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The Canopy of a Temperate Floodplain Forest

Results from five years of research at the Leipzig Canopy Crane

Edited by:

Martin Unterseher
University of Leipzig, Germany

Wilfried Morawetz
University of Leipzig, Germany

Stefan Klotz
Helmholtz Centre for Environmental Research – UFZ

Erik Arndt
Anhalt University, Bernburg, Germany

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We dedicate this book to the late Prof. Dr. Wilfried Morawetz, who died too young and unfortunately did not live to see its publication. Without his visionary enthusiasm, leading to the setup of two canopy crane research facilities (Surumoni and LAK), the world of canopy research would definitely be the poorer. His passing away leaves a big void in canopy science.

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Addresses of contributors

Erik Arndt
Anhalt University of Applied Sciences
Department LOEL
Strenzfelder Allee 28
D-06406 Bernburg, Germany
E-mail: earndt@loel.hs-anhalt.de

Stephanie Bartel
Section Tropical Ecology
Max-Planck-Institute for Limnology
August-Thienemann-Straße 2
D-24306 Plön, Germany
E-mail: bartel@mpil-ploen.mpg.de

Detlef Bernhard
Molecular Evolution and Animal Systematics
Institute of Biology II
University of Leipzig
Talstraße 33
D-04103 Leipzig, Germany
E-mail: bernhard@rz.uni-leipzig.de

Roland Brandl
Department of Animal Ecology
Phillips University Marburg
Karl-von-Frisch-Straße
D-35032 Marburg, Germany
E-mail: brandlr@staff.uni-marburg.de

Martin Brändle
Department of Animal Ecology
Phillips University Marburg
Karl-von-Frisch-Straße
D-35032 Marburg, Germany
E-mail: braendle@staff.uni-marburg.de

Oliver-D. Finch
Terrestrial Ecology Working Group
Faculty V, Biology and Environmental-Sciences
University of Oldenburg
D-26111 Oldenburg, Germany
E-Mail: oliver.d.finch@uni-oldenburg.de

Andreas Floren
Department of Animal Ecology
and Tropical Biology
Biozentrum Am Hubland
Julius-Maximilians University Würzburg
D-97074 Würzburg, Germany
E-mail: floren@biozentrum.uni-wuerzburg.de

Uta Fröhlich
Department of Systematic Botany
and Botanical Garden
Institute of Biology I
University of Leipzig
Johannisallee 21-23
D-04103 Leipzig, Germany
E-mail: sunny.uta@web.de

Matthias Gorny
Institute of Geography
University of Leipzig
Johannisallee 19a
D-04103 Leipzig, Germany
E-mail: Mattes.Gorny@directbox.com

Axel Gruppe
Department of Animal Ecology
TU München
Am Hochanger 13
D-85354 Freising, Germany
E-mail: gruppe@forst-tu-muenchen.de

Stephan Hielscher
Anhalt University of Applied Sciences
Department LOEL
Strenzfelder Allee 28
D-06406 Bernburg, Germany

Anja Homscheid
Waaggasse 16
91083 Baiersdorf, Germany
E-mail: anja-homscheid@gmx.net

Peter J. Horchler
Section Ecological Interactions
German Federal Institute of Hydrology
Am Mainzer Tor 1
D-56068 Koblenz, Germany
E-Mail: horchler@bafg.de

Anke Jentsch
Disturbance Ecology and Vegetation Dynamics
Department Conservation Biology
Helmholtz Centre for Environmental Research – UFZ

Permoserstraße 15
D-04318 Leipzig, Germany
E-mail: anke.jentsch@ufz.de

Claudia Jesche
Molecular Evolution and Animal Systematics
Institute of Biology II
University of Leipzig
Talstraße 33
D-04103 Leipzig, Germany
E-mail: cljesche@web.de

Stefan Klotz
Department of Community Ecology
Helmholtz Centre for Environmental Research – UFZ
Theodor-Lieser-Straße 4
D-06120 Halle, Germany
E-mail: stefan.klotz@ufz.de

Annett Krüger
Institute of Geography
University of Leipzig
Johannisallee 19a
D-04103 Leipzig, Germany
E-mail: akrueger@rz.uni-leipzig.de

Sven Kupillas
Anhalt University of Applied Sciences
Department LOEL
Strenzfelder Allee 28
D-06406 Bernburg, Germany
E-mail: sven.kupillas@web.de

Jan Mitscherling
Department of Systematic Botany
and Botanical Garden
Institute of Biology I
University of Leipzig
Johannisallee 21–23
D-04103 Leipzig, Germany
E-mail: kjewitsch@yahoo.de

Peter Nagel
Institute of Biogeography
Department of Environmental Sciences
University of Basel
St. Johanns-Vorstadt 10
CH-4056 Basel, Switzerland
E-mail: peter.nagel@unibas.ch

Hans Neumeister
Institute of Geography
University of Leipzig
Johannisallee 19a
D-04103 Leipzig, Germany
E-mail: neumeist@rz.uni-leipzig.de

Pia Parolin
Section Tropical Ecology
Max-Planck-Institute for Limnology
August-Thienemann-Straße 2
D-24306 Plön, Germany
E-mail: pparolin@mpil-ploen.mpg.de

Ingo Rieger
Fledermaus-Gruppe Rheinfall
Chratzhöfli 4
CH-8447 Dachsen, Switzerland
E-mail: rieger@adikom.ch

Markus Rohrschneider
Universität Leipzig
Institut für Informatik
PF 100920
D-04109 Leipzig, Germany
E-mail: r77markus@googlemail.com

Barbara Rudolph
Department of Systematics
Biocenter Klein Flottbek
University of Hamburg
Ohnhorststraße 18
D-22609 Hamburg, Germany
E-mail: b.rudolph@botanik.uni-hamburg.de,
BarbaraRudolph@gmx.de

Haike Ruhnke
Department of Community Ecology
Helmholtz Centre for Environmental Research – UFZ
Theodor-Lieser-Straße 4
D-06120 Halle, Germany
E-mail: ruhnke@genalis.de

Martin Schädler
Department of Animal Ecology
Phillips University Marburg
Karl-von-Frisch-Straße
D-35032 Marburg, Germany
E-mail: schaedler@staff.uni-marburg.de

Ronald Schiller
Naturkundemuseum Leipzig
(Natural History Museum Leipzig)
Lortzingstraße 3
D-04105 Leipzig, Germany
E-Mail: RonaldSchiller43@t-online.de

Carsten Schmidt
Molecular Evolution and Animal Systematics
Institute of Biology II
University of Leipzig
Talstraße 33

D-04103 Leipzig, Germany
E-mail: carstenLE@web.de

Claudia Schöne
Department of Systematic Botany
and Botanical Garden
Institute of Biology I
University of Leipzig
Johannisallee 21–23
D-04103 Leipzig, Germany
E-mail: claudi.schoene@gmx.de

Carolin Seele
Max Planck Institute for Biogeochemistry
Hans-Knöll-Straße 10
D-07745 Jena, Germany
E-mail: cseele@bgc-jena.mpg.de

Andreas Sickert
Stadt Leipzig
Abteilung Stadtforsten
Stadtforstamt und Forstbehörde
Teichstraße 20
D-04277 Leipzig, Germany
E-mail: abt.stadtforsten.gfa-leipzig@t-online.de

Peter Sprick
Curculio-Institut (CURCI e.V.)
Weckenstraße 15
D-30451 Hannover, Germany
E-mail: psprickcol@t-online.de

Kathrin Stenchly
Molecular Evolution and Animal Systematics
Institute of Biology II
University of Leipzig
Talstraße 33
D-04103 Leipzig, Germany
E-mail: stenchly@yahoo.de

Ophir Tal
Institute for Plant Sciences
Faculty of Agriculture
Hebrew University
76100 Rehovot, Israel
E-mail: o4s.tal@gmail.com

Martin Unterseher
Department of Systematic Botany
and Botanical Garden
Institute of Biology I
University of Leipzig
Johannisallee 21–23
D-04103 Leipzig, Germany
E-mail: unterseher@uni-leipzig.de

Anna Maria Vogt
Department of Systematics
Biocenter Klein Flottbek
University of Hamburg
Ohnhorststraße 18
D-22609 Hamburg, Germany
E-mail: fb0a014@botanik.uni-hamburg.de

Winfried Voigt
Institute of Ecology
Friedrich Schiller University Jena
Dornburger Straße 159
D-07743 Jena, Germany
E-mail: Winfried.Voigt@uni-jena.de

Foreword

Welcome of the Head of Environment, Public Order and Sports.

Why the city of Leipzig supports the Leipzig Canopy Crane Project? Leipzig's floodplain forest is in many aspects a worldwide uniqueness.

While most of the cities are happy if they are surrounded by many forests, most of Leipzig's floodplain forest stretches across the densely populated urban area. Therefore it is an intensively used recreation area for our citizens, which has to match a lot or requests, like hiking, cycling, jogging, riding, or making campfire.

But Leipzig's floodplain forest is also an area with a huge biodiversity. More than 40 tree species, 100 breeding birds, many rare butterflies and beetles are registered in large numbers that are unique in Central Europe. Nevertheless the natural scenery is also characterised by intensive, but sustainable forestry operations producing valuable timber an other products, e.g. seeds, for hundreds of years.

The city of Leipzig, one of the biggest non-state owners in the floodplain forest, takes care for the guarantee of its recreation function, for the conservation of its biodiversity, and for the sustainable utilisation of its products. But without comprehensive knowledge of the forest ecosystem it is not possible ot match and balance the functions mentioned before. Therefore the Leipzig Canopy Crane Project is not only an interesting research project, which is supported by the city of Leipzig, but also a tool to gain new fundamental insights into the functioning of our woods. This is of crucial importance in order to make well-founded decisions which can effect the Leipzig floodplain forest in many ways.

This is the reason, why the city of Leipzig will furthermore support the Leipzig Canopy Crane Project within the scope of its possibilities.

Inge Kunath
Head of Environment, Public Order and Sports

Preface

The Leipzig Canopy Crane (LAK) project started in March 2001. Since then it is one of few scientific ventures in temperate regions that focuses on biological diversity in tree crowns and it is the first that investigates the ecosystem riparian forest both on the forest floor and in the forest canopy. As every project designed for long-term ecological studies, the LAK project saw its first years in the meticulous survey and monitoring of the investigation site, which is an indispensable necessity for subsequent studies of functional aspects, interdependencies of organisms and structural components.

This volume presents a comprehensive overview of the main scientific activities from studies of soil reliefs over tree genetics and tree phenology to arthropods, bats, and fungi that populate the forest canopy.

This book is designed to meet the attention of scientists involved with canopy research. As it also aims inspiring every ecologist, a brief summary of past and present scientific activities in forest canopies follows this chapter. We hope that it will help the unprovided reader getting familiar with foggers, climbing gear, and canopy cranes.

The first chapter "Soil attributes, stand structure, and aspects of forest regeneration" imparts detailed knowledge of basic components of the investigation site. Starting with high scale soil reliefs, soil topography, and changes in soil compositions (KRÜGER *et al.*) the reader will also learn about the high diversity of woody plant species in the investigated area (SEELE), of vertical light transmittance patterns (HORCHLER), and of the canopy surface structure of the forest stand (ROHRSCHNEIDER *et al.*) as a fundamental basis for the following papers of species diversity, distribution of organisms, and organismic interaction. Knowledge of forest regeneration dynamics is of outstanding value in the context of the LAK project that functions only in conjunction with the city's forestry (see foreword by Inge Kunath). HOMSCHEID & HORCHLER examined patterns of leaf fall, whereas the paper by SCHÖNE & JENTSCH provides detailed information about the history, the current situation, and succession tendencies of Leipzig's riparian forests and highlights the influence of brown coal mining activities, river straightenings and air pollution over the ecosystem.

By getting to the second chapter "Tree phenology, genetic variation, and herbivory", the reader likewise reaches the forest canopy. TAL & MORAWETZ supply evidence that investigating processes in the canopy – in that case flowering and fruiting phenology – is needed to understand patterns that are observable on the forest floor (e.g. seedling establishment). TAL & MORAWETZ elaborate complex gender distributions among tree species and individual trees. The study of PAROLIN *et al.* present a starting point for further investigation of somatic mutation within trees. Slowly but surely, we come up to the huge world of canopy arthropods. MITCHERLING & HORCHLER assessed the extent of herbivory as a key process in forest ecosystems, ecosystem compartments and trophic levels across space and time by inspecting damage of living foliage in the canopy. Another study of herbivory focused on the leaf quality of a single tree species with respect to palatability of leaves and larvae development in time and space (RUHNKE *et al.*).

The third chapter is almost completely dedicated to studies of arthropod diversity and distribution within the canopy. On the basis of standardised sampling protocols (ARNDT & UNTERSEHER), the papers easily can be compared with each other and stress once more the importance of a forest rich in tree species and structural components for the sustainment of biodiversity. Using a combination of different trap types a comprehensive analysis of the diversity of spiders from the trunk layer and the canopy was realised by Stenchly et al. The study of bugs (Heteroptera) was conducted in the canopy layer and assessed the tree association of the insects (ARNDT *et al.*). The Investigation of GRUPPE also focused on one taxon, the Neuropterida, which can be generally regarded as poorly studied. His results revealed an inter alia separation of the neuropterid communities on different tree species. Because of a large amount of dead branches in the canopy, it was assumed that the diversity of arthropods, which depend on this substrate is also high. SCHMIDT *et al.* confirm this hypothesis. He and his colleagues could identify 175 species of xylobiontic beetles (Coleoptera). Within the ecological guild of mycetophageous beetles they found significant differences in numbers of species on different tree species building bridges to the mycological studies of UNTERSEHER & TAL at the end of the chapter. ARNDT & HIELSCHER studied a second group of Coleoptera, the ground beetles (Carabidae). The species set of the canopy could be divided into several ecological groups, such as strictly arboricolous species as well as species with ground-canopy interactions.

FRÖHLICH *et al.* assessed the diversity of nocturnal macro-Lepidoptera. With around 1000 individuals analysed they make first statements of spatio-temporal activity patterns of these organisms. FLOREN & SPRICK finally knocked down more than 95 000 arthropods by means of fogging canopy trees close to the crane site in spring 2003. They present an exhaustive overview of arthropod diversity in this central European forest canopy and point to the great importance of the organisms for many processes in the ecosystem.

Studies of vertebrates are almost completely missing in this volume, though there is considerable activity of squirrels, tree frogs, and of course, of birds in the canopy of the crane site. In 2003 the work of a diploma student revealed an extraordinary species richness and abundance of bats. Within only one vegetation period she could detect 15 species (about 75% of all species recorded in Saxony) and distinct niche separation at the crane site (FICHTNER 2004, unpublished diploma thesis). RIEGER & NAGEL take up this study and present own data gathered during an intensive monitoring period of two weeks. As a result, they obtained an impression of the daily "when" and the three-dimensional "where" of bats in a temperate deciduous forest. First results from an ornithological study in spring 2005 indicate a high number and density of bird species with distinguishable activity patterns in different forest patches and tree species.

We are indebted to many colleagues and institutions who contributed with great efforts to the successful start of the Leipzig Canopy Crane (LAK) Project and the realisation of the present volume: all contributors to this book; the Helmholtz Centre for Environmental Research – UFZ for funding the first six years through the projects UFZ-16/200 and UFZ-04/2004; the Faculty of Biology, Pharmacy and Psychology and the Department of Planning and Technology (Dezernat Planung und Technik, Abt. Betriebstechnik und Betriebsfhrung) of the University of Leipzig for further financial support; the Environmental Protection Office (Amt für Umweltschutz, Leipzig), the Office for Green Spaces, Department of Urban Forests (Grünflächenamt, Abt. Stadtforsten, Leipzig), and the Botanical Garden (Förderverein des Botanischen Gartens, Leipzig) for financial, technical and personnel support over the last seven or more years; the regional council (Regierungspräsidium, Leipzig) for providing the required permissions for our investigations in the protected forest area; Peter J. Horchler, the first coordinator of the project. We thank Kronen – Verlag, Hamburg for providing the beautiful, introductory illustrations for each of the three parts.

Finally, we are especially grateful to Mr. Andreas Sickert, Head of the Department of Urban Forests Leipzig. His great personal effort, his professional and profound suggestions and recommendations throughout the years contributed largely to the scientific concepts of the LAK Project.

MARTIN UNTERSEHER
WILFRIED MORAWETZ
STEFAN KLOTZ
ERIK ARNDT
Leipzig, Germany

A short introduction to canopy science

Martin Unterseher

Figure 1 – Panorama view of the riparian forest canopy at the crane site in Leipzig.

BEGINNINGS

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 20th 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 20th 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) revolutionised the perception of ecological processes and abiotic parameters high above the forest.

CLIMBING FOREST TREES

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). With their work Perry and his colleagues are exceedingly responisble that the vertical stratification of tropical forests is generally accepted in tropical biology nowadays (e.g. De Vries *et al.* 1997; Schulze *et al.* 2001)

FOGGING TREE CROWNS

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).

CANOPY CRANES

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).

TOPICS OF CANOPY RESEARCH

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 2006; 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 2006), 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 2006).

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.

TO BE CONTINUED

Apart from this brief overview of a fascinating and important science, 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; and Lowman & Rinker 2004), including free online material (Basset *et al.* 2003). Because research in the treetops additionally is full of emotional sensations (e.g. floating above the forest canopy, Fig. 1) the media regularly approach our scientific activites with impressiv documentaries in television (e.g. ZDF[1] and BBC[2]). On the other hand, scientists too are trying to enhance the public awareness 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 Lowman 2005[3]).

Recent studies such as that of gliding ants in tropical forests (Yanoviak *et al.* 2005) or the influence of elevated CO_2 on mature forest stands (Körner *et al.* 2005) demonstrate that many more unexpected phenomena in the canopy still await the impartial scientist.

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Part I

Description of the canopy crane investigation site

1 Soil attributes, stand structure, and aspects of forest regeneration

Contents

1.1 High scale diversity of soil and relief attributes in the LAK investigation area

Annett Krüger[1], Matthias Gorny & Hans Neumeister

Investigation of soils influenced by groundwater is an essential precondition for characterising the ecological aspects of the floodplain forest closed to Leipzig. The effects of vegetation in the Lowlands of the rivers Elster and Luppe (northwest of Leipzig) on soil distribution and micro-relief were examined, and also as part of this present study, attributes of the topsoil zones as well as features of the sediments and relief were analysed in high scale in their spatial heterogeneity. 12 soil profiles were analysed along a catena on the basis of German soil taxonomy and investigated in respect of parameters such as soil form, soil type, substrate type, hydromorphy and grain sizes. Tachymeter measurement revealed extremely varied forms of relief. In the area of the LAK, height differences of almost 3 m (from 100.7–103.05 m above sea level) were analysed. Following on from these differences in relief, the results of the profile probes substantiate a multi-layered soil construction within a very confined space. Soil distribution in the area under investigation shows the occurrence of Brown Vega and Vega gleys developed on fluvial clay over pleictocence terrace gravel and sands. The soils show clear differences, particularly in grain composition. Soil horizonts depths also vary, as do their sequences. Changes in the hydrological system in the Leipzig Lowlands due to groundwater reduction as a result of the embankment, channelling and construction of the New Luppe in 1934–1936 are already having a marked effect on the soil attributes. A continued absence of inundation dynamics could ultimately lead to the loss of typical floodplain soil attributes.

INTRODUCTION

High scale analysis of topsoil attributes is an essential precondition for characterising the onsite conditions of the floodplain forest with a particular focus on vegetation. Vegetation type and density has a considerable decisive influence on the entry of rainwater with substances it contains into the soil, and should therefore be assessed as a significant factor for the development of nutrient concentrations in the soil solution. Turnover of this substances in the soil depends on soil parameters. Time and space depending topsoil attributes have a key function in the process.

There is a multitude of written material concerning soil attributes and substance conversion in flooding plains nearly town. Only a few results concerning heterogeneity and temporal variability in high scales of certain soil parameters in flood plains have been published so far (Neumeister et al. 2000, Franke & Neumeister 2000). Works concerning influences on topsoil attributes in flood plains of the White Elster due to inundation events (Krüger & Neumeister 2000), as well as due to substance inputs from stem and dripp from branches and leafs, have been presented by Neumeister (1999). Within the context of the LAK project, the opportunity presents itself to demonstrate relationships between crown dripping, stem flow and troughflow in their spatial and temporal diversity, and finally to demonstrate their feedback to soil attributes and vegetation. The investigations in the“Soil” sub-project in the LAK research are taking place with the objectives of **(i)** analysing interrelations between topsoil attributes, micro-relief and vegetation features and **(ii)** analysing and describing the spatial heterogeneity of the soil attributes (soil form, soil and substrate type, hydromorphy, pH value, humus content, geochemical composition).

