for Germany so far, was described in detail.

A definite species list of wood decay fungi from the canopy of the LAK investigation site was published in 2005. Among the 108 species in 77 genera corticioid fungi (e.g. Corticiaceae, Stereaceae, Hymenochaetaceae) were most abundant with 37 species, pyrenomycetes were present with 18 species, and both groups clearly outnumbered other divisions of macrofungi. Agaric fungi (Agaricales and Cortinariales) were scarce. Species with minute basidiomes dominated the fungal composition of these orders. Agarics with larger sporomes were found only once and were restricted to strongly decayed branches in shaded canopy areas. This is a feature that is different from patterns of occurrence of wood decay fungi on the forest floor, where exposed "mushrooms" clearly are more diverse. In this paper the α-diversity was discussed using species-accumulation curves as a tool to estimate species richness. One important result within the framework of this study is the large number of rarely recorded species (singletons and doubletons) – 61% – that occurred despite the enormous sampling efforts. In consequence, all species-accumulation curves shown in the paper continue to rise almost linearly, which means that many more samples have to be collected before species saturation can be approached and a serious number of total species richness can be given for that particular canopy.

This result stands in contrast to the findings of the study of MMLO on dead decorticated twigs from the canopy in which 37 different taxa were isolated. Estimations of species richness showed that this particular habitat was investigated sufficiently to recover a majority of the likely species – 42 to 45 – depending on the diversity index used.

Communities of wood decay fungi showed distinct variations both in species richness and composition with respect to the tree species, height in the canopy, stage of decay, and branch diameter. Pyrenomycetes and their anamorphs (mostly Coelomycetes) dominated the mycobiota on thin, exposed twigs at great heights, indicating their ability to overcome extended periods of drought and high levels of solar irradiance. Some taxa of Tremellales (*Exidia* spp.), Orbiliales (*Hyalorbilia inflatula*, *Orbilia* spp.) or Agaricales (*Episphaeria fraxinicola*, *Cyphellopsis anomala*, *Lachnella* spp.) also exhibit features that enabled them to develop in lesser protected habitats in tree crowns.

It is worthwile to compare the substrate specificity of MMLO with that of lignicolous fungi. Wood-dwelling fungi show distinct adaptations to their host trees. In consequence the investigated tree species differed with respect to their mycota both in species number and species composition. The highest species richness and the highest density of fruit bodies was observed on *Tilia cordata*. Dead branches of *Acer pseudoplatanus* turned out to be the least populated habitats in the canopy. There was virtually no overlapping

in the species composition of fungi on *A. pseudoplatanus*, *Fraxinus excelsior*, *Quercus robur*, and *T. cordata*. Fungal indicator species could be significantly assigned to six of the nine investigated tree species. In contrast to that, no clear preferences for certain tree species could be found for MMLO. Instead, they responded to the mostly plant-independant parameters stage of decay, water holding capacity, and pH value. The only exception, the observed specificity of *Stemonitis pallida* for *Q. robur* was due to the more acidic, heavily decayed branches from oak trees.

Therefore, decaying wood as a substrate seems to be much more uniform among tree species for superficially living organisms like MMLO than for wood decay fungi where clear host preferences could be well documented. Please refer to the corresponding articles in this thesis for an exhaustive discussion of the phenomena.

In the paper "Influence of small-scale conditions on the diversity of wood decay fungi in a temperate, mixed deciduous forest canopy", climatic and structural peculiarities of the ecosystem compartment 'forest canopy' are shown, and their effect on the ecology of canopy fungi are discussed. Given that the upper canopy is widely composed of young, thin twigs, and exposed to high illumination levels, to strong winds, and heavy rainfall, fungi living in this particular habitat need adequate adaptations to the extreme weather conditions and the limited substrate availability. Contrarily, inner and lower canopy layers are formed by a broad range of thin twigs and thick branches with a patchwork of sunny and shady places that provide many different ecological niches for wood decay fungi. With respect to small-scale temperature and relative humidity, marked differences existed between forest floor and upper canopy layers that persisted on smaller scales and on different aspects of single branches (north, south, east, west). As it is dicussed in the article, the climatic features in the canopy are an important factor determining the spatio-temporal patterns of distribution of organisms dwelling in tree tops.