MATERIALS AND METHODS

In collaboration with the Green Space Office of Leipzig (“Grünflächenamt”) and its department “urban forests”, the soils in the area surrounding the crane in the Burgaue (being part of the Elster-Luppe floodplain northwest of Leipzig) were analysed under consideration of sedimentological, relief and soil view point in March 2003. In this context the parameters soil type, soil form, substrate type, hydromorphy, colour and humus content was analysed according German soil taxonomy (Arbeitsgruppe Boden 1994) along a catena within the crane plot. The

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[1] corresponding author

soil profiles were analysed from north to south along the y-25 mark (northing 45 21 613), with a bore hole of up to two metres in depth drilled approximately every 20 m. The micro-relief was mapped by means of tachymeter recordings: the swivel range of the tower crane is marked on the ground every 10 m. These markings were chosen as co-ordination points for recording the relief of the total crane area.

RESULTS AND DISCUSSION

The vertical diversity of surface-proximate subsoil in the investigation area

The flood plains of the White Elster, the Pleisse, the Luppe and the Parthe conjoin in the area of the present city of Leipzig, in the lowlands of the same name. Due to the early settlement of the loess areas south of Leipzig from approximately 6 000 BC, the associated clearing of the forests located there and incipient agronomic utilization or Holocene climatic fluctuations (Fuhrmann 1999), a 2–4 m thick layer of fluvial brown sediments over Pleistocene and Holocene gravel came into being in the present flood plain area as a result of erosion with correlated sedimentation (Neumeister 1964).

The development of the Elster-Luppe flood plain in its present form was shaped in the Pleistocene era, in particular during Germany's last great ice age (90 000 to 10 000 years before the present day, according to Eissmann 1994). First the rivers spread erosion detritus from the mountain ranges across several kilometres and up to 8 m thick. Gritty and (as a result of decreasing water flow) sandy sediments deposited themselves over these layers. On top of that sediments, in the Elster-Pleisse flood plain, the reddish-brown, clayey-silty, fluvial-alluvial clay-sediments as base for the soil development in the Leipzig flood plains.

The formation of the fluvial loamy sediment is therefore connected with human settlement. Clearances in the Elster and Pleisse catchment area from the early Atlantikum 5 000 to 6 000 years ago provided favourable conditions for the erosion of the now exposed soil by rainwater in the hydrological catchment. The rivers picked up the eroded soil particles and carried them in the form of a suspension into the floodplains. When the highfloods ebbed, the suspended material was deposited outside the river beds. As can be traced in a 5-step scheme one can see stages of floodplain development (Eissmann 1997, adapted from Hiller, Litt & Eissmann 1991).

A second principal phase for the accumulation of fluvial loamy sedimentscame in the period between 1 350 and 900 B.C. (subboreal). This took place in parallel with the Bronze Age settlement of the Elster-Pleisse area. From 8 A.D., the time of increasing agriculture, the suspended material transported by the rivers grew again, and flood loam formation grew with it. Thanks to river adjustments and hydraulic engineering measures in Leipzig's Elster-Luppe flood plain, fluvial loam sedimentation which might still be possible today due to prevailing geological conditions can be described as minimum. High flood events have been prevented technologically.

Development of the Elster-Luppe flood plain near Leipzig over the past 100 years

The present appearance of the Leipzig floodplains is characterised by numerous impacts by humans on the water balance of the flood plain system. Up to the middle of the 1930s the fluvial loam sedimentation process was relatively continuous (Gutte & Sickert 1998). Up until then, an exceedingly species-rich hardwood plain with oak, elm, hornbeam, maple and ash had been developing, promoted by forestry since the 16th century. The formation of an extraordinarily species-rich hardwood floodplain in addition to the softwood plain was made possible by the prevailing dry conditions. In phytogeographical terms, the Elster-Pleisse flooding forest (Querco-Ulmetum) is given the suffix allietosum for the facies-forming wild garlic there (*Allium ursinum*). In the 1930s, the high floods were broken with the construction of the new Luppe and the construction of retention systems at the upper parts of the Elster and Pleisse (Fig. 1).

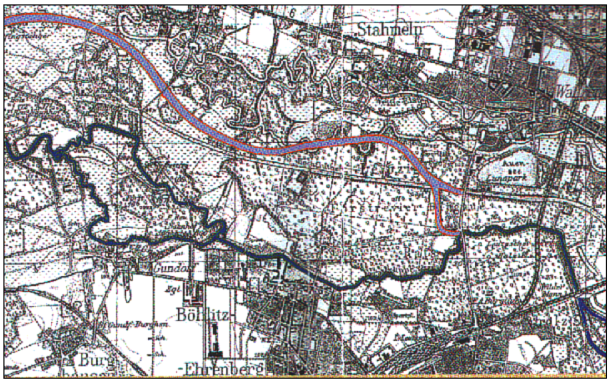

Figure 1 – Development of the rivers Luppe und Weiße Elster in the northern part of Leipzig Lowland. Map from: Topographic card from Saxony, scale 1 : 25 000, number 4 639 (Leipzig ouest), made from the year 1907. The river Neue Luppe builded in the years 1934–1936 is already marked. The river Alte Luppe shows as an natural river with meanders.

The increasing of the Neue Luppe as an artificial drain led to a reduction in groundwater. Natural watercourses and their bayous dried out as a result. The soil attributes changed, formerly strongly groundwater influenced soils became increasingly drier. Since vegetation interacts strongly with the soil, the change in the hydrological conditions ultimately had a detrimental effect on both flora and fauna of the wetland biotopes. Today, efforts are being made to boost the hardwood flood plain by means of annual inundation measures (e.g. increasing the proportion of oaks). The Leipzig flooding forest can therefore be viewed as relatively natural.

However, due to their proximity to the city of Leipzig and its polluters, primarily including industry and brown coal open-cast mining, traffic and municipal domestic fuel, the floodplains have had their diversity and functionality impaired since the beginning of industrialisation by a continuous input of pollutants (Krüger, Haase & Neumeister 1999). As part of the atmospheric pollution of the floodplain areas of Leipzig, in addition to carbon dioxide and low-lying ozone, heavy metals and organic airborne pollutants, acids and acid-forming emissions in particular (particularly, increasingly, NO_x; German Federal Office Environment and Geology, LfUG 1997) play a large part. While a decrease in SO_x emissions can be observed due to the switch in fuel from coal to other energy sources, a rise in nitrous oxides can be recognized in the Leipzig area since 1990.

Soil formation and distribution in the Burgaue near Leipzig

Soils are the result of the co-action between different soil-forming factors rocks (sediments), relief, vegetation, climate, water, and human influence, which vary spatially and temporally. Depending on their specificities, a spatially heterogeneous pattern of soil forms arises, with different physical/chemical attributes which control substance turnover and transport processes in the soil.

In older written material, floodplain soils are described as alluvial soils. A floodplain made up of unregulated flowing watercourses is characterised by periodic and irregular inundations. Varying water levels lead to increased anaerobic, respectively aerobic conditions and to a change in the physico-chemical control factors (Rinklebe, Heinrich & Neue 2000). Considered at the micro level, the relief attributes in floodplains therefore play a significant role for longer periods of waterlogging at increasingly anaerobic conditions in the soil and therefore lead to an altered, redox potential-dependent substance dynamics. Taking the example of the 90 m x 120 m crane plot, the localized interaction of relief, soil attributes and vegetation was investigated for this reason. The possible effective range of the tower crane is marked on the ground every 10 m. These markings were chosen as co-ordination points for the tachymeter recording of the overall crane plot. More precise measurement reveals a highly diverse relief (Fig. 2). The tachymeter recordings show relief forms such as small dents, weakly pronounced hills, dissected ridges, bayou systems and others. The appearance of isolated and dissected full forms, as well as of level and channelled relief units, supports the image of a locally diverse landscape. In respect of tendency to slope, more pronounced westerly-exposed and flatter easterly-exposed inclines are detected around the channels. It is evident that the area under investigation rises slightly to the south. Relief differences of almost 3 m appear in the area under investigation, heights above sea level fluctuate from 100.7 m–103.5 m. Here it should be noted that the elevation in the middle of the height profile is the artificial mound left by the crane markings.

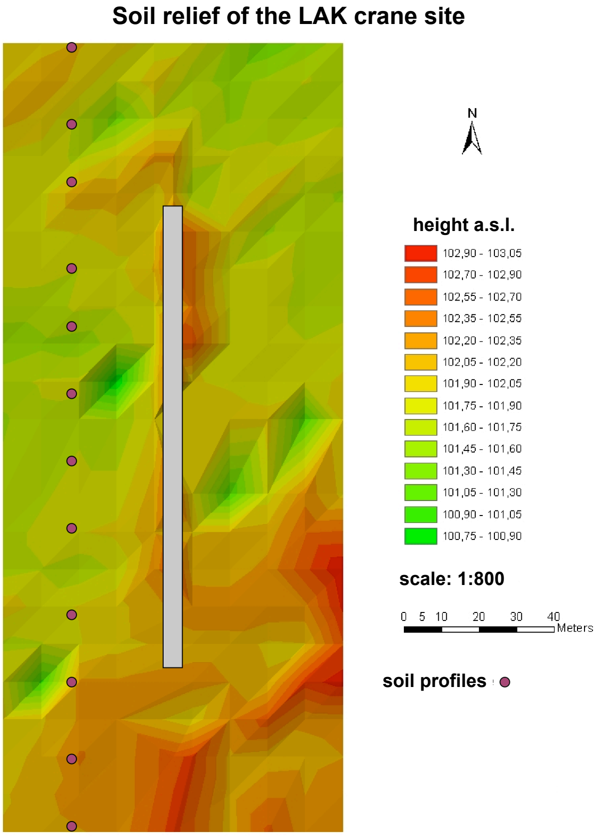

Figure 2 – Topographic map for the area of LAK. Measuring of the morphological differences using Tachymeter investigations. The height above sea level are shown in meter.

Spatial heterogeneity is reflected visibly in vegetation (Seele, this volume). Relief-related and pedogenetic variety enables different habitats for fauna and flora to co-exist within a very confined space. Varied dependencies and back-couplings, combined with high spatial heterogeneity, give rise to a complex structure of events, processes and effects. The effect of localised relief differences and diverse vegetation attributes on soil attributes was analysed in the next step.

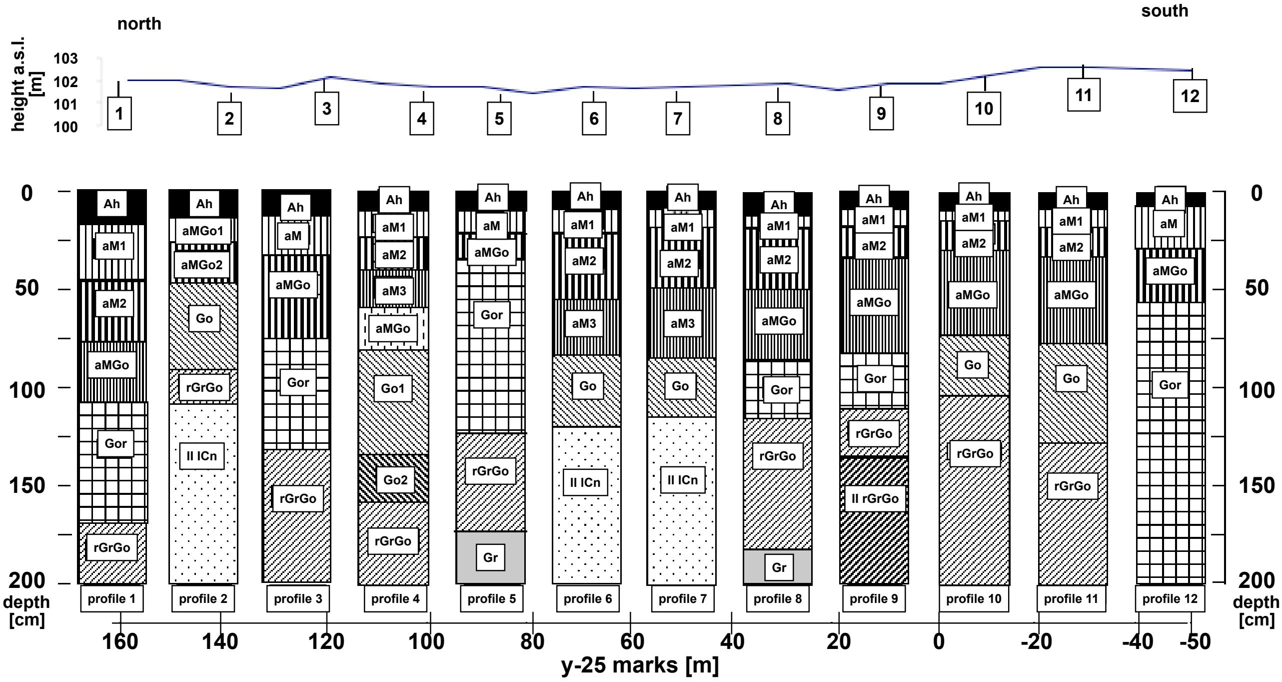

Figure 3 – Soil profiles in the catena of the LAK area. Soil profiles were picked off using Pürckhauer gadget in the line of the y-25 m plot from the LAK area. On the top is shown the height a.s.l. in metre from the several soil profiles. Description of the soil profiles number 1 to number 12 are given in the appendix. In this figure the occuring soil horizons are shown.

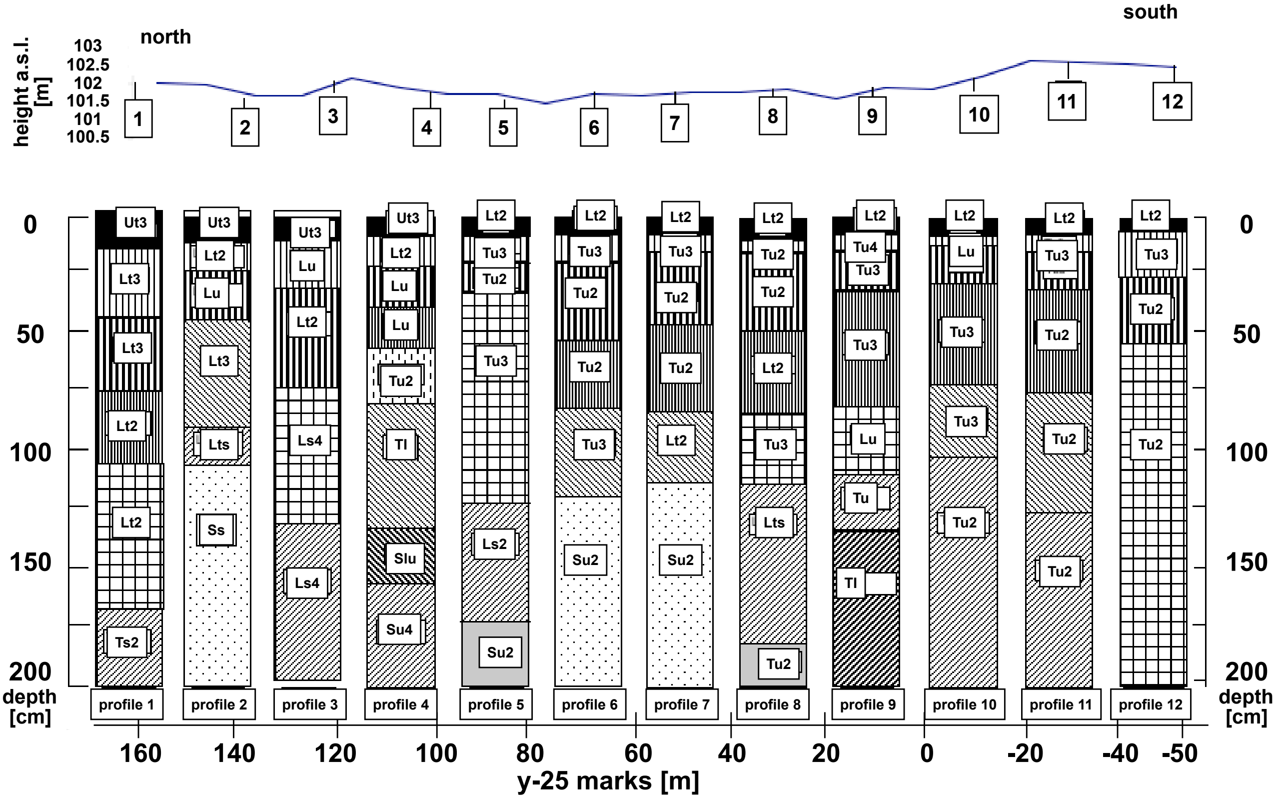

Figure 4 – Grain sizes from soils in the catena of the LAK area. Soil profiles were picked off using Pürckhauer gadget in the line of the y-25 m plot from the LAK area. On the top is shown the height a.s.l. in metre from the several soil profiles. Description of the soil profiles number 1 to number 12 are given in the appendix

Fluvial clays, whose soil in lower-lying areas mostly represent Vega Gleys or, in more elevated relief positions, Brown Vegas made up of fluvial clay to fluvial silt, dominate almost totally in the Leipzig floodplain areas. (Haase, Schneider & Neumeister 2000, Krüger & Neumeister 2000). The results of the soil recordings along the catena in the LAK investigation area (Fig. 3) confirm these expectations.

All 12 profiles show the typical formation of Vega Gleys from fluvial silt and clay over Pleistocene terrace gravel and sands (Appendix). Based on the individual soil profiles it can be established that the soil consists of up to 13 different soil types (Fig. 4).

Down to a depth of one metre, the profiles can be divided into three groups: for profiles 1–3, a humic topsoil zone (Ah) made up of silty material (Ut3) and mixed by burrowing creatures is found over the strongly to moderately clayey, partly silty loam in the aM to aM-Go zones. Profile 4 reveals from a depth of approximately 60 cm under the silty to slightly clayey loams of the aM zones a 85 cm thick, silty-clayey sediment (Tu2) in the aM-Go zone. The silty substrates of profiles 1–3 and profile 4 are no longer found in the topsoil (Ah zones) in profiles 5–12 (level ground); here, slightly to moderately silty clay is overlaid by loamy substrate (Lt2 to Lu). Further substrate differences can be seen in the lower part of the profiles. Comparing with the investigations by Eissmann (1997), the conclusion can be drawn that fluvial loam from profiles 2 and 4–7 are overlaid by re-deposited valley sands.

On the basis of the catena it can further be established that not only thickness of horizons, but also soil horizon succession is highly diverse. It can be seen clearly that the Ah zone becomes thinner towards the south. While its thickness in profile 1 is 15 cm, it reaches a thickness of just 6 cm in profile 12, 120 m away. Fluvial sediments are observed at the aM horizon, characterised by the high release of iron oxide as a soil-forming process. In parts, these are more then 80 cm thick and, due to their colour and sometimes varying substrate, reveal multi-phase formation (aM1–aM3).

In profiles 1–5 and 8–12 we find a transitional horizon (aM-Go) from the solum sediment to the groundwater influenced Go horizon. Here begins the periodically well-ventilated and hence rusty (due to oxidized iron) groundwater seam. These transitional zones can be encountered down to a depth of 70 cm to some 105 cm. Among them can be found either a distinctive Go horizon (> 10 surface area% rusty flecks in the groundwater range), or a transitional zone between a Go and Gr zone. These groundwater-influenced horizons show an uneven distribution right across the entire catena, allowing no particular pattern to be drawn. The only observation possible is that the groundwater range can be highly varied locally. For profiles 6 and 7 the aM horizon changes directly into a Go horizon. Due to the fluvial silty II ICn horizon (valley sand) present at these drilling points of some 120 cm depth, the stagnant groundwater is able to drain off quickly.

Due to the valley sands ('Talsande' in the sence of geological mapping) in profiles 6 and 7, which overlie fluvial loam or represent valley sand remnants, this area was not influenced by groundwater even in earlier times (at least down to a depth of two metres). In contrast to this is profile 2. Here, a thin, relictic groundwater influenced horizon (r GrGo) has formed over the coarse sand (II ICn), which can probably be attributed to its comparatively low height in the terrain. Apart from this, indications of a relictic groundwater zone which was created as a result of regular floods before groundwater was reduced around Leipzig (water regulation in flood plains) are revealed by all other soil profiles apart from profile 6, 7 and 12. This relictic zone leads to the conclusion that the subsoil was formerly much more waterlogged and provided the basis for a lush softwood floodplain forest. This horizon, too, runs very unevenly and is highly distinctive along the catena.

A pale Gr horizon has formed in profiles 5 and 8 beneath the relictic groundwater zone. It arose under reduced circumstances, since iron is distributed finely in the constantly saturated subsoil and colours the soil grey. It is remarkable that this Gr horizon only appears for two of a total of twelve profiles and only from a depth of approx. 173 cm.

The results of the catena investigations show multi-layered soils in a very confined space. Furthermore, the relictic groundwater horizon and today's far deeper Gr horizon bears witness to the change in ground water ratios from the formerly much more widely-spread softwood plain forest to the onsite attributes of the present hardwood plain forest. The soils, an integral indicator, reflect the fact that today's appearance of the Elster-Luppe flood plain is characterised by numerous attacks by humans on the water balance of the floodplain system. A continued absence of inundation dynamics could ultimately lead to the steady loss of decisive aspects of the flooding forest vegetation.

The effects on soil and vegetation attributes of the change in groundwater status as a result of groundwater reduction – with the construction of the Luppe dam or a potential groundwater increase as a result of renaturation projects (e.g. refilling the Burgaue brook) – form the subject of current and planned investigations at the Institute of Geography. Varying water levels lead to alternate anaerobic, respectively aerobic conditions. This change in physico-chemical control factors can, as the existing results substantiate, have a marked effect on soil features. Formerly strongly groundwater influenced soils have become increasingly drier. This fact is reflected by the appearance of rGr-Go horizons at deeper relief positions, i.e. relictic groundwater influenced soil horizons with reduction to increasing oxidation features. The extent to which the change in groundwater level in the last 69 years – since the Luppe dam was completed – is already having a marked effect on the soil's hydromorphy features, is to be the subject of further investigations.

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Appendix – Description of the soil profiles 1 to 12.

Profile 1

x-25; y160; Right-value: 45 21 613; Hight value: 56 92 464; Height a.s.l.: 102.07 m
soil type: brown Vega
soil form: brown Vega developed from fluvial silt and loam over relictic gley developed from fluvial clay
border bioturbation: 30 cm

	horizon	depth [cm]	colour	particel size	features	organic matter
1	Ah	0-15	10YR3/4	Ut3	branch-rests	middle humic
2	aM1	15-45	10YR4/4	Lt3		weak humic
3	aM2	45-76	10YR4/6	Lt3		very weak humic
4	aM-Go	76-107	7.5YR4/6	Lt2	iron oxide	humus- free
5	Gor	107-159	7.5YR4/4	Lt2	iron oxid, manganese oxide	humus-free
6	rGrGo	159-198	7.5YR5/4	Ts2		humus-free

Profile 2

x-25; y138; Right-value: 45 21 613; Hight value: 56 92 442; Height a.s.l.: 101.72 m
soil type: Floodplain Gley
soil form: Floodplain Gley developed from fluvial Loam over pleictocene sand
border bioturbation: 19 cm

	horizon	depth [cm]	colour	particel size	features	organic matter
1	Ah	0-13	10YR3/4	Ut3	branch-rests	middle humic
2	aMGo1	13-25	10YR4/4	Lt2	iron oxide	weak humic
3	aMGo2	25-46	10YR4/4	Lu	iron oxid, manganese oxide	very weak humic
4	Go 46-91	7.5YR4/6	Lt3	iron oxid, manganese oxide	humus-free	
5	rGrGo	91-107	7.5YR5/4	Lts	iron oxide	humus-free
6	II lCn	107+	7.5YR4/6	Ss		humus-free

Profile 3

x-25; y120; Right-value: 45 21 613; Hight value: 56 92 424; Height a.s.l.: 102.18 m
soil type: brown Vega
soil form: brown Vega developed from fluvial loam and loam over relictic gley developed from fluvial loam
border bioturbation: 19 cm

	horizon	depth [cm]	colour	particel size	features	organic matter
1	Ah	0-12	10YR3/4	Ut3	branch-rests	middle humic
2	aM	12-33	10YR4/4	Lu	iron oxide	weak humic
3	aMGo	33-85	7.5YR4/4	Lt3	iron oxide	very weak humic
4	Gor	85-132	7.5YR4/6	Ls4	iron oxide	humus-free
5	rGoGr	132-196	7.5YR4/6 7.5YR5/3	Ls4	iron oxide	humus-free

Profile 4

x-25; y100; Right-value: 45 21 613; Hight value: 56 92 404; Height a.s.l.: 101.74 m
soil type: Gley-Vega
soil form: Gley-Vega developed from fluvial Loam and clay over relictic Gley out of terrace stones and sand
border bioturbation: 21 cm

	horizon	depth [cm]	colour	particel size	features	organic matter
1	Ah	0-9	10YR3/3	Ut3	branch-rests, leaves	middle humic
2	aM1	9-22	10YR4/4	Lt2		weak humic
3	aM2	22-40	10YR4/3	Lu		very weak humic
4	aM3	40-59	10YR4/3	Lu		very weak humic
5	aMGo	59-81	7.5YR4/4	Tu2	iron oxide	humus-free
6	Go1	81-144	7.5YR4/4	Tl	iron oxid, manganese oxide	humus-free
7	IIGo2		7.5YR5/6	Slu	iron oxid, manganese oxide	humus-free
8	rGrGo		10YR5/4	Su4		humus-free

Appendix continued – Description of the soil profiles 1 to 12.

Profile 5

x-25; y84; Right-value: 45 21 613; Hight value: 56 92 388; Height a.s.l.: 101.52 m
soil type: Vega-Gley
soil form: brown Vega-Gley developed from fluvial loam and clay over relictic gley developed from fluvial loam and sand
border bioturbation: 22 cm

	horizon	depth [cm]	colour	particel size	features	organic matter
1	Ah	0-10	10YR3/3	Lt2	branch-rests, leaves	middle humic
2	aM	0-22	10YR4/4	Tu3		weak humic
3	aM-Go	22-34	7.5YR4/4	Tu2	iron oxide	very weak humic
4	Gor	34-123	7.5YR4/6	Tu2	iron oxid, manganese oxide	humus-free
5	rGrGo	123-173	7.5YR5/4	Ls2	iron oxid, manganese oxide	humus-free
6	Gr	173+	10YR6/4	Su2		humus-free

Profile 6

x-25; y68; Right-value: 45 21 613; Hight value: 56 92 372; Height a.s.l.: 101.76 m
soil type: Gley-Vega
soil form: Gley- Vega developed from fluvial loam and clay over pleistocene sand
border bioturbation: 22 cm

	horizon	depth [cm]	colour	particel size	features	organic matter
1	Ah	0-7	10YR3/4	Lt2	branch-rests, leaves	middle humic
2	aM1	7-22	10YR4/4	Tu3	iron oxide	weak humic
3	aM2	22-55	10YR5/4	Tu2	iron oxide	very weak humic
4	aM3	55-82	7.5YR4/4	Tu2	iron oxide	humus-free
5	Go	82-120	7.5YR4/6	Tu3	iron oxid, manganese oxide	humus-free
6	II lCn	120+	n.d.	Tu2		humus-free

Profile 7

x-25; y50; Right-value: 45 21 613; Hight value: 56 92 359; Height a.s.l.: 101.79 m
soil type: Gley-Vega
soil form: Gley- Vega developed from fluvial loam and clay over pleistocene sand
border bioturbation: 19 cm

	horizon	depth [cm]	colour	particel size	features	organic matter
1	Ah	0-8	10YR3/4	Lt2	branch-rests, leaves	middle humic
2	aM1	8-19	10YR4/4	Tu3	iron oxide	weak humic
3	aM2	19-51	7.5YR5/4	Tu2	iron oxide	very weak humic
4	aM3	51-83	7.5YR4/4	Tu2	iron oxide	very weak humic
5	Go	83-116	7.5YR5/6 7.5YR4/6	Lt2	iron oxid, manganese oxide	humus-free
6	II lCn	116+		Su2		humus-free

Profile 8

x-25; y30; Right-value: 45 21 613; Hight value: 56 92 334; Height a.s.l.: 101.89 m
soil type: Vega-Gley
soil form: brown Vega-Gley developed from fluvial loam over fluvial clay
border bioturbation: 19 cm

	horizon	depth [cm]	colour	particel size	features	organic matter
1	Ah	0-12	10YR3/4	Lt2	branch-rests, leaves	middle humic
2	aM1	12-19	10YR4/4	Tu2		weak humic
3	aM2	19-50	10YR5/4	Tu2	iron oxide	very weak humic
4	aMGo	50-85	7.5YR3/4	Lt2	iron oxide	humus-free
5	Gor	85-115	7.5YR4/6 7.5YR5/6	Tu3	iron oxid, manganese oxide	humus-free
6	rGrGo	115-179	7.5YR5/4 7.5YR5/6	Lts	iron oxid, manganese oxide	humus-free
7	Gr	179+	7.5YR5/3	Tu2	iron oxide	

Appendix continued – Description of the soil profiles 1 to 12.

Profile 9

x-25; y10; Right-value: 45 21 613; Hight value: 56 92 314; Height a.s.l.: 101.91 m
soil type: Vega-Gley
soil form: brown Vega-Gley developed from fluvial loam and clay over fluvial clay
border bioturbation: 16 cm

	horizon	**depth [cm]**	**colour**	**particel size**	**features**	**organic matter**
1	Ah	0-8	10YR3/4	Lt2	branch-rests, leaves	middle humic
2	aM1	8-18	10YR4/4	Tu4		weak humic
3	aM2	18-33	10YR5/4	Tu3	iron oxide	very weak humic
4	aMGo	33-82	10YR5/4	Tu3	iron oxide	humus-free
5	Gor	82-111	7.5YR4/6	Lu	iron oxid, manganese oxide	humus-free
6	rGrGo	111-135	7.5YR5/4 7.5YR4/4	Lu	iron oxid, manganese oxide	humus-free
7	II rGrGo	179+	7.5YR4/4	Tl	iron oxid, manganese oxide	

Profile 10

x-25;y-10; Right-value: 45 21 613; Hight value: 56 92 294; Height a.s.l.: 102.24 m
soil type: Vega-Gley
soil form: brown Vega-Gley developed from fluvial loam over fluvial clay
border bioturbation: 26 cm

	horizon	**depth [cm]**	**colour**	**particel size**	**features**	**organic matter**
1	Ah	0-9	10YR3/4	Lt2	branch-rests, leaves	middle humic
2	aM1	9-15	10YR4/4	Lu		weak humic
3	aM2	14-30	10YR4/4	Lu	iron oxide	very weak humic
4	aMGo	30-72	7.5YR5/4	Tu3	iron oxid, manganese oxide	humus-free
5	Go	72-104	7.5YR4/3	Tu3	iron oxid, manganese oxide	humus-free
6	rGrGo	104+	7.5YR5/3	Tu2		humus-free

Profile 11

x-25; y-30; Right-value: 45 21 613; Hight value: 56 92 274; Height a.s.l.: 102.57 m
soil type: Vega-Gley
soil form: brown Vega-Gley developed from fluvial loam over fluvial clay
border bioturbation: 19 cm

	horizon	**depth [cm]**	**colour**	**particel size**	**features**	**organic matter**
1	Ah	0-9	10YR3/4	Lt2	branch-rests, leaves	middle humic
2	aM1	10-18	10YR4/4	Tu3		weak humic
3	aM2	19-33	10YR4/4	Tu3	iron oxide	very weak humic
4	aMGo	33-78	7.5YR5/4	Tu2	iron oxide	humus-free
5	Go	78-128	7.5YR4/3	Tu2	iron oxid, manganese oxide	humus-free
6	rGrGo	128+	7.5YR5/3	Tu2	iron oxide	humus-free

Profile 12

x-25; y-50; Right-value: 45 21 613; Hight value: 56 92 254; Height a.s.l.: 102.47 m
soil type: Vega-Gley
soil form: brown Vega-Gley developed from fluvial loam over fluvial clay
border bioturbation: 29 cm

	horizon	**depth [cm]**	**colour**	**particel size**	**features**	**organic matter**
1	Ah	0-6	10YR3/4	Lt2	branch-rests, leaves	middle humic
2	aM1	6-29	10YR3/4	Tu3		weak humic
3	aMGo	29-57	7.5YR5/4	Tu2	iron oxide	very weak humic
4	Gor	57+	7.5YR5/3	Tu2	iron oxid, manganese oxide	humus-free

1.2 Tree species composition of the LAK investigation site

CAROLIN SEELE

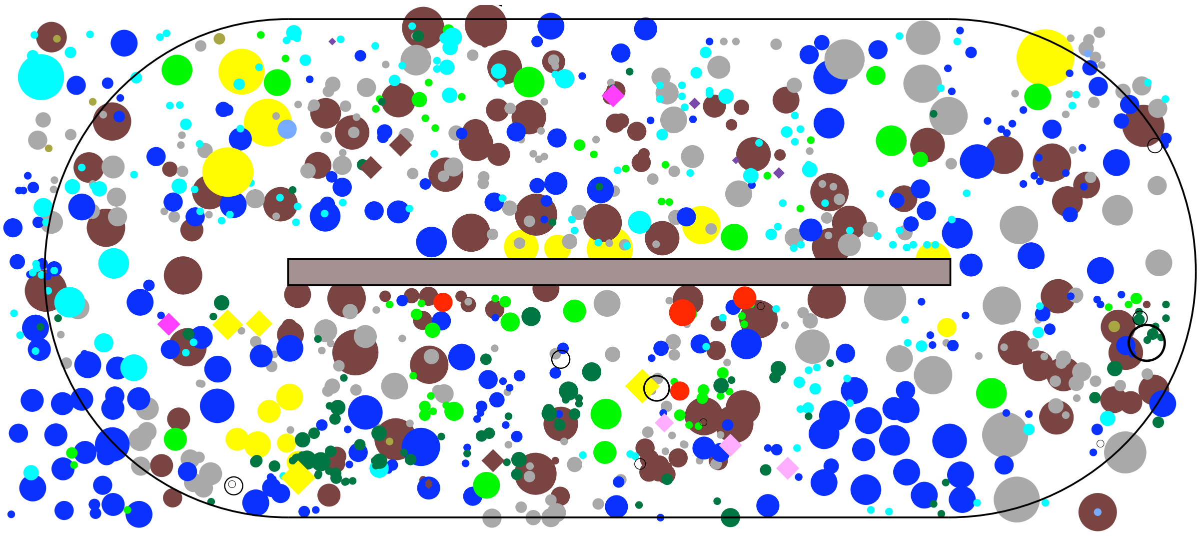

Figure 1 – Species composition and position of the tree stems at the crane site. The different size of the circles indicate different stem diameters. Colour code of the five most dominant tree species: blue = *Acer pseudoplatanus*; brown = *Fraxinus excelsior*; grey = *Tilia cordata*; turquoise = *Acer platanoides*; green = *Carpinus betulus*.

SHORT COMMUNICATION

Every tree with a stem diameter at breast height (dbh) > 5 cm was acquired in an area of 1.81 ha, including the crane site with 1.65 ha. The exact position of every single tree was measured, as well as their dbh, the height to the base of the crown, and the total height of the trees. Based on these parameters the stand structure was analysed on community and species level.

The species list (Table 1) shows the occurrence of typical taxa of a riparian forest but also some introduced neophytes.

In the year 2003 there existed 906 living trees at the investigated site (1.81 ha; dbh > 5 cm) which belong to 16 species. All stems occupied a basal area of 63.1 m^2. This is accordant to a stand density of 500 tree individuals ha^{-1}, a basal area of 34.9 m^2 ha^{-1}, and a diversity of 14 tree species ha^{-1}.

The ecologically most important species at the investigated site are *Acer pseudoplatanus*, *Fraxinus excelsior*, and *Tilia cordata* (Fig. 2). *Acer* and *Tilia* reach their highest Importance Value (IVI; Importance Value Index) due to the large number of individuals, whereas *F. excelsior* belongs to the most dominant trees of the investigated forest stand because of its basal area.

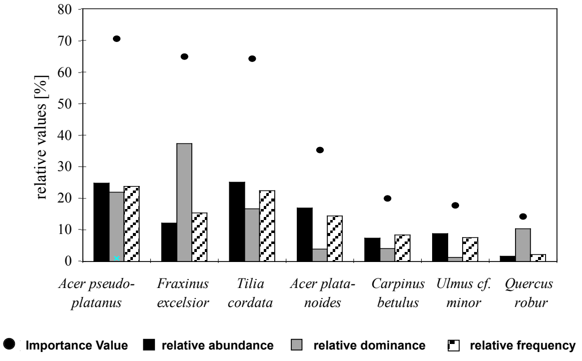

Figure 2 – Most important tree species of the investigated site.

The dbh-class distribution of *Acer pseudoplatanus*, *Acer platanoides*, *Tilia cordata*, and *Carpinus betulus* shows a negatively exponential curve progression which can be well compared to that of independently regenerating species (Fig. 3). Most individuals group in classes with low dbh values. With increasing stem diameter the number of individuals of the corresponding tree species decreases exponentially. *Acer platanoides* stands out by its very large number of individuals with dbh values between 5 and 10 cm and a very low number of individuals with thicker stems. The extensive absence of old trees shows that *A. platanoides* did not belong to the dominant species about 100 years ago and that the actual conditions at the investigation site promote a massive propagation of this species.

Fraxinus excelsior shows a bimodale dbh-class distribution with two peaks at 20–35 cm and 60–75 cm dbh, respectively, and an equal distribution of individuals in classes with very low, medium, and very large stem diameters. This indicates that a natural regeneration of the population virtually does not occur, although the site conditions should promote this species (see below). The damages caused by roe deer surely plays an important role in the regenerating capacities of *F. excelsior* and *Quercus robur*. Another likely explanation of this unusual distribution of dbh-classes in the stand is the history of forestry in this area. Before the 19^{th} century, *F. excelsior* did not occur naturally in the lowland riparian forests of Leipzig and was planted in several phases, two of them could be visible until now as the peaks of dbh-classes.

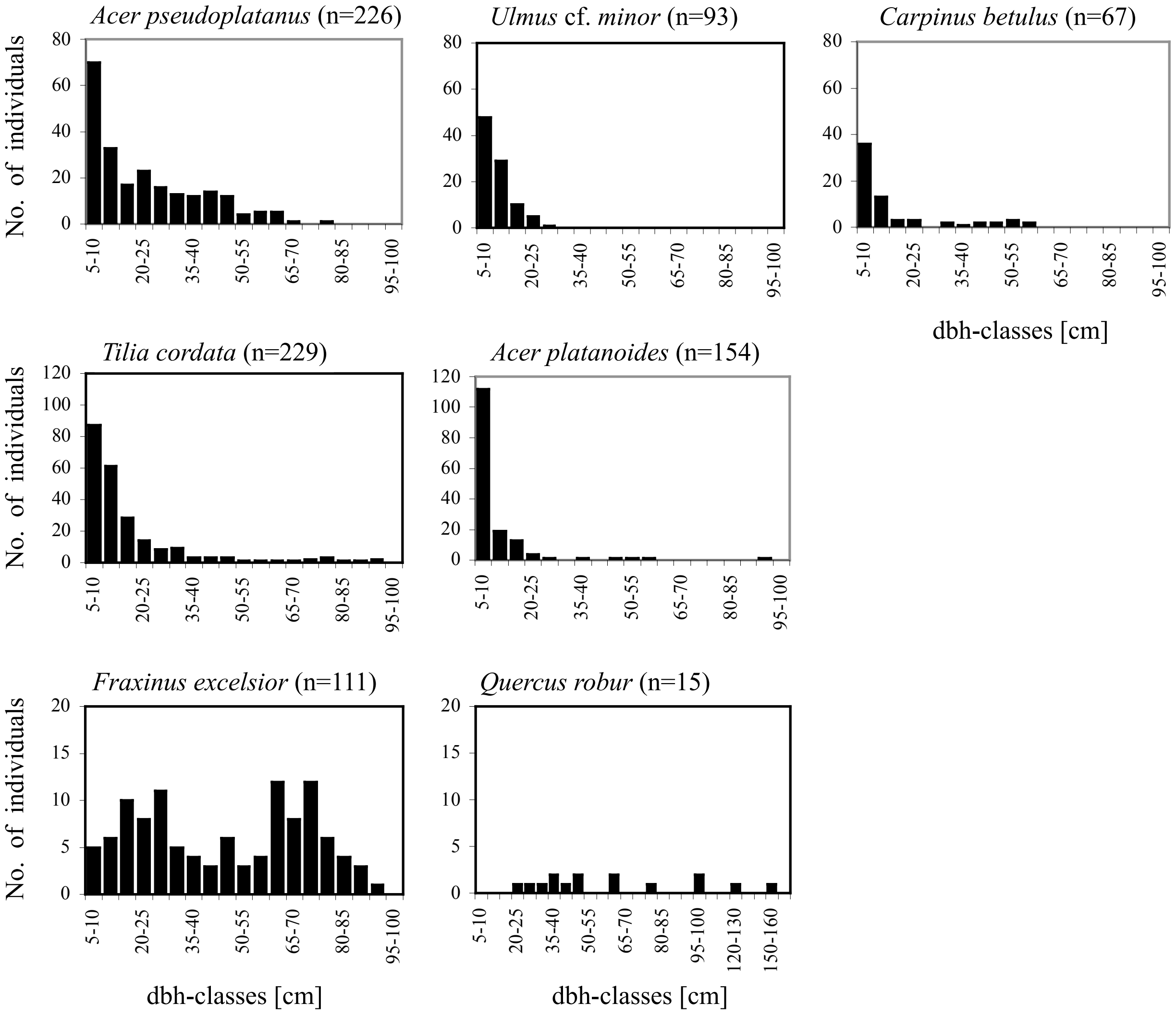

Figure 3 – DBH-class distribution of the seven most important tree species.