In the short article from the ICAN newsletter *What's up?* finally, *one* particular example of dozens or hundreds of potentially different small-scale habitats in *one* canopy is given. The description of a tiny fragment of a decayed branch from a cherry tree (*Cerasus avium*) makes us realise that it is almost impossible to reveal every single pattern of organismical behaviour in environmental sciences.

Considering that wood decay fungi and fungus-like organisms in the canopy are an inconspicuous but important component of the biota of forest ecosystems, that are also associated with other organisms such as canopy arthropods, investigation of the diversity and ecological patterns of fungi in the canopy may be crucial to the understanding of foodwebs and their links between canopy and soil (wood endophytes start growing on attached branches and, if branches drop, most likely complete life-cycles on the ground). The varying microclimatic conditions caused by the structural complexity of the forest canopy, together with the broad range of available substrates, lead to the suggestion

that the diversity of fungi and fungus-like organisms is high in the canopy, and that the ecological phenomena are highly variable and provide a rich source for further investigations.

The amount of studies and papers that deal with wood decay, leaf-parasitic, endophytic, or epiphyllous fungi, with lichens or other small organisms such as myxomycetes or nematodes still is evanescent. As the implementation of molecular techniques into ecological sciences is enhanced, these organisms probably are the forthcoming protagonists of canopy research.

Curriculum vitae

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PERSONAL DATA

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EDUCATION

1981 - 1985	Basic school in Kuppenheim/Oberndorf
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1996 - 1998	University of Karlsruhe, Germany SS 1996: Chemistry (Diploma) WS 1996 - SS 1998: Biology (Diploma)
WS 1998 - SS 2002	Eberhard-Karls-University of Tübingen Biology (Diploma) 22^{th} of March 2002: final examinations (Botany, Parasitology, and Biochemistry), grade 'very good' (1.0)
May 2002 - December 2004	PhD-student at the Department of Systematic Botany and Botanical Garden, University of Leipzig

DIPLOMA THESIS

Title	Investigations of Entomopathogenic Fungi Isolated from Soils of the Brazilian Cerrado
Nov. 2000 - April 2001	Field studies in Brazil and cooperation with Dr. Wolf Christian Luz, Professor at the Federal University of Goiânia, Brazil.

Reviewer	Dr. Jörg Grunewald, University of Tübingen (first review) Prof. Dr. Franz Oberwinkler, University of Tübingen (second review)
Grade	very good (1.0)

DISSERTATION

Title	Fungi and Fungus-like Organisms in a Temperate Deciduous Forest Canopy
Beginning	May 2002
Supervisors	Prof. Dr. Wilfried Morawetz, University of Leipzig Dr. Peter Otto, University of Leipzig

TECHNICAL AND PROFESSIONAL SKILLS

Graphics, Layout	LaTeX, iWork, RagTime, Microsoft Office, Adobe Photoshop, Adobe Illustrator
Statistics	PC-Ord, Canoco 4.5 for Windows, R, EstimateS, IndVal, Le Progiciel R
Office, Databases	iWork, OpenOffice, RagTime, Microsoft Office, MySQL
July 2004 - August 2005	Organisation Committee of the 4^{th} International Canopy Conference in Leipzig, 10-17 July 2005
January 2005 - present	Scientific coordination of the Leipzig Canopy Crane (LAK) Project

LANGUAGE SKILLS

German	native
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Brazilian Portuguese	basic knowledges

Erklärung (Declaration)

Erklärung

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Hiermit verpflichte ich mich zur Einhaltung der in der Dissertationsordnung der Fakultät für Biowissenschaften, Pharmazie und Psychologie der Universität Leipzig aufgeführten Präambel zu den Prinzipien guter wissenschaftlicher Praxis. Die Promotionsordnung ist bekannt und wird von mir anerkannt.

Martin Unterseher Leipzig, im Januar 2006