The individuals of *Ulmus* cf. *minor* represent basically an independantly regenerating population. The lack of old trees with thick stems is by reason of the dutch elm disease that appeared from the 1960s on.

The population of *Q. robur* does not regenerate naturally. Young plants of this species are completely lacking and there exist only a few but very old trees with very large dbh values. This population structure shows that *Q. robur* belonged to the dominating tree species in earlier times and that actual conditions prevent a natural regeneration of this species.

Due to anthropogenic factors since the last century, there exist a change with respect to species composition in the Leipzig floodplain forest in general. The forestry measures changed from 'Mittelwald-' (coppice-with-standards forests) to 'Hochwaldwirtschaft' (high forests) during the 18^{th} century. This promoted the propagation of shadow-tolerant species such as *Acer* spp. and *Fraxinus excelsior*. In contrast, the growth of species with light-induced germination such as *Carpinus betulus* and *Q. robur* were repressed. The discontinuation of regular inundations as a result of river straitenings enhanced the accumulation of species with a low tolerance against indundations (*Acer* spp.). Additionally a distinct number of nitrophile species could be identified which is due to a growing nutrient input, especially *Acer platanoides* and *Sambucus nigra*.

To conclude, a shift can be observed from a stand rich in *Quercus* and *Ulmus* species towards a forest rich in *Acer* and *Fraxinus*.

Table 1 – Woody species from the investigated forest stand. *: neophytes, **: with only one individual (dbh < 5 cm).

Family	**Species**
Aceraceae	*Acer campestre*
	Acer platanoides
	Acer pseudoplatanus
Corylaceae	*Carpinus betulus*
Fabaceae	*Robinia pseudoacacia**
Fagaceae	*Quercus robur*
	*Quercus rubra**
Hippocastanaceae	*Aesculus hippocastanum**
Oleaceae	*Fraxinus excelsior*
	*Fraxinus pensylvanica**
Rosaceae	*Cerasus avium*
	Crataegus sp.
	*Sorbus aucuparia***
Salicaceae	*Populus x canadensis**
Tiliaceae	*Tilia cordata*
Ulmaceae	*Ulmus cf. minor*
	Ulmus glabra
Caprifoliaceae	*Sambucs nigra*
Celastraceae	*Euonymus europaea*
Cornaceae	*Cornus sanguinea*
Corylaceae	*Corrylus avellana*

1.3 Assessment of vertical forest layers by measurements of light transmittance

Peter J. Horchler

Most forests do show a vertical layering or stratification. This is most obvious in tropical rain forests. It has been stated that temperate forest have a less pronounced stratification, which might be due to an even aged stand structure, at least for the central European often highly managed forests. Detecting this vertical layering, and especially relating it to the question of niche partitioning among forest organisms, causes practical problems including the scaling problem. I tried to get a first assessment of the vertical stratification of the Leipzig forest by measuring the light conditions at different height levels in summer 2003. This was realised conducting 12 detailed PAR measurements along vertical transects, using the canopy crane system. The results revealed a pattern, which seems to be generally applicable in forests. The light conditions in the forest understorey up to ca. 7 m are uniformly dark without high variations. Above this zone, I found one with intermediate but highly varying light levels up to ca. 26 m. Above this zone the light is bright and more constant. Of course there are deviations at a local scale, e.g. in case of tree-fall gaps. These findings set the physical frame for further research concerning niche partitioning among forest organims.

INTRODUCTION

A vertical structuring of forests into several layers has early been recognised especially in tropical rain forests (Richards 1996). There exist the hypothesis that this physical layering would provide additional niche space especially for small forests organisms like arthropods or even birds (e.g. Terborgh 1992). This so called stratification of organisms would hence contribute to the high overall diversity of rain forests. Examples for such a stratification were found e.g. by Perry (1987), who identified certain species of Hymenoptera to be specific to distinct vertical forest layers in Costa Rica. Yet it remained a bit vague, which factors might be responsible for the observed differences. Among those, mostly differences in the distribution of resources (flowers, prey) have been debated. Potential other factors are predator avoidance, but also differences in important microclimatic parameters like temperature, air humidity, light conditions, and wind. Most of the microclimatic factors are correlated. So far only few attempts have been made to try to directly correlate those abiotic factors to vertical differences in arthropod communities, which is mainly due to the inaccessibility of the canopy.

MATERIALS AND METHODS

I took advantage of the existing Leipzig Canopy Crane enabling to lift the crane's gondola virtually to any point in the forest canopy (Morawetz & Horchler 2003). I used the TRAC™-system (Leblanc *et al.* 2002), to measure flux densities (μmol m^{-2} s^{-1}) of photosynthetically active radiation (PAR) on a high-resolution time scale (32 sec^{-1}). I carried out continuous measurements from the forest ground up to the outer canopy at 12 sites within the forest in the study area (Fig. 1). These measurements were conducted in June 2003 around noon (12:00 h to 14:00 h, CET) at clear sky conditions and bright sunshine.

For subsequent analysis the maximum value of each measurement was taken as 100% transmittance of PAR. Since the crane's gondola moves at a more or less constant speed, and the maximum height it reaches is known, I could calculate the mean transmittance (% PAR of max.) and its standard deviation (SD) for every height metre.

RESULTS AND CONCLUSIONS

While every transmittance profile showed quite a high variation mostly in the middle and upper part, the mean curve (Fig. 2) resembles the curve of asymptotic light absorption.

At the forest ground it shows a very low transmittance (1–5%) and little variation up to a height of ca. 7 m. Above this, up to ca. 26 m I found increasing mean values (10–50%) with a very high variation. The upper zone (26–31 m) is characterised by high transmittance levels with decreasing variation.

Hence, the forest stand can roughly be subdivided in a lower dim zone, a transition zone and a bright zone. This seems to be a universal pattern of many forests from the boreal zone (Parker 1997) to the tropics (Anhuf & Rollenbeck 2001). Deviations from this pattern are found in two measurements in tree-fall gaps, where brighter light conditions are found also near the ground.

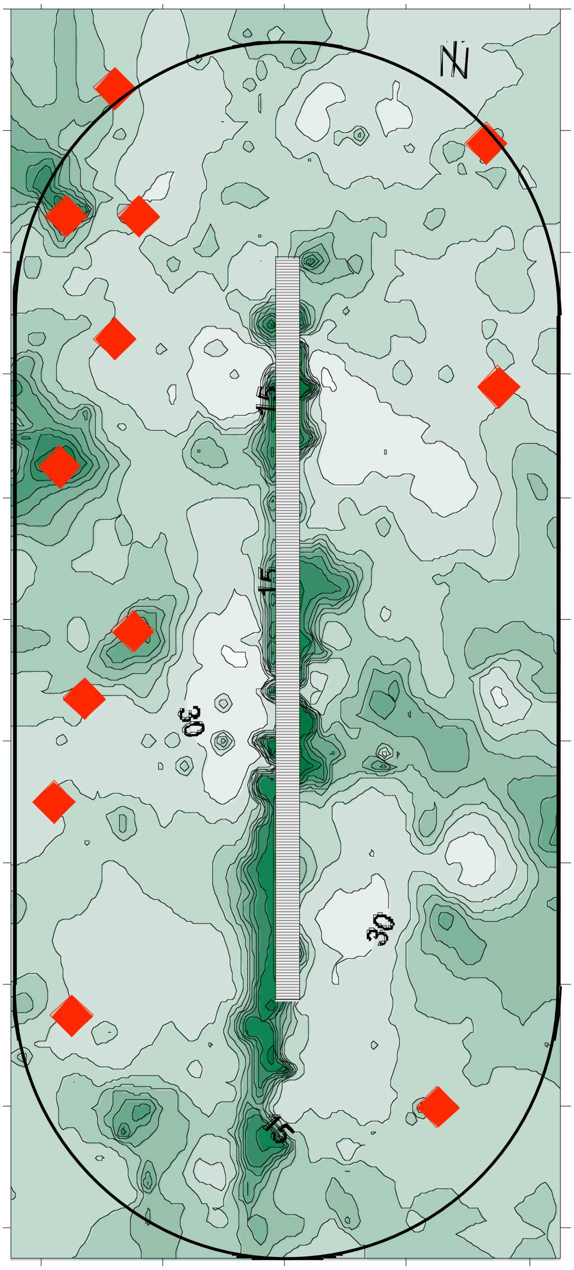

Figure 1 – Location of the 12 sites (red diamonds) for PAR measurements within the crane plot. The shading pattern with isolines represents the canopy surface height (deep green = low height, light green = tall height; compare Rohrschneider this volume). The large ellipsoid outer line delimits the area reached by the crane.

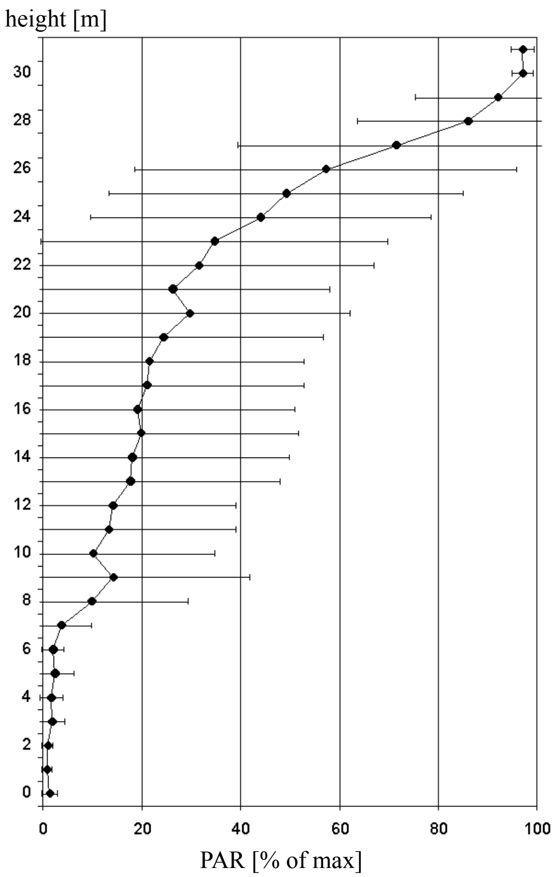

Figure 2 – Transmittance values (% of maximum) of photosynthetically active radiation (PAR) at different heights in the forest canopy. At 12 sites continuous measurements (32 sec^{-1}) have been carried out while moving the crane's gondola vertically from the forest ground up to the outer canopy. The dots represent mean values per height metre (ca. 200 measurement values) the bars represent the standard deviation. The line connects the mean values to show the trend. Note the lower dim zone up to ca. 7 m, the transition zone with a high light variation up to ca. 26 m, and the bright upper zone with less variation.

I could also find a notable difference in single transmittance curves between different tree species. A profile measured within a stand of *Quercus robur* L. (> 200 years old) showed generally much more variation than one taken within a stand of *Fraxinus excelsior* L. (> 130 years old).

The data presented here provide a base for future work at the Leipzig Canopy Crane site as well as for similar forest stands. Microclimatic measurements can be correlated to PAR data in order to check for the indicative power of measurements of transmittance, which can easily be carried out.

Furthermore, it remains to be tested if forest organisms respond to the three light zones found here, as well as to finer differences like those found between

Quercus robur and *Fraxinus excelsior* stands. Some evidence for a positive correlation of transmittance values with the degree of folivory at leaves of *Acer pseudoplatanus* was already found (Mitscherling & Horchler, this volume).

Contrarily to statements that temperate forest may lack a pronounced stratification of forest organisms (e.g. Basset *et al.* 2003), I believe that more evidence will be found for such a stratification at the Leipzig site, just as it was found at a temperate cool, mixed deciduous forest in Northern Japan (Tanabe 2002; Murakami & Hiura 2003).

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1.4 Measurement of the canopy height and visualisation of its surface structure

Markus Rohrschneider[1], Peter J. Horchler & Wilfried Morawetz

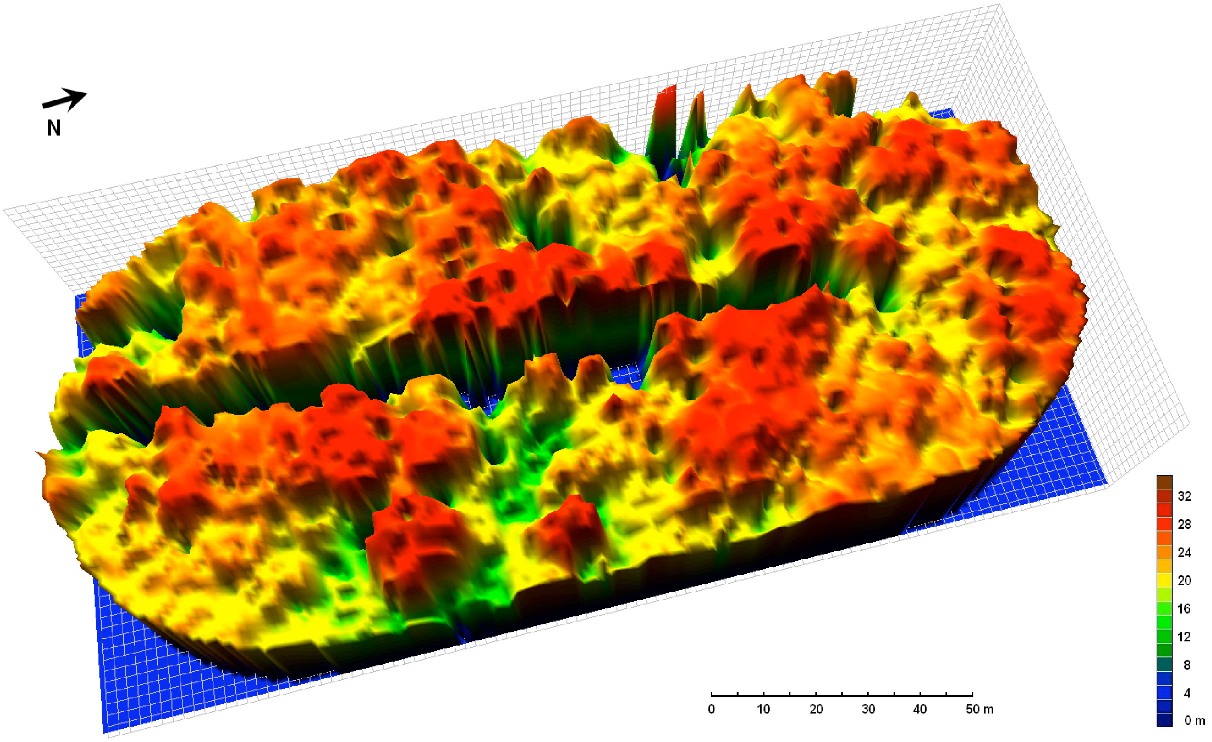

Figure 1 – Surface model of the upper crown area.

SHORT COMMUNICATION

The surface of the canopy crown is commonly considered as being quite smooth. Though, canopies of natural mixed forest are often clearly structured. A detailed knowledge of the forest and canopy structure provides excellent baseline information for many ecological studies such as microclimatic and plant-physiological research.

By using the Leipzig Canopy Crane facility, we measured the height difference between the crown surface and the crane jib on an area of approx. 1.6 ha. The distance between the measuring points was 2.0 by 2.0 m along the rectangular side of the rail track. In the case of the northern and southern curve, it was more convenient to approximate the linear 2 by 2 grid by polar coordinates. If the distance between two measuring points fell below 1.2 m, points were omitted (Fig. 2). In the next step, the mesh was converted into a rectilinear grid (1 by 1 m) by bilinear interpolation. To visualise the height profile, a simple height field function of an OpenGL implementation for Borland Delphi was used taking advantage of the sampling step performed earlier (Fig. 1). Besides the height field visualisation, simple summary statistics were calculated to characterize the topography. The maximum height was 35.5 m, mean 24.5 m, median 25.8 m and the standard deviation, also termed "rugosity" (Parker & Russ 2004) of 5.74 m (Variation coefficient 23.4%).

One further characteristic parameter is the Gap Fraction, which describes the fraction of canopy area with

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[1] corresponding author

a height less than one meter. In the area of interest (excluding artificial gaps, i.e. rail, paths) the gap fraction was approx. 1.3% (198 m^2 of 15 212 m^2).

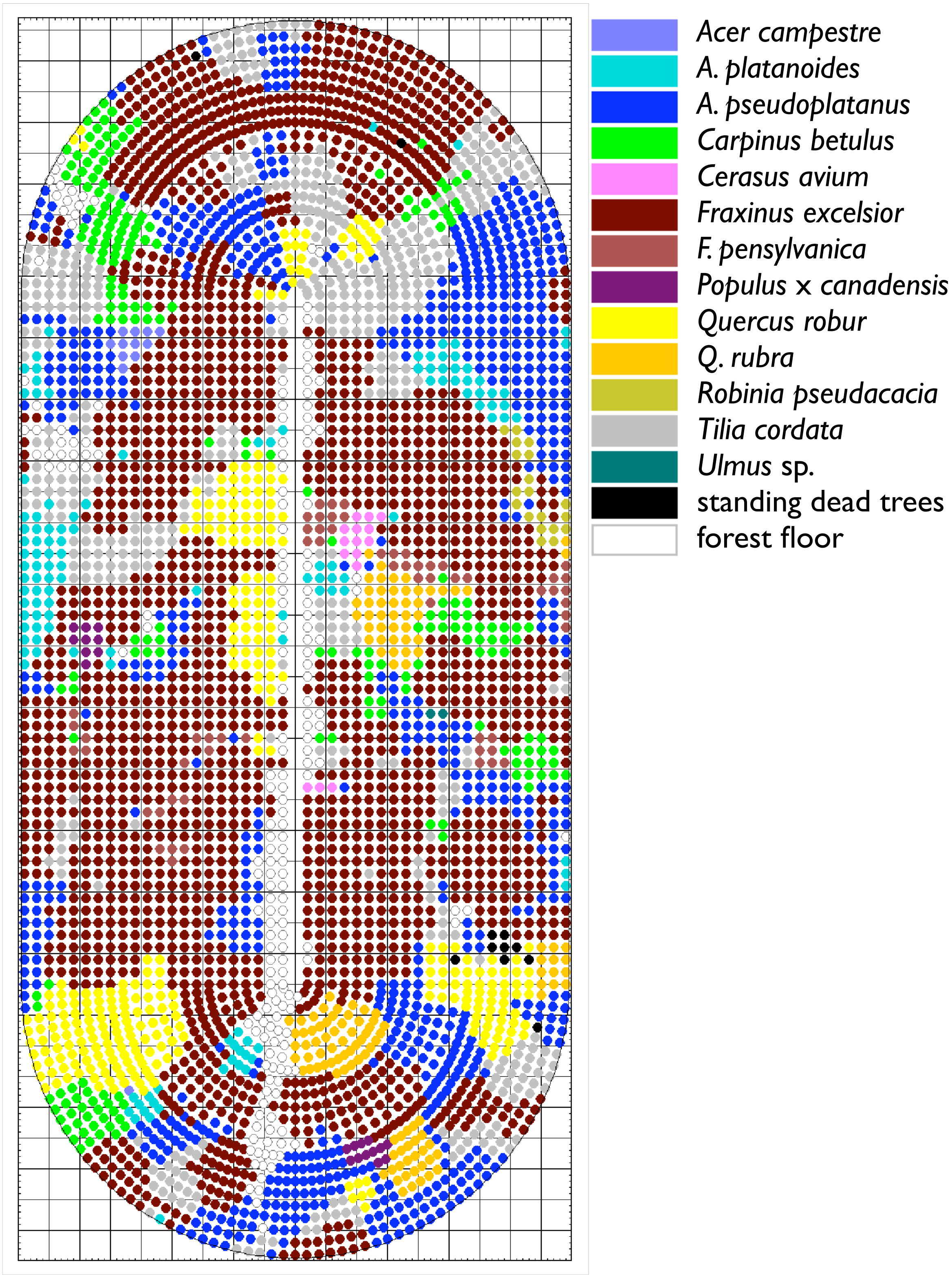

Fig. 2 – Position of the measuring points on the plot. Tree species are colour coded. The underlying grid is 5 x 5 m.

The species distribution with their fraction of the surface area and the heights distribution is shown in Fig. 3.

The topographic image reveals a rather heterogenous structure of the upper crown surface. The previously mentioned values are basic parameters suitable to compare different forests regarding their structure. Local barriers, e.g. for pollination, can be examined with the topographic maps and competition between individuals regarding light or space can be modelled. In this respect, the contact between individual tree crowns is of interest. Based on the height data and including the species information, those contacts are subject to further investigation.

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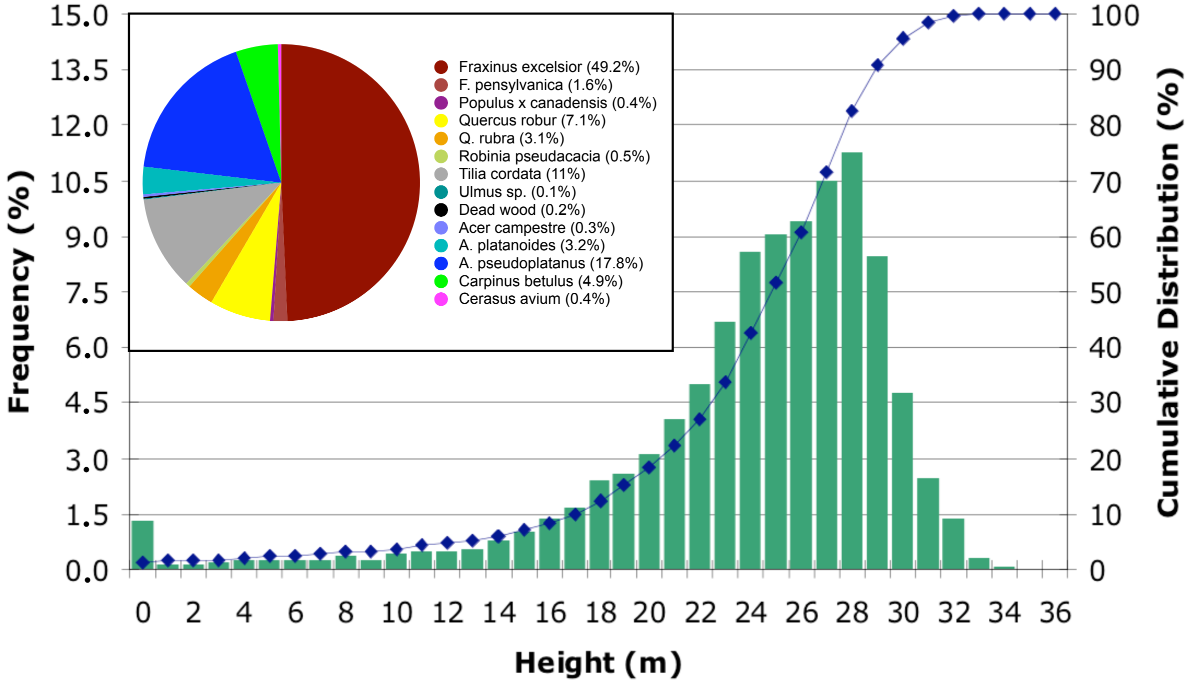

Fig. 3 – Distribution of canopy species, heights, and cumulative distribution (Hypsograph). Inset: surface area cover (%) of the canopy species.

1.5 Tree seedling establishment and pattern formation–regeneration dynamics of a floodplain forest in central Europe (Germany)

Claudia Schöne & Anke Jentsch[1]

We obtained a differentiated profile concerning the establishment and pattern formation of tree seedlings in a floodplain forest near Leipzig. Irrespective of species composition, seedlings and saplings are not distributed homogeneously, but distributed in clumps up to distances between 8 m and 14 m across a floodplain forest area. The seedlings and saplings differ species-specifically with reference to the distance at which their distribution patterns become emergent. Dispersal strategies help to explain the seedling patterns found. For some species, the spatial pattern of seedlings correlates positively with the canopy space from a distance of 2 m onwards (e.g. *Quercus robur*, *Acer pseudoplatanus*), for others, negatively (e.g. *Acer platanoides*, *Fraxinus excelsior*). The spatial pattern of saplings correlates negatively with the distribution of adult trees for nearly all species. This points to the effective factors at different times in the life cycle: seed production, dispersal distance, sheltered positions for germination, competition for resources. As expected, the examined tree species have different dispersal mechanisms, fruit weights and fruit quantities. The wind-dispersed, light and hence low-resource fruits are produced by adult trees in large quantities, but only show a low germination rate (max. 1.4%). Species with low fruit production show a significantly higher germination rate (max. 8%).

INTRODUCTION

Tree species composition in a German floodplain forest near Leipzig has undergone remarkable changes in the past 100 years: the proportion of oaks (*Quercus robur*), whose regeneration has practically ceased for decades, and of elms (e.g. *Ulmus glabra*) has declined sharply, while by contrast the proportion of maple (*Acer platanoides*, *Acer campestre*) and ash (*Fraxinus excelsior*) has increased. Due to the absence of flooding and due to general eutrophication, the Norway maple in particular (*Acer platanoides*) has been finding its way into the floodplain forest ever more forcefully in recent decades (Müller & Zäumer 1992).

The aim of this study is to analyse the regeneration capacity of floodplain forest tree species under the current conditions and to quantify the spatial patterns of the seedling establishment that takes place. The interest is also to find out whether stand of species that have become rarer, such as oak and elm, recover by means of successful regeneration. Germination and seedling establishment is the most sensitive phase of the life cycle of most tree species.

Analysing the regeneration capacity of the Leipzig floodplain forest is of particular nature conservational interest, since various initiatives are striving to restore the floodplain forest to its original dynamics and species composition (Teubert 1994). Past changes and damage can be attributed for the most part to the drying out of the floodplains, due to human influences (such as the settlement and leisure activity of more than 500 000 inhabitants of the neighbouring city of Leipzig) on the one hand, and on the other, to the rising area of the earth and the distancing from the water table ascribable to the rivers' natural tide dynamics and sedimentation (Haase 1999). As a result of decades of pollutant seepages originating from industrial and transportation use, construction activity and open-cast brown coal mining in the southern region of Leipzig, heavy metals, flying ash remnants and organic pollutants had amassed in forest soils and floodplain waters in addition (Haase & Schneider 2001).

Dispersal, germination and establishment of tree seedlings

In angiosperms, which are the subject of this study, diaspores assist in dispersal and reproduction. Their aim, with the aid of various dispersal mechanisms, is to reach and colonise potential locations. Often, favourable positions with an appropriate microclimate and availability of resources for colonisation are rare, unstable, unevenly distributed or only available

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[1] corresponding author

temporarily. Among other things, the morphology and seasonality of fruits are decisive for dispersal opportunities and methods. In addition, heavy rainfall and, particularly in the floodplain, inundations play a significant role in transportation. Once the diaspores have reached a favourable location for germination, metabolism by means of respiratory energy conversion is activated either immediately or following a period of rest, and the germination phase begins. First, the reserve substances in the seedling's endosperms are mobilised and used up. This event is defined as the beginning of germination (LARCHER 1994). Photosynthetic activity for autotrophic feeding of the seedling begins only once the cotyledons have turned green, or the first green leaves have appeared, respectively, and the germination procedure is concluded. This phase is described as initial growth (URBANSKA 1992). In addition to abiotic environmental factors, neighbouring plants in particular play an important role in successful seedling establishment. This role can be both stimulating, for example by protecting against direct solar radiation, or inhibiting, for example due to strong competitive pressure. From a spatio-temporal point of view, therefore, natural regeneration is an extremely heterogeneous procedure (Küssner & Wagner 2002). It is dependent upon the number and distribution of mother trees as well as upon the heterogeneity of environmental factors such as free space, soil, light, nutrient and water supply, phytophagous species and inter- and intra-species competition.

The mortality rate of seedlings is determined by the density of the seedling pool in forests (STRENG *et al.* 1989, KÜSSNER 2003). Since mortality rates are species-specific, species composition during the course of the regeneration of seedlings to saplings can vary considerably. This transitional phase is principally characterised by competition processes (COLLINS 1990, JONES *et al.* 1994, GEORGE & BAZZAZ 1999).

Spatial patterns

Ecologists study spatial patterns in order to find clues to underlying mechanisms (PERRY *et al.* 2002). Patterns are variation in density in comparison with randomly distributed individuals (DUTILLEUL & LEGENDRE 1993). Thus, various patterns can result from plant distributions originating from different processes and conditions which have an effect on various scales. Analysis of the resulting spatial structures can provide evidence of the existence of these underlying processes. A regular distribution of individuals can, for example, be an indication of strong competition for homogeneously distributed resources. Of course, different processes can lead to the same spatial pattern (WIEGAND 2002). Methods for the analysis of spatial point patterns, based on Ripley's K function, have seen a rapid development in recent years (PERRY *et al.* 2002) and are now widespread.

In order to quantify spatial pattern, it is necessary to use suitable area extent for the examination which is actually capable of capturing the mechanisms having an effect at a defined scale (JUHÁSZ-NAGY & PODANI 1983). In the present study, the task was to quantify the establishment, dynamics and spatial pattern formation of tree seedlings of the most prominent tree species of the floodplain forest near Leipzig, *Acer platanoides*, *Acer pseudoplatanus*, *Quercus robur*, *Fraxinus excelsior*, *Carpinus betulus*, *Ulmus* sp., and *Tilia cordata* in their current state.

We assume that the various tree species have different regeneration strategies. Therefore, we state the following hypotheses: **(1)** Irrespective of species composition, seedlings and saplings are not homogeneously distributed across a floodplain forest area. **(2)** Patterns of seedlings and saplings differ according to species. **(3)** The spatial distribution of seedlings and saplings of one species is independent of the spatial distribution of adult trees of the same species. **(4)** Fewer seedlings of the same species establish beneath the mother trees, due to intra-species competition for resources between life stages.

MATERIALS AND METHODS

The study site is located in the Leipzig hardwood floodplain (Burgaue nature reserve, 102 m a.s.l.) directly at the Leipzig Canopy Crane on the south-eastern edge of the central German semi-arid region and is only inundated at peak tide. Mean annual rainfall is approximately 500 mm, mean annual temperature 8.9 °C (ZÄUMER 1996). The plots in our study site cover 30 m x 100 m, so 3 000 m^2, which were divided by a fine grained grid measuring 1 m x 1 m.

Data aquisition: spatial patterns

In order to record the spatial patterns of adult trees, their seedlings and saplings, the exact location of these units of *Acer platanoides*, *Acer pseudoplatanus*, *Quercus robur*, *Fraxinus excelsior*, *Carpinus betulus*, *Tilia* sp. and *Ulmus* sp. was noted on a map between May and August 2002. Subsequently, the data were transferred to a binary list with co-ordinates. Further, all offsprings were recorded according to their size class: seedlings up to a height of 20 cm , saplings at a height of 21 cm–50 cm and saplings at a height of 51 cm–100 cm . Growth height is used as an indirect measurement for age, using internode compression with an accumulation of bud scales and scars, which always appears at the beginning and end of a vegetation period (Troll 1954). The age of all units was determined on the basis of 10 individuals from each species and from each size class. All positions of adult trees, seedlings and saplings were depicted on species-specific maps, in order to generate digital point patterns of all individuals according to category. A circle with a radius of 5 m was drawn around the adult trees as an idealised canopy perimeter for determining seedling density beneath adult trees. This circle corresponds to a area of 78.54 m^2. In overlapping areas of several adult trees, half of the seedlings were ascribed to each adult tree. On indicating the number of seedlings per area content, all data were standardised to an area measuring 10 m^2 in order to ensure comparability with other investigations.

Data analysis: mortality rate, establishment rate, spatial statistics

Species-specific mortality rate was calculated from the distribution of size classes. The establishment rate equals the proportion, as a percentage, of saplings 51 cm–100 cm in size compared with the number of seedlings in the youngest stage, which was standardised respectively as 100%.

Analysis of spatial patterns was conducted by means of spatial statistics using PROGRAMITA (Wiegand 1999). Several methods were combined in the process.

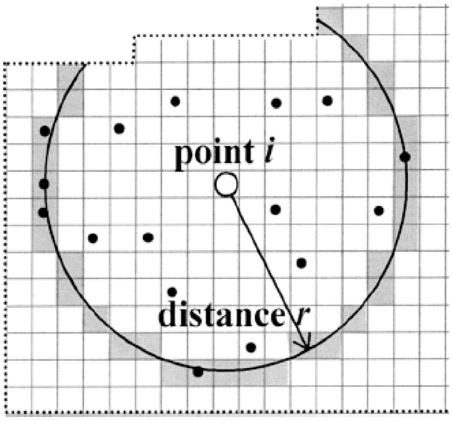

Figure 1 – The O-ring statistic is based on the distance between all point pairs of a pattern and counts the data points on a ring with a distance r from every data point. It describes typical features of point patterns across a range of distance scales and is therefore able to discover mixed patterns, e.g. scattering on smaller and clumping on larger distances (Wiegand & Moloney 2004).

(A) The positions of seedlings and adult trees were characterised by means of Ripley's K and L function for uni- and bivariate statistics along a series of scales. Thus, clumping or scattering can be quantified up to a distance r.

(B) In parallel to the K function, Wiegand-Moloney's O-ring statistic was used (Fig. 1), a density-probability function with interpretation of the neighbouring density. It conveys the expected number of points (tree seedlings of one species) on a distance r (metres), departing from an arbitrary point (seedling or adult tree), divided by pattern intensity λ. At its maximum, radius r is half the width of the shorter investigation area boundary (Wiegand 2004). In this study radius r = 10 m and a confidence interval of 0.05 was chosen.

(C) Since we assume that data points outside the investigation area contribute significantly to the characterisation of the pattern, we adjusted the edge. For this purpose a buffer zone of the size of the maximum radius distance r was created around the main investigation area. However, only points which lie within the actual investigation area of 3 000 m^2 were used for point pattern analysis.

(D) In order to test the homogeneity of individual species, or to discover "holes" of extremely small point density in the investigated patterns, homogeneity tests were carried out. In order to keep to the methods developed for homogeneous patterns, it is possible to define homogeneous sub-areas of one heterogenic point pattern and analyse the spatial structure there (Pelissier & Goreaud 2001). This result is a null model, which is not tested randomly, but according to first order heterogeneity. In accordance with the "first order heterogeneity" null model, the Monte Carlo simulation thus distributes the simulated points (seedlings) while randomly taking account of the first order heterogeneity across the investigation area. In order to obtain representative data, 99 repetitions were selected.

The maps depict **(1)** first order density in colours of the spectrum (blue: low density, pink: high density), and diagrams showing **(2)** the distribution frequency of the data points within the circles with radius r in all cells of the investigation area; the **(3)** expected distribution frequency under complete spatial randomness (CSR); and the **(4)** expected Poisson values for the test whether the seedlings of the tree species are distributed across the area homogeneously. For the point pattern analysis, therefore, the seedling pattern of one species was tested 99 times against the created null model, or seedling and adult tree patterns tested against each other, respectively. Analysis was conducted as to whether the seedling patterns are clumped, random or regular, and up to which distances, or on which scales, respectively, the patterns become emergent. Moreover, it can be tested whether the pattern of seedlings is significantly spatially correlated with the pattern of adult trees.

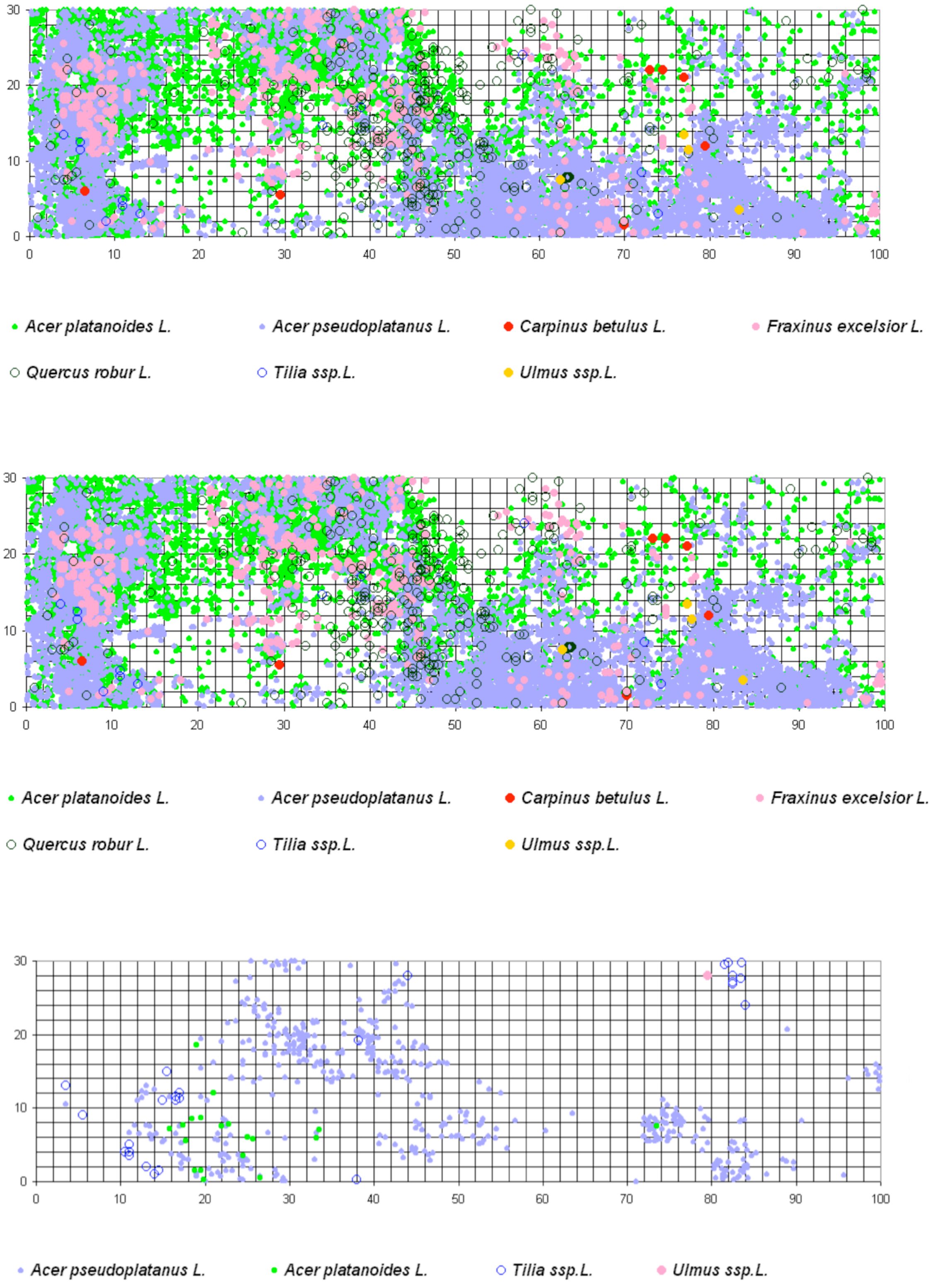

Figure 2 – Top: Individual density of seedlings (up to 0.2 m growth height); Middle: medium-sized saplings (0.2 m–0.5 m growth height); Bottom: tall saplings (0.5 m–1.0 m) of various tree species in a 3 000 m^2 floodplain forest area near Leipzig in 2002.

Table 1 – Number, proportion [%] and density [m^2] of seedlings and adult trees of various species in a floodplain forest measuring 3 000 m^2 in size near Leipzig.

Tree species	Number of seedlings	Proportion of seedlings [%]	Density of seedlings [m^2]	Number of trees	Proportion of trees [%]	Density of trees [m^2]
Quercus robur	377	2.15	0.13	2	1.20	0.01
Acer platanoides	7757	44.15	2.59	46	27.71	0.02
Acer pseudoplatanus	8821	50.21	2.94	27	16.27	0.01
Fraxinus excelsior	548	3.12	0.18	21	12.65	0.01
Ulmus sp.	5	0.03	0.01	7	4.22	0.01
Tilia sp.	51	0.29	0.02	50	30.12	0.02
Carpinus betulus	9	0.05	0.01	13	7.83	0.01
Sum	17.568	100.00	5.9	166	100.00	0.1

Table 2 – Diaspore type, seed weight, dispersal mechanism and shade tolerance of seedlings from 7 floodplain forest tree species. Seed weights are taken from Luftensteiner 1982, seed quantities per "standard adult tree" from the following authors: [a]: Tal 2003, [b]: Küssner 2002 in Roloff *et al.* 2002. n.i.: "not indicated".

Tree species	Diaspore type	Weight [mg]	Dispersal type	Seed quantity
Quercus robur	single-seeded nuts	n.i.	Falling / animal	1 000[a]
Acer platanoides	winged fissile fruit	134.5	Wind	10 000[a]
Acer pseudoplatanus	winged fissile fruit	128.6	Wind	10 000[a]
Fraxinus excelsior	winged nuts	74.8	Wind / animal	76 000[a]
Ulmus sp.	winged nuts	n.i.	Wind	114 000[b]
Tilia sp.	winged nuts	181.0	Wind / root growth	11 000[b]
Carpinus betulus	nuts with bearing leaf	56.8	Wind / animal	n.i.

RESULTS

Age and establishment of seedlings

In 2002, a total of 17 568 seedlings and 166 adult trees from seven different species were detected on a 3 000 m^2 section of floodplain forest (cf. Table 1). This corresponds to an average seedling density of 5.9 per m^2 and a ratio of 106 seedlings per adult tree. 16 578 seedlings alone belonged to the genus *Acer* (*Acer platanoides* 7 757 seedlings = 44.15%, *Acer pseudoplatanus* 8 821 seedlings = 50.21%), that is 94.4% of the total number of all seedlings. 27.71% of adult tree individuals belonged to *Acer platanoides* and 30.12% of adult tree individuals to *Tilia cordata*, 26.3% to *Acer pseudoplatanus.*

The age of the detected seedlings and saplings up to a size of 1 m differed clearly among the tree species investigated. Seedlings from the current vegetation period only were found of *Quercus robur.* Seedlings and saplings of other tree species covered a larger age range: individuals of *Fraxinus excelsior* were detected from freshly germinated up to 15 years of age, of *Acer platanoides*, *Acer pseudoplatanus*, and *Tilia cordata* from freshly germinated up to 25 years old, of *Carpinus betulus* from freshly germinated up to 4 years old. *Ulmus* sp. showed freshly germinated individuals up to 20 cm in size, and in size group 0.5 m to 1 m exclusively, highly deformed plants with an age of at least 15 years.

All individuals with a growth height between 0.5 m and 1.0 m are deemed established. This height was achieved by only 3.3% of all mapped seedlings and saplings. Numbers of individuals were distributed in the three size classes as follows: 15 114 seedlings up to 0.2 m, 2 430 saplings between 0.2 m and 0.5 m, 503 saplings between 0.5 m and 1.0 m. The mortality rate from germination to establishment varied among the floodplain forest species: *Acer platanoides* 88% (100% from seedling to sapling), *Acer pseudoplatanus* 82% (94%), *Quercus robur* 77% (100%), *Ulmus* sp. 75% (75%), *Carpinus betulus* 71% (100%), *Fraxinus excelsior* 70% (100%). Only for *Tilia cordata* was the mortality rate zero overall. The mortality rate up to saplings of 1.0 m growth height was therefore 100% for all species, except for *Acer pseudoplatanus* 94%.

Pattern formation and dynamics of seedling establishment

Maps of the spatial patterns of seedlings (up to 0.2 m growth height), small saplings (0.2 m–0.5 m growth height) and tall saplings (0.5 m–1.0 m) on the

3 000 m^2 floodplain forest area are depicted in Fig. 3. The declining density of individuals from seedlings to saplings of all tree species in the floodplain forest can be seen clearly. Furthermore, a clear clumping of seedlings occurred on various scales. However, this pronounced spatial clumping likewise declined during the course of seedling establishment. It can be assumed that there is already high density competition at the germination stage, dominating the most sensitive phase in the life cycle of several floodplain forest species.

Location of the seedlings in relation to adult trees

The spatial location of the seedlings varies widely among the various species. Of *Quercus robur*, 90% of all seedlings were found directly beneath the idealised canopy space, of *Fraxinus excelsior* just 10% in the 5 m radii around the adult trees (Fig. 2). Of *Tilia cordata*, *Carpinus betulus*, and *Ulmus* sp., only slightly more seedlings were found within the idealised canopy space than in the rest of the floodplain forest area. A random, mutually independent distribution of life stages dominated in *Acer platanoides* and *Acer pseudoplatanus*. Literature references to diaspore type, seed weight and dispersal mode of all investigated tree species are listed in Table 2.

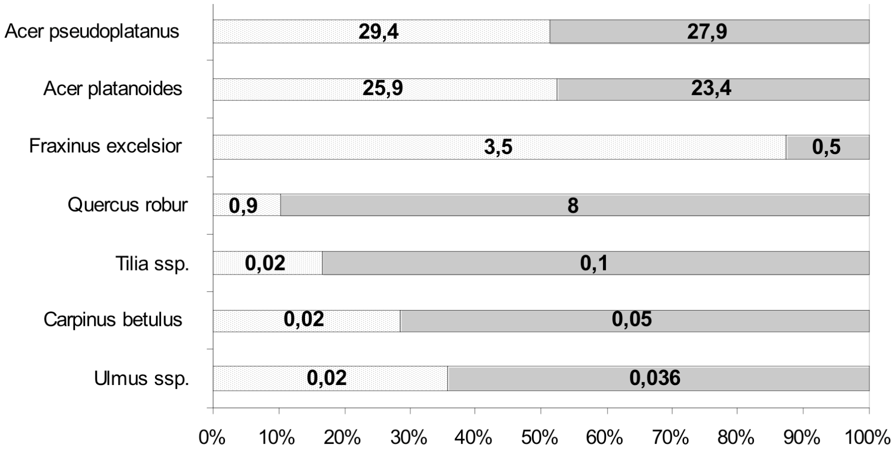

Figure 3 – Proportion of all seedlings and saplings inside and outside the idealised canopy space of the species-specific mother tree (radius r = 5 m).

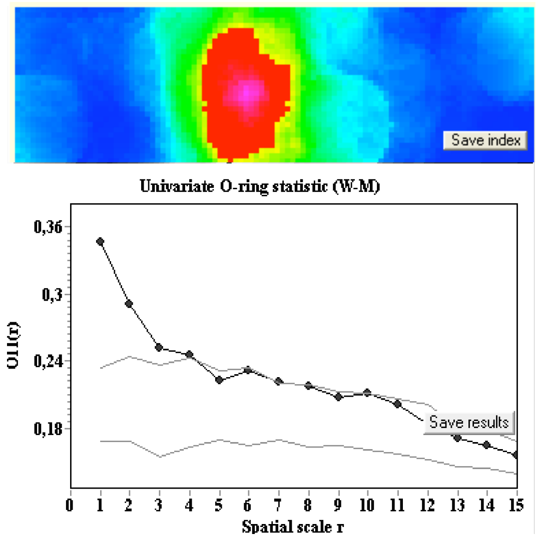

Figure 4 – *Quercus robur* seedlings (up to 0.2 m). Top: Depiction of seedling density (first order heterogeneity). Bottom: Scale emergence of the pattern by means of univariate O-ring statistics.

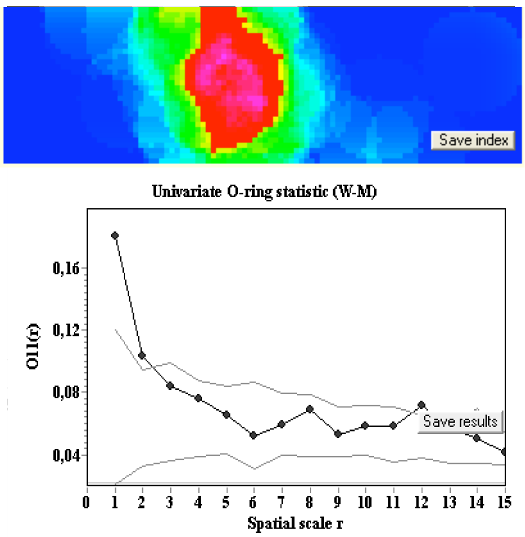

Figure 5 – *Quercus robur* saplings (0.2 m–0.5 m). Top: Depiction of sapling density (first order heterogeneity). Bottom: Scale emergence of the pattern by means of univariate O-ring statistics.

Species-specific pattern formation of various life stages of the floodplain forest trees

The following is a visual depiction and discussion of the spatial patterns of all seedlings and saplings of the floodplain forest species with strong regeneration (depiction for species with a pronounced seedling emergence as indirect density distribution in accordance with "first order heterogeneity", for species with very low seedling emergence, with direct location). Visual depiction was omitted for tree species with very low seedling emergence.

Quercus robur

The spatial pattern of seedlings of *Quercus robur* is clearly clumped up to a distance of 4 m, thereafter randomly distributed (Fig. 4). The average number of seedlings in a circle with a radius of 10 m around one single seedling was 38. Seedling emergence is at its highest immediately where the two adult trees stand. The spatial distribution of saplings (0.2 m–0.5 m) shows clumping on two different scales: from 0 m-2 m and from 12 m–14 m (Fig. 5). This life stage has its highest density in places with low seedling emergence and at a larger distance from adult trees. Saplings with a growth height of 0.5 m–0.1 m were not found. Overall, the distribution of seedlings and saplings of the genus *Quercus robur* in the floodplain forest shows a pattern intensity of $\lambda = 0.24$. Comparison of the spatial distribution of seedlings and adult trees results in a highly significant 1st order correlation for distances around adult trees of between 4 m–9 m, for older seedlings (up to 0.5 m growth height) for distances from 2.5 m–4 m and 2^{nd} order for distances from 5.5 m–8 m (Fig. 6). Significant spatial clumping of seedlings around adult trees is therefore recognisable for both life stages.

Acer platanoides

The spatial pattern of seedlings of *Acer platanoides* is clearly clumped up to a distance of 7.5 m, thereafter randomly distributed (Fig. 7). The average number of seedlings in a circle with a radius of 10 m around one single seedling was 785. Seedlings only appear in a scattered manner where adult trees stand most densely. However, in contradiction to this a particularly high seedling density can be seen in the vicinity of the largest adult tree.

The spatial pattern of saplings (0.2 m–0.5 m) is likewise clumped up to a distance of 6.5 m (Fig. 8). This life stage has its highest density in places with low seedling emergence and at a larger distance from adult trees. The spatial pattern of saplings with a growth height of 0.5 m–0.1 m is scattered in a totally random manner and also not correlated with the pattern of adult trees (Fig. 9).

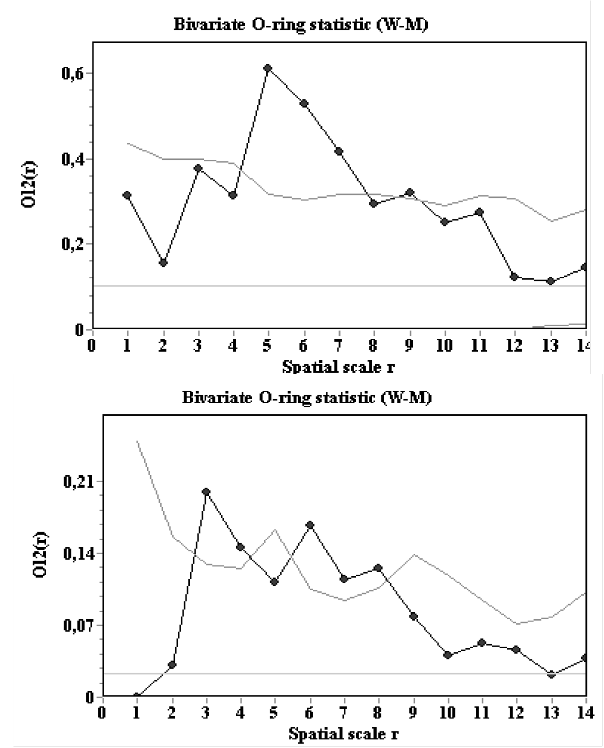

Figure 6 – Bivariate analysis of the patterns of seedlings and adult trees of *Quercus robur*. Top: Seedlings up to 0.2 m growth height with adult trees, bottom, saplings of 0.2 m–0.5 m growth height with adult trees.

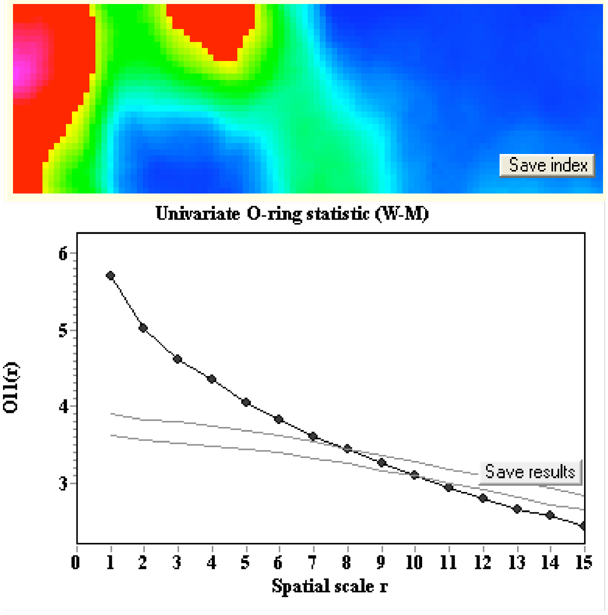

Figure 7 – *Acer platanoides* seedlings (up to 0.2 m). Top: Depiction of seedling density (first order heterogeneity). Bottom: Scale emergence of the pattern by means of univariate O-ring statistics.

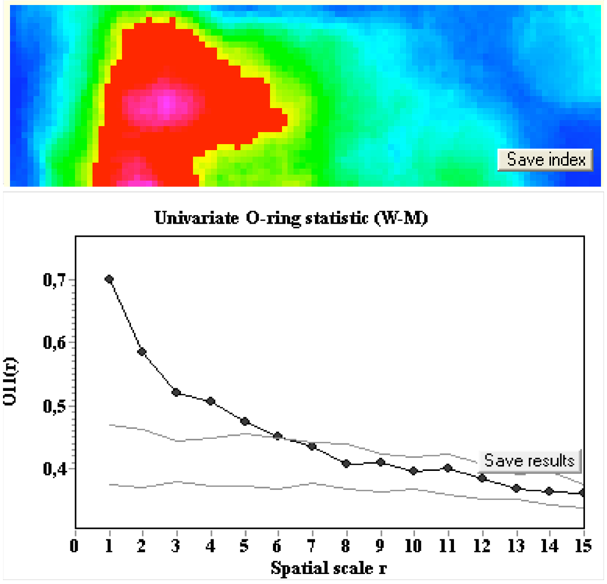

Figure 8 – *Acer platanoides* saplings (0.2 m–0.5 m). Top: Depiction of sapling density (first order heterogeneity). Bottom: Scale emergence of the pattern by means of univariate O-ring statistics.

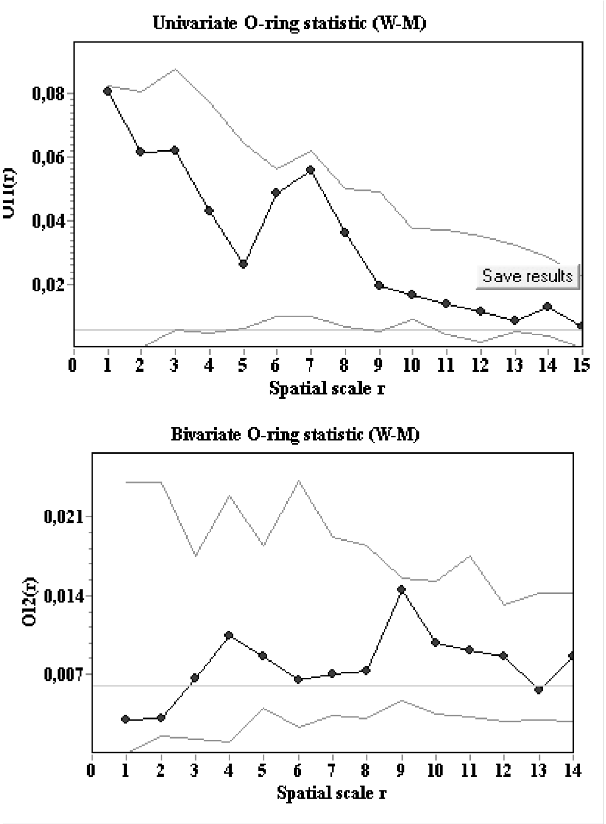

Figure 9 – *Acer platanoides* saplings (0.5 m–1.0 m)-top: scale emergence of the pattern by means of univariate O-ring statistics; bottom: bivariate analysis of saplings and adult trees.

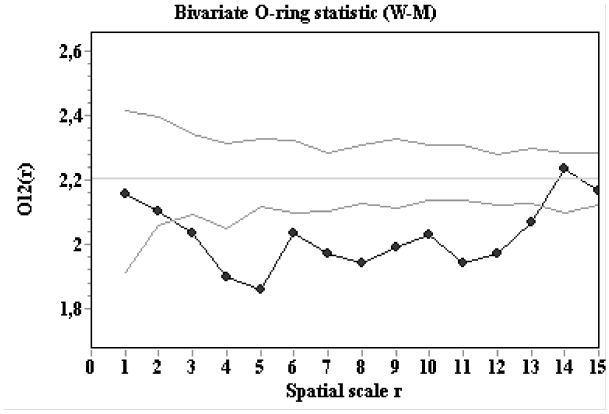

Figure 10 – Bivariate analysis of all seedlings and adult trees of Acer platanoides.

Overall, the distribution of seedlings and saplings of the genus *Acer platanoides* in the floodplain forest shows a pattern intensity of $\lambda = 3.90$. Comparison of the spatial distribution of seedlings and adult trees results in a random relationship up to a distance of 2.5 m, mutual rejection between 2.5 m and 13.5 m, and a random relationship again thereafter (Fig. 10). Therefore, no significant spatial correlation between the distribution of seedlings or saplings and the canopy of adult trees can be recognised.

Acer pseudoplatanus

The spatial pattern of seedlings of *Acer pseudoplatanus* is clearly clumped up to a distance of 10.5 m, thereafter randomly distributed (Fig. 11).

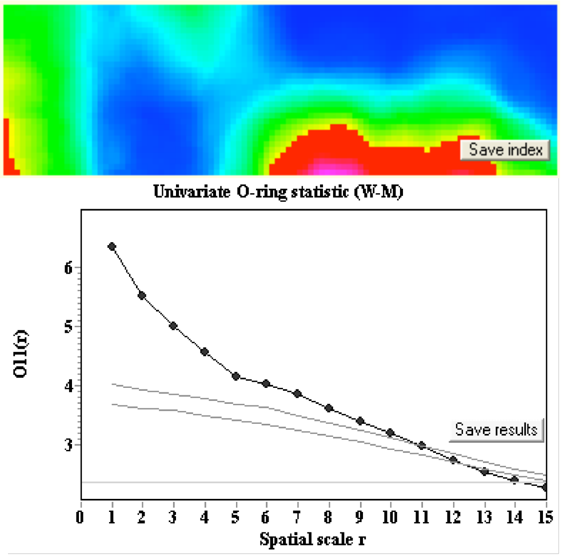

Figure 11 – *Acer pseudoplatanus* seedlings (up to 0.2 m). Top: Depiction of seedling density (first order heterogeneity). Bottom: Scale emergence of the pattern by means of univariate O-ring statistics.

The average number of seedlings in a circle with a radius of 10 m around one single seedling was 893.

Seedlings achieve their highest density where adult trees also stand most densely. The spatial pattern of saplings (0.2 m–0.5 m) is likewise clumped up to a distance of 7.5 m (Fig. 12). This life stage has its highest density in places with low seedling emergence and at a larger distance from adult trees. The spatial pattern of saplings with a growth height of 0.5 m-0.1 m is clumped up to a distance of 5 m (Fig. 13). Overall, the distribution of seedlings and saplings of the genus *Acer pseudoplatanus* in the floodplain forest shows a pattern intensity of $\lambda = 3.85$. Comparison of the spatial distribution of seedlings and adult trees results in a random relationship up to a distance of 8.5 m, then a spatial correlation at a distance between 8.5 m and 13 m. With reference to the distribution of saplings of growth height 0.2 m–0.5 m, rejection from the adult trees is clear up to a distance of 3.5 m, in saplings of growth height 0.5 m–1.0 m rejection up to distance of 6 m (Fig. 14).

Fraxinus excelsior

The spatial pattern of seedlings of *Fraxinus excelsior* is clumped up to a distance of 8.5 m, thereafter randomly distributed (Fig. 15). The average number of seedlings in a circle with a radius of 10 m around one single seedling was 55. There are no seedlings to be found in the immediate vicinity of the adult trees. The spatial pattern of saplings (0.2 m–0.5 m) is likewise clumped up to a distance of 6 m (Fig. 16). This life stage has its highest density at a larger distance from the adult trees. Saplings with a growth height of 0.5 m–0.1 m were not found. Overall, the distribution of seedlings and saplings of the genus *Fraxinus excelsior* in the floodplain forest shows a pattern intensity of $\lambda = 0.31$. Comparison of the spatial distribution of seedlings and adult trees results in a significant rejection up to a distance of 15 m, then a random relation of both patterns. With reference to the distribution of seedlings of growth height 0.2 m–0.5 m, only a random relation to the distribution of adult trees is indicated (Fig. 17).

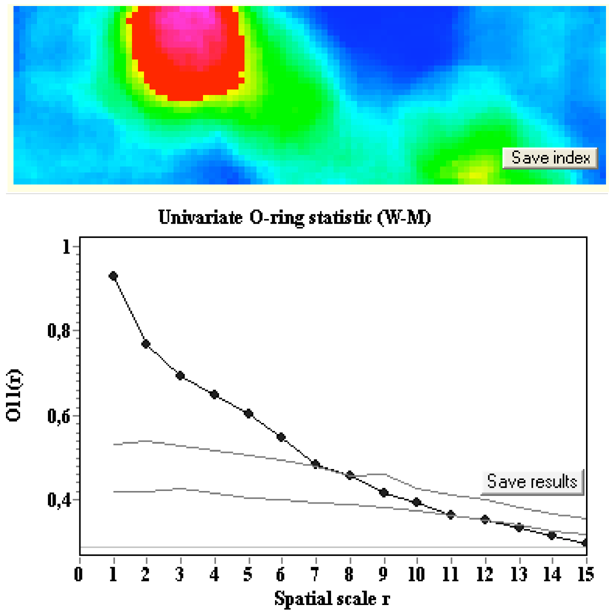

Figure 12 – *Acer pseudoplatanus* saplings (0.2 m–0.5 m). Top: Depiction of sapling density (first order heterogeneity). Bottom: Scale emergence of the pattern by means of univariate O-ring statistics.

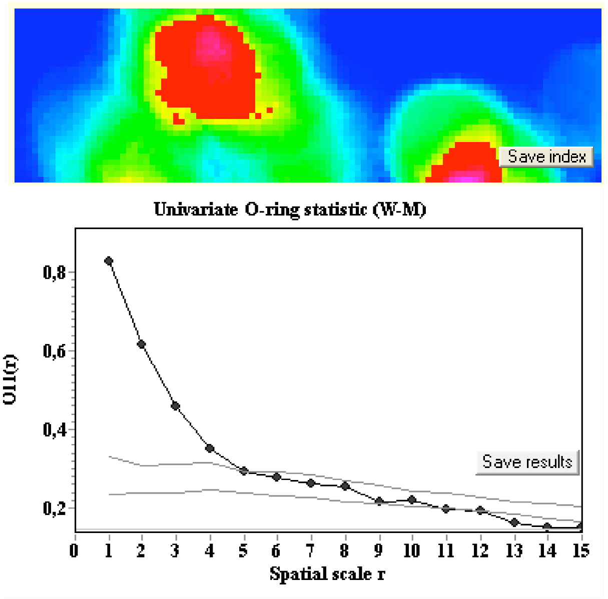

Figure 13 – *Acer pseudoplatanus* saplings (0.5 m–0.1 m). Top: Depiction of sapling density (first order heterogeneity). Bottom: Scale emergence of the pattern by means of univariate O-ring statistics.

Ulmus sp.

In total, only five *Ulmus* seedlings were found on the investigation area, of which four were at the youngest stage (Fig. 18). They are minutely represented on the area, with 0.03% of all seedlings. The seedlings are unevenly distributed in the northern part of the area, with a maximum distance of 20 m from the adult trees.

Tilia cordata

In total, 51 *Tilia* seedlings were found on the investigation area, of which 12 were at the youngest stage. They therefore present 0.3% of all seedlings on the area. On consideration of Fig. 19, it can be seen that many of the seedlings were able to establish themselves and the mortality rate is practically 0%. In most cases, the seedlings can be found in the immediate vicinity of adult trees.

Carpinus betulus

In total, nine *Carpinus betulus* seedlings were found on the investigation area, of which seven were at the youngest stage. They therefore present 0.05% of all seedlings on the area. On consideration of Fig. 20, it can be seen that the seedlings are distributed unevenly across the area, and both in the immediate vicinity of the adult trees and farther away. The spatial pattern of *Carpinus betulus* seedlings is therefore distributed randomly across the overall area.

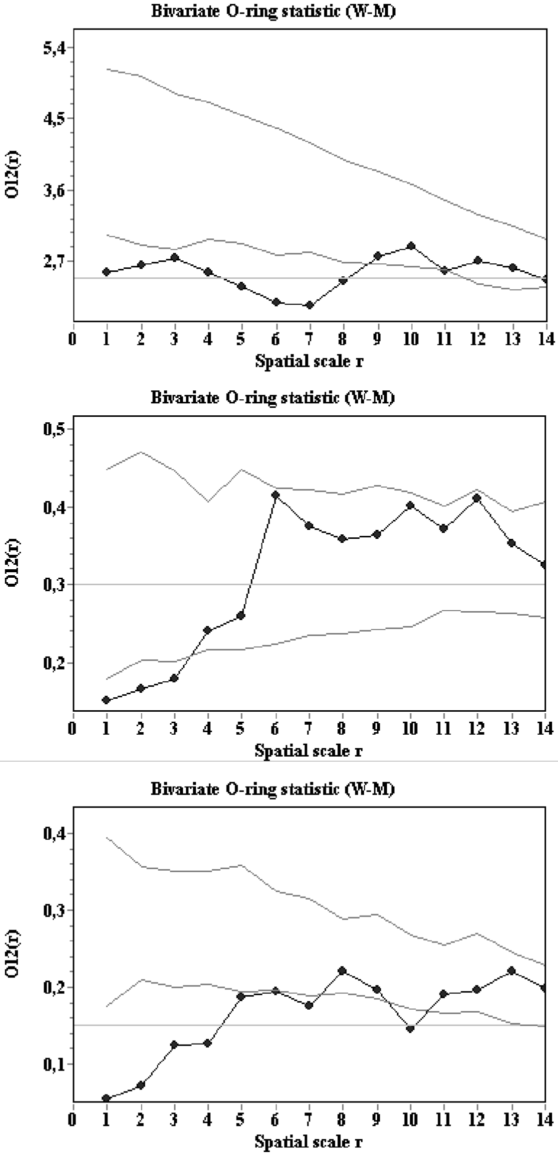

Figure 14 – Bivariate analysis of the patterns of seedlings and adult trees of *Acer pseudoplatanus*. Top: Seedlings of up to 0.2 m growth height with adult trees; middle: Saplings of 0.2 m–0.5 m growth height with adult trees; bottom: saplings of 0.5 m–1.0 m height.

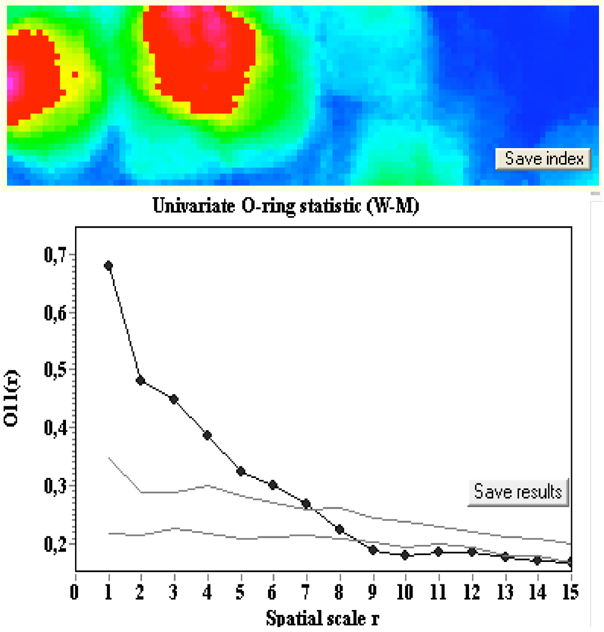

Figure 15 – *Fraxinus excelsior* seedlings (up to 0.2 m). Top: Depiction of seedling density (first order heterogeneity). Bottom: Scale emergence of the pattern by means of univariate O-ring statistics.

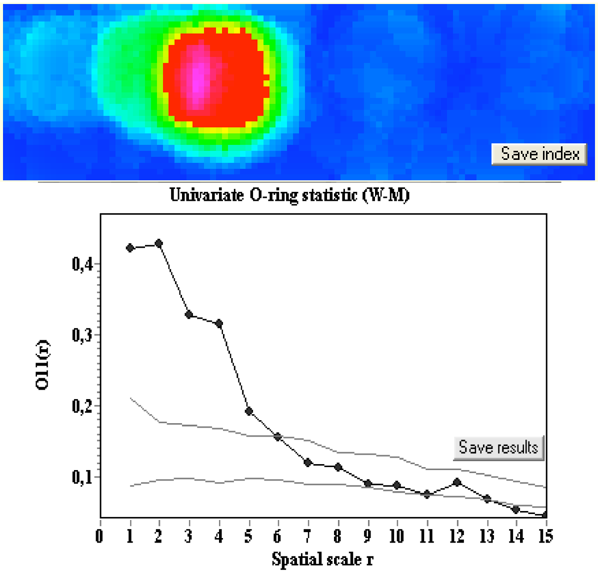

Figure 16 – *Fraxinus excelsior* saplings (0.2 m–0.5 m). Top: Depiction of sapling density (first order heterogeneity). Bottom: Scale emergence of the pattern by means of univariate O-ring statistics.

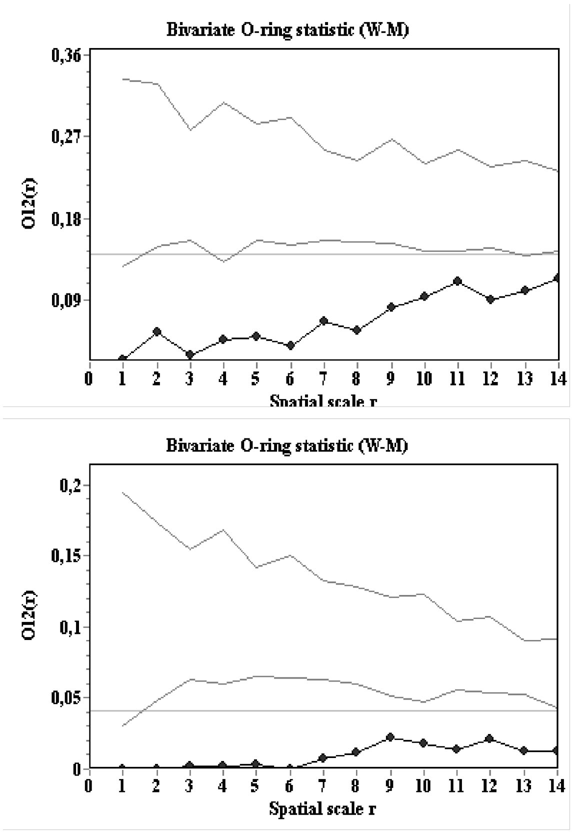

Figure 17 – Bivariate analysis of the patterns of seedlings and adult trees of *Fraxinus excelsior*. Top: Seedlings of up to 0.2 m growth height with adult trees, bottom, saplings of 0.2 m–0.5 m growth height with adult trees.

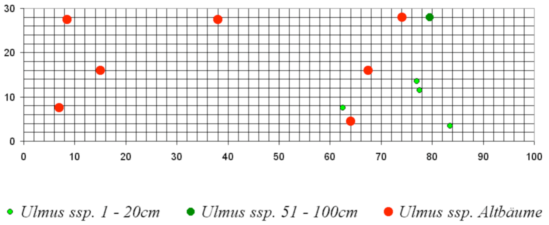

Figure 18 – Investigation area with location of adult trees and seedlings in various age stages of *Ulmus* sp.

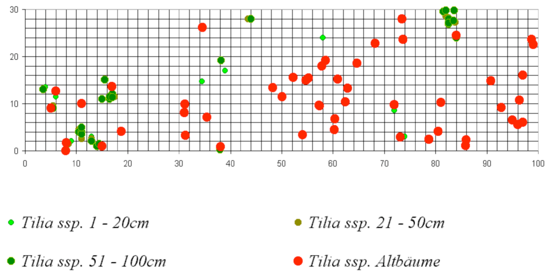

Figure 19 – Investigation area with location of adult trees and seedlings in various age stages of *Tilia* sp.

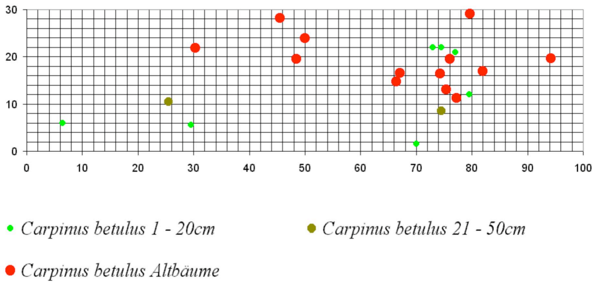

Figure 20 – Investigation area with location of adult trees and seedlings in various age stages of *Carpinus* sp.

Summary of the results

Sycamore (*Acer pseudoplatanus*) regenerates and establishes itself most strongly in the Leipzig floodplain forest. The originally untypical Norway maple (*Acer platanoides*) is likewise commonly represented in the understory vegetation. Oak (*Quercus robur*) and ash (*Fraxinus excelsior*) germinate frequently, but are rarely able to establish themselves as saplings. Hornbeam (*Carpinus betulus*) produced only few seedlings. Elm (*Ulmus* sp.), whose stand was severely decimated by Dutch elm disease in the 1960s, likewise rarely shows seedlings despite a number of adult trees in the area. In the case of lime trees (*Tilia* sp.), all seedlings appear to establish themselves, but it is yet to be clarified whether these arose from root offshoot or actually seeds.

The distribution pattern of seed varies highly when the individual species are compared. With reference to the spatial distribution of seedlings, saplings and adult trees, clumped patterns appear for sycamore and Norway maple, for oak and ash trees. Significant correlation between seedling pattern and adult tree pattern was found in oak and sycamore. Norway maple shows a random distribution of seedlings in relation to adult trees: ash trees, on the other hand, a significant rejection of both.

DISCUSSION

Establishment and dispersal of tree seedlings

Indicators of the change in vegetation composition in the Leipzig floodplain forest in the last 100 years include the migration of warmth-loving tree species such as *Acer platanoides* and the absent regeneration of *Quercus robur* and *Ulmus* sp. 28% of all living adult trees belong to the species *Acer platanoides*. However, they only have a seedling establishment rate of 0.3%. By contrast, the typical floodplain forest species *Acer pseudoplatanus* have a seedling establishment rate of 91%. Evidently, although *Acer platanoides*, originally not a native of the Leipzig floodplain forest, shows many adult trees in the area due to absent inundations, reduction of the water table and increasing eutrophication (Müller 1992), it is barely able to regenerate and is therefore on the decline again due to the current revitalisation measures. *Quercus robur* and *Fraxinus excelsior*, both of them typical floodplain forest representatives, show only comparatively weak regeneration, *Ulmus* sp. and *Carpinus betulus* practically none at all. This result confirms the assertion by Roloff *et al.* (2002) that the seedlings of *Quercus robur* are unable to establish themselves, probably due to too thick understory vegetation. Naturally, the data presented here only represent a snapshot of the seedling vegetation. Abundant years, such as occur for *Quercus robur* or *Carpinus betulus*, or years in which fewer seedlings grew, were not taken into account. The too-low sample number of *Ulmus* sp., *Carpinus betulus*, and *Tilia* sp. has resulted in uncertainty in the interpretation (in the statistical sense), due to which no representative results could be obtained.

Competition, allelopathy and other factors

As Collins (1990) and Jones *et al.* (1994) state, the first phase of regeneration is the most sensitive, with the highest mortality rate. In the investigation area, the highest mortality rate in six of the seven species occurred within the first vegetation period. According to Küssner 2003 , this is primarily conditioned by the lack of light, which is a limiting factor for the survival of young trees. Allelopathic effects, too, can lead to seedling mortality, even though this has not yet been proven for central European deciduous forests. Thus, root and leaf shedding and flushing of anorganic or organic substances from fresh or fallen leaves by rain can be responsible for the death of seedlings in the immediate vicinity of adult trees. Where it has been investigated so far, the allelopathic substances involve aetheric oils, alkaloids, cumarin derivatives, glycoside or phenol derivatives (Ise 2001). For example, in fallen leaves there is abscisic acid, which has an inhibitory effect on growth and metabolism. Haase & Schneider (2001), during investigations in the Leipzig floodplain forest, found a strong acidity of trunk off-flows, particularly in *Quercus* and *Fraxinus*, which may have prevented seedling establishment in the direct surroundings of the adult trees. Furthermore, the accumulation of seedlings in the immediate vicinity of the mother plant results in intra-species competition not only with the mother plant, but also among seedlings of the same species (Webb 1966). According to Howe & Smallwood (1982) it is necessary for many species, if they are to disperse and establish successfully, to escape the direct environment of the mother plant. High intra-species root competition (Beyschlag 1999) leads to a high die-off rate where there is high seedling density (Büren-Rieder 2000), as can be found for both *Acer* species. On consideration of the maps showing the distributions of seedlings and saplings, it is striking that most saplings establish themselves at larger distances from the adult trees and in places where the understory vegetation is not so dense. At the same time, this indicates a high mortality rate in places with a high seedling density.

Regeneration strategies

Different strategies of fruit dispersal, seed dormancy, shade tolerance and growth likewise play a decisive role for germination and seedling establishment. With the exception of *Quercus robur* all investigated trees are dispersed by wind and have lightweight fruits with a flight organ. When compared, *Carpinus betulus* and *Fraxinus excelsior* can both theoretically fly the farthest. Yet, various dispersal strategies exist in turn even among the anemochorous species. Gliding fliers, of which the genus *Ulmus* is one, have a large flight organ and a light seed. Dynamic fliers, which include the genera *Acer*, *Tilia* and *Carpinus* as spiralling fliers and the genus *Fraxinus* as a spinning flier, execute rotary movements during flight (Schmidt 2002). The effect of this is that *Fraxinus excelsior* is indeed able to fly far due to the lightness of its fruit, but at the same time has the highest rate of descent (214 cm s^{-1}) (Schmidt 2002). Both *Acer* species have a significantly higher weight, yet their rate of descent is only between 107 cm s^{-1} and 115 cm s^{-1}. Thus, the dispersal distance of *Fraxinus excelsior* is smaller than that of *Acer* and *Carpinus*. The average dispersal distance of *Fraxinus excelsior* was ascertained at 52 m, while most fall up to 20 m around the mother tree (Wagner 1997). This smaller dispersal ability is compensated by the fact that the fruits are able to remain hanging on the tree for up to more than 200 days, even throughout the winter. (Schmidt 2002). On the other hand, these dispersal distances apply for lone-standing trees or sparse forest stands. Therefore it can be assumed that, within a highly dense floodplain forest stand, long-distance dispersal by wind can be largely disregarded since flight distances do no differ significantly from the carrying distance by birds and squirrels. The ecological significance of the mass of the units dispersed lies in the fact that this determines nutrient provision for the seedling (Harper *et al.* 1970). Thus, *Quercus robur* with its large, heavy acorns has an enormous energy reserve for the seedling. This is proven by the high germination rate, which in the investigation area is

188 seedlings per *Quercus robur* adult tree and is only higher in *Acer pseudoplatanus* (280). If the numbers of formed fruits, which in the case of *Quercus* are estimated at only a few 1 000, (Tal pers. comm.), are taken into account, this results in a germination rate of 8% (*Acer pseudoplatanus*, on the other hand, approx. 1.4%).

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2 Tree phenology, genetic variation, and herbivory

Contents

2.1 Reproductive biology of the main tree species at the canopy crane investigation site

Ophir Tal[1] & Wilfried Morawetz

The reproductive processes of trees are a key component in the forest ecosystem, as they support the persistence of the trees and are the basis for their numerous interactions with other organisms. This chapter presents general findings about the sexual systems, flowering phenology and fruit and seed production of the four dominating tree species in the stand. *Fraxinus excelsior* is polygamous, *Acer* spp. heterodichogamous, *Tilia cordata* andromonoecious, and tree gender correlates with tree size, manifesting an individual based variability. *Fraxinus excelsior* flowers every year in a high intensity and its flowering phenology is sensitive to climate whereas the flowering phenologies of *Acer* spp. and *Tilia cordata* are quite constant in duration but strongly change intensity between years. This variability implies a differentiated pattern of floral resources in space and time. Corresponding to flowering phenology, *Fraxinus excelsior* is also the major fruit producer in the stand, followed by *Tilia cordata*. *Acer pseudoplatanus* is the least productive species. The results demonstrate the high complexity of the reproductive biology of the tree species and the large spatial and temporal variability in resources they present to other organisms. The paper enhances the high conservation value of the Leipzig floodplain forest, and the importance of relating to the individual trees when studying interacting organisms.

INTRODUCTION

Trees are the largest organisms of a forest, and as such they are the basis for most of the biological interactions in it. The reproductive biology of the trees determines on the long range the constitution of the forest and on the short range it is the basis to different biotic interactions around the flowers and fruit (Röhrig & Bartsch 1992).

The LAK project concentrates on studying biological diversity in the forest and the ecological processes in it (Morawetz & Horchler 2003). The diversity of tree species is relatively high, and is considered a basis for the diversity of smaller organisms in the forest. In this chapter, we present some further, intraspecific diversity of the trees that is observed by examining their reproductive biology.

Reproductive biology includes the study of the sexual system, flowering phenology, pollination and fruit and seed production (Richards 1997):

(1) The sexual system of a species concerns the gender distribution of flowers on the plant and their functionality (Richards 1997). The genera *Fraxinus* and *Acer* are both renown for the large diversity of sexual systems they present, and were thus an object for at least ten taxonomical studies each, most of which however in artificial or immature stands, and without canopy accessibility to large trees (e.g. De Jong 1976; Wallander 2001, respectively).

(2) Flowering phenology, especially in early spring, is among the most climate sensitive biological processes (Fitter & Fitter 2002). As such it is strongly connected to microclimate (Stoutjesdijk & Barkman 1992) and may be used to indicate climate change (Roetzer *et al.* 2000). It also has a strong influence on reproductive success and genetic diversity of the offspring (Fox 2003).

(3) Pollination is an intriguing contact zone between plants and insects (Faegri & van der Pijl 1966; Proctor *et al.* 1996). Plants may depend on different insects and in different measures for successful reproduction, or they may rely predominantly on wind pollination (Culley *et al.* 2002). All three studied genera present a diversity of strategies in this respect (Eisenhut 1957; Ogata 1967; De Jong 1994; Fromm 2001; Wallander 2001). Insects depend on floral resources for their own reproductive processes.

(4) Fruit and seed production are the result of the above-mentioned characters, and represent the future growing potential of the trees. At the same time they are a resource for different animals. Masting (fluctuating synchronous fruit production) is found in forest trees (Herrera *et al.* 1998) and is supposed to

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[1] corresponding author

be linked with fluctuating weather (Kelly & Sork 2002), satiation of predators (Ostfeld & Keesing 2000), and wind pollination (Smith *et al.* 1990).

These topics were studied in the last four years in the main tree species in the plot - *Fraxinus excelsior* L. (Oleaceae, common ash, Esche), *Acer pseudoplatanus* L. (Sapindaceae, sycamore maple, Bergahorn), *Tilia cordata* Mill. (Malvaceae, small-leaved lime, Winterlinde), and *Acer platanoides* L. (Norway maple, Spitzahorn), in practically all canopy trees in the plot (Seele and Rohrschneider, this volume).

The aim of this paper is to present the intraspecific variability and overview data on the reproductive characteristics of these species.

MATERIALS AND METHODS

The study site is the investigation plot of the Leipzig Canopy Crane, located at the edge of the Leipzig floodplain forest (see details in Morawetz & Horchler 2003). The crane enables access to ca. 1.6 ha of canopy, up to the height of 32 m. Most canopy trees of the studied species were inspected during 2002 to 2005 (Table 1) and their gender distributions, flowering phenologies, pollination levels, insect in inflorescences and fruit and seed production were recorded and analysed (Tal 2006). Data of tree height and stem diameter was taken from Seele (2004) and the crown area (included in the canopy's upper surface) was measured by outlining the tree crowns on an aerial photo. Data on individual trees is available from the corresponding author. Table 1 presents the number of studied trees after study year and topic.

F. excelsior is a polygamous species, trees were categorised as: **(1)** Males, with no or less than 1% hermaphrodite flowers. **(2)** Male-biased hermaphrodites with mostly male flowers but more than 10% hermaphrodite flowers (with large anthers and small but functional pistils). **(3)** Balanced hermaphrodites with all flowers hermaphrodite (balanced morphology). **(4)** Female-biased hermaphrodites with reduced but mostly functional anthers and large pistil. **(5)** Females with almost no stamens (when existing rudimentary).

Inflorescences of *A. pseudoplatanus* and *A. platanoides* usually include male and female flowers but in anthesis only one gender is presented at a time, synchronously in the tree (De Jong 1976; Cruden 1988). Trees are either protandrous (male then female, commonly followed by a second male phase), protogynous (female then male), or male.

Tilia cordata is considered hermaphrodite (Pigott 1991).

The intensity of flowering for each tree was categorised after the proportion of buds with inflorescences as full (> 50%, usually over 80%), partial (10–50%, usually around 30%), scant (less than 10%, usually 1–5%, on single twigs), or no flowering. We gave efforts to scrutinize each tree both during flowering and at fruit ripening.

Fruit amount was quantitatively assessed by direct counting of infructescences or twigs in a part of the crown and assessing the number of subunits in the whole canopy (in large trees subunits were counted at two levels). The estimated error is 50%, i.e. an assessment of total fruit on a tree of 100 000 means the actual number is between 50 000 and 200 000 (Tal 2003). Samples of ripe fruits were checked for seeds (details in Tal 2006).

Table 1 – Number of studied trees after species, year of study and theme. Intensity of flowering and number of fruit include non-flowering and non-fruiting trees, respectively.

	Theme of study			
Species and year	**Tree gender**	**Intensity of flowering**	**Flowering time**	**Number of fruits**
F. excelsior 2002	68	69	38	21
F. excelsior 2003	64	64	48	21
F. excelsior 2004	66	71	63	21
F. excelsior 2005	91	97	90	26
A. platanoides 2004	8	8	8	8
A. platanoides 2005	6	10	1	10
A. pseudoplatanus 2004	53	50	53	47
A. pseudoplatanus 2005	60	65	52	74
T. cordata 2004	9	30	9	30
T. cordata 2005	9	30	9	30

RESULTS

In *F. excelsior*, about a half of the trees in the stand were predominantly male, the other half were mostly different types of hermaphrodite trees, with only 6% of the trees being purely female. Most of *A. pseudoplatanus* were protandrous and most *A. platanoides* were protogynous. *T. cordata* trees had a large proportion of male flowers beside the hermaphrodite flowers, a sexual system termed andromonoecy (Fig. 1).

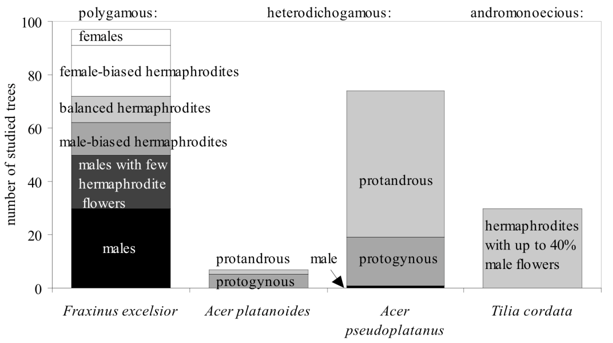

Figure 1 – Gender distribution in the studied species and number of studied trees.

The largest *F. excelsior* trees in the stand were male. Males (and male-biased hermaphrodites) were significantly larger than other hermaphrodites and females (10% in stem diameter, t-test p = 0.03 and 3% in tree height, Mann-Whitney rank sum test, p = 0.007) among the larger canopy trees (stem diameter greater than 40 cm, tree height greater than 28 m, 68% of all canopy trees). However, in respect to all canopy trees, there was no significant difference between the gender groups (Mann-Whitney rank sum test, p = 0.22 for stem diameter, p = 0.10 for tree height, in total 97 trees).

However, taking only canopy trees with stem diameter larger than 30cm, no significant difference was found (t tests for stem diameter and tree height p=0.2 and 0.4 respectively). Protogynous *A. pseudoplatanus* trees were larger than protandrous trees (25% in stem diameter, t-test p = 0.007; 10% in tree height, Mann-Whitney rank sum test p = 0.045, 18 protogynous, 50 protandrous trees). However, taking only canopy trees with stem diameter larger than 30 cm, no significant difference was found (t-tests for stem diameter and tree height; p = 0.2 and 0.4 respectively).

F. excelsior flowered in a constant high intensity in four years whereas the other three species fluctuate in the years of study (Fig. 2). 80% of *F. excelsior* trees at least flowered fully. All male trees flowered fully every year, whereas some of the fruit producing trees flowered at a low intensity in some of the years. 2004 was a full flowering year for the other three species, whereas 2005 a weak flowering year for them. The *Acer* species suffered increased herbivore damage (mainly caused by aphids) to the flowers in 2005, the year of weak flowering.

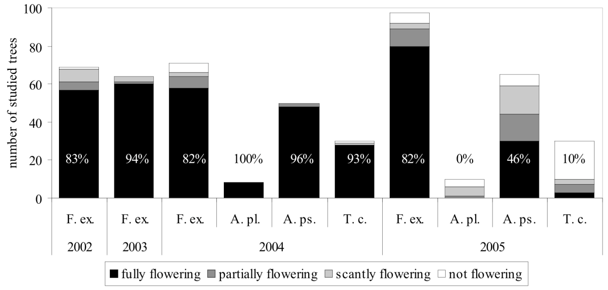

Figure 2 – Flowering intensities of the studied species. The number of trees is separated after four intensity levels, and the percent of fully flowering trees from total is noted. F. ex.: *Fraxinus excelsior*, A. pl.: *Acer platanoides*, A. ps.: *Acer pseudoplatanus*; T. c.: *Tilia cordata*

T. cordata trees flowering in 2005 were significantly higher and with thicker stems than trees not flowering in 2005 (Mann-Whitney rank sum test, $p < 0.001$, $p < 0.001$ respectively, 35 trees). The large flowering trees are all in the northern part of the plot, whereas the central and southern parts of the plot had exclusively small non-flowering *T. cordata.*

Flowering duration was most variable in the early flowering *F. excelsior* and quite constant in the later flowering *Acer* spp. and *T. cordata.* The former flowered in the end of March to mid April during 3–8 weeks in different years, *A. platanoides* in mid April for three weeks, *A. pseudoplatanus* in May for 4–5 weeks and *T. cordata* in mid June to mid July for 3–4 weeks in different years.

Table 2 – Correlations of fruit production per tree and tree dimensions (Pearson product moment coefficients); ns: not significant, *: p<0.05, **: p<0.01, ***: p<0.001.

Species	Correlated crop	Tree height	Stem diameter	Crown area
Fraxinus excelsior	maximal per tree	ns	ns	0.44 *
Acer pseudoplatanus	2004	0.32 *	0.38 *	0.55 ***
Tilia cordata	2004	0.52 **	0.58 **	0.76 ***

F. excelsior produced the largest number of fruit in the plot. Both the annual seed production and the year-to-year constancy were superior to *A. pseudoplatanus* and *T. cordata*. The latter followed in fruit quantity, and *A. pseudoplatanus* produced the smallest crop, with a large proportion of seedless fruit (Fig. 3).

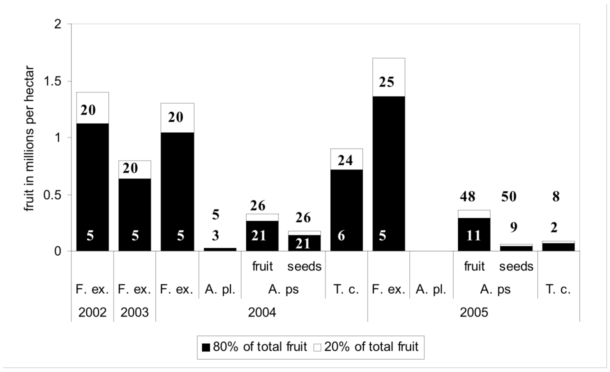

Figure 3 – Overall fruit production in the stand in millions per hectare for studied years and species. The lower numbers are the number of trees producing 80% of total fruit (trees with greatest number of fruit) and the upper numbers are of trees producing the rest 20%. F. ex.: *Fraxinus excelsior*, A. pl.: *Acer platanoides*, A. ps.: *Acer pseudoplatanus*; T. c.: *Tilia cordata*

In the major fruit producers, *F. excelsior* and *T. cordata*, the crop was produced by a small proportion of the trees. In these species the number of seeds is equal to the number of fruit, whereas in the least productive *A. pseudoplatanus* less than one seed per fruit are produced.

Large fruit production is correlated with tree size, and is especially well explained by crown area, as presented in Table 2.

DISCUSSION

This paper presents the characteristics of reproductive biology of the main species in the stand, encompassing ca. 200 canopy trees (Table 1) and applying intensive observations using the high canopy accessibility provided by the LAK crane. The results exemplify the large interspecific diversity of the species in the forest, implying a high conservation value (PRIMACK 2002, BROWN *et al.* 1997). Some of the complexity arises from the mature status of the forest, thus underlining its value (BROWN *et al.* 1997).

The gender distributions of *F. excelsior* and *Acer* spp. (Fig. 1) are similar to those described by WALLANDER (2001) and DEJONG (1974) respectively, whereas andromonoecy in *T. cordata* is described for the first time (PIGOTT 1991; FROMM 2001), cryptic andromonoecy was reported for the close relative *T. japonica* by ITO & KIKUZAWA (1999) and ITO (2002).

The correlation of tree gender types with vegetative characteristics (Table 2, see also PAROLIN *et al.*, this volume) as well as their effects on sex-dependent biotic interactions (WARDLE 1961; HARGASIM 1977; DELPH 1999; VERDÚ 2004; TAL 2006), and possibly on variability in vegetative tissue in respect to herbivores (ÅRGEN *et al.* 1999; VERDÚ *et al.* 2004; RUHNKE *et al.* this volume) implies that tree gender should be taken into account in the study of inter- and intraspecific variability in biotic interactions.

The flowering and fruiting of *F. excelsior* in a more or less constant intensity and constant high flowering intensity of males (Fig. 2) contrast other studies of *F. excelsior* which report a two-year cycle (TAPPER 1996; WALLANDER 2001), and may result from the maturity of the forest. The contrast between wind pollinated species producing a large crop every year and insect pollinated species producing fluctuating crop (Fig. 3) counters the idea that masting is associated with wind pollination (KELLY & SORK 2002). Fluctuating flowering intensity may have strong effects on flower visitors as well as on flower and fruit foragers (OSTFELD & KEESING 2000), especially if these are not very mobile or if these phenomena are synchronised in the forest.

The flowering duration in *F. excelsior* is the most variable, reflecting the sensitivity of this early flowering species to macro- and microclimate. Flowering duration in *Acer* spp. is relatively constant and may be related to its heterodichogamy, which requires synchronisation within and among trees (RENNER 2001). Flowering duration has important implications to the degree of synchronicity between individual trees and thus to the gene flow in the population (WILLSON & BURLEY 1983; PRIMACK & KANG 1989) which are discussed for *F. excelsior* and *A. pseudoplatanus* in TAL (2006). The finding that in *F. excelsior* and *T. cordata* most yield is produced by the few largest trees in the stand has implications both to the genetic variability of the stand and demonstrates the importance of the struggle for space among canopy trees (FRECH *et al.* 2003).

F. excelsior is the most prolific fruit producer in the plot (Fig. 3). Both the maximal fruit production and the constancy of yield are much larger than the ones of the other species. *A. pseudoplatanus* produces a lower fruit crop and a still lower seed crop than *F. excelsior* and *T. cordata*, whereas its seedlings are the most abundant on the forest floor (SCHÖNE & JENTSCH, this volume). This indicates that vegetative competition is more important than reproductive competition in determining the species composition of the stand.

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2.2 Phenotypical and genetic variation of Fraxinus excelsior L. at the LAK site

Pia Parolin[1], Ophir Tal, Stephanie Bartel, Anna Maria Vogt & Barbara Rudolph

In the forest of the "Leipzig Canopy Crane Project" (LAK), the common ash (*Fraxinus excelsior*) is the dominant tree species. This ash population is most likely the result of different phases of plantings after 1800. In the LAK study plot, 64 adult individuals exceeding 22 m in height and a large number of seedlings and saplings show a high phenotypic variation. In the present study, the genetic variation of the semi-natural population of *F. excelsior* is analysed. The main questions are whether phenotypic variation is reflected by a genotypic variation, and how large the genetic variability of the population is. The establishment of microsatellite and AFLP markers for analyses of the LAK ash population is described as well as first results. One main result is that the ash population possesses an astonishingly high level of genetic variation within this population, especially regarding the putative origin and strong selection of this forest during the last centuries. Because of this high variability in microsatellite markers all individuals analysed in this first screening could be identified via individual DNA fingerprinting. After a first test of utility of microsatellite and AFLP markers a screening of a set of 77 individuals of the LAK plot containing 220 samples is in progress. Additionally to the comparison of the geno- and phenotypic variability of the ash population – especially in floral phenology – in future studies it is planned to compare this semi-natural with a natural population, and based on the high genetic variability, investigate the role of somatic mutations in genetic diversity.

INTRODUCTION

The ash trees in the Leipzig Canopy Crane Project (LAK) are the dominant species in the tree canopy (see Seele and Rohrschneider, this volume). They show great phenotypical variation: the sex distribution and floral phenology of *Fraxinus excelsior* was studied in detail by O. Tal within the context of a master thesis (Tal 2003 and this volume). Results of this work show that among the 64 adult individuals (> 22 m in height), a large variation in the development of floral sex (female, male, androgynous, female-androgynous, male-androgynous) was predominant (Fig. 1, 2). Even considering various levels – single flowers, florescence, tree, subpopulation or stand – a high variability was revealed and interesting distribution patterns emerged; but these appear to be typical for ashes (Binggeli & Power 1991, Wallander 2001). As Darwin wrote in 1877: "As far as the sexual relations of flowers are concerned, Linnaeus long ago divided them into hermaphrodite, monoecious, dioecious, and polygamous species. This fundamental distinction, with the aid of several subdivisions in each of the four classes, will serve my purpose; but the classification is artificial, and the groups often pass into one another". This last case also applies for the common ash. Functionally, trees have a defined sex; yet morphologically they are characterised by many deviations.

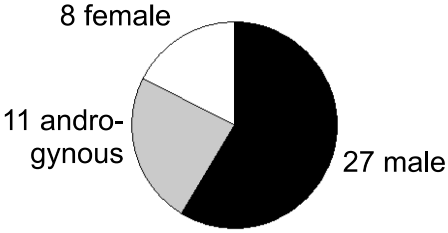

Figure 1 – Quantitative distribution of flower gender in the analysed LAK ash population (Tal 2003).

On the other hand, it is as yet unknown how large the genetic variability of the investigated population is. As early as the 19th century, *F. excelsior* was not an uncommon species in Leipzig (Gläser 2001), but little is known about the origin of the LAK and neighbouring forest. The ash trees of the LAK may possibly have been planted: diameter and height distribution reveal two groups (Fig. 3, 4; Seele, this volume), one

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[1] corresponding author

group with individuals which are approx. 100–200 years old, and a second with 50–60 year-old trees. 200 years ago, the ash tree was presumably rare in the Leipzig floodplain forest (Gläser 2001). Being promoted (directly by planting and indirectly by river adjustment), most of the trees probably reproduced from local populations, as well as domestic gardens (Gläser pers. comm.).

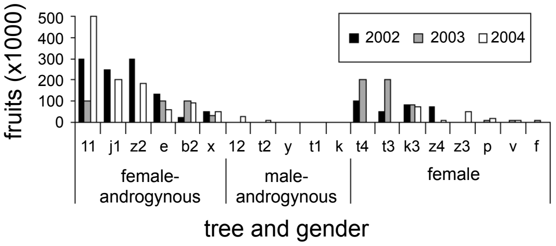

Figure 2 – Sex of the tree, defined by the produced fruits; mean of the years 2002–2004 from fruits of 19 ash trees (in thousand) (Tal 2003).

Further, there is one adult and five younger trees of *F. pennsylvanica* in the investigated floodplain plot, being planted and introduced from the USA, which also possibly reproduce. This could lead to a hybridisation between the species, which is however improbable according to Wallander (pers. comm.), since *F. excelsior* and *F. pennsylvanica* belong to two different sections of the genus (Wallander in preparation).

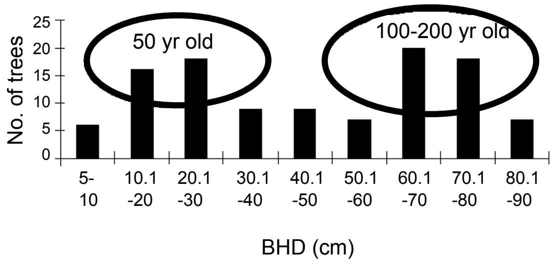

Figure 3 – Distribution of diameter at breast height (dbh) of the LAK trees: two phases of planting become evident (Seele 2004; see also this volume).

However, membership of various sections of a species or various genera must not be an exclusion criterion for hybridisation events, as examples of natural hybrids in Asteraceae (examples: Molloy 1995, Okada *et al.* 1997), Caricaceae (van Droogenbroeck *et al.* 2004) Brassicaceae (Heenan 1999) or Orchidaceae (Abele *et al.* 2005) have shown. "Consideration of Proposals for Amendments of Appendices I and II"[2] alone shows a multitude of intergeneric hybrids in *Cattleya*, *Cymbidium*, *Dendrobium*, *Oncidium*, and *Vanda* (all Orchidaceae).

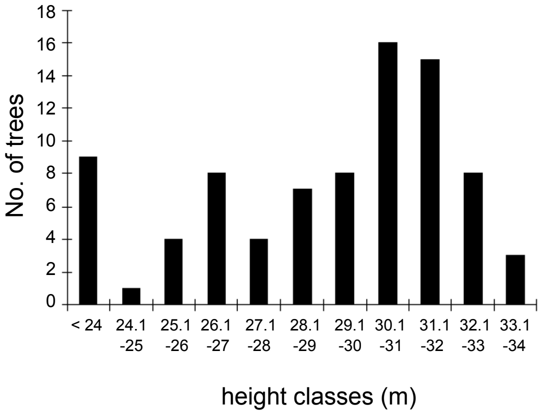

Figure 4 – Height distribution of the LAK trees (Seele 2004; see also this volume).

The aim of the current investigations is to examine the genetic variability of the LAK ash population. For this purpose, the genetic differences within the overall adult population are first investigated and the genotypic and phenotypic variations (Tal 2003) were compared. The *F. excelsior* population in the LAK was examined on the basis of a combination of microsatellite markers (SSR: simple sequence repeat) (Litt & Luty 1989, Weber & May 1989, Jeandroz *et al.* 1995, 1996; Brachet *et al.* 1999, Lefort *et al.* 1999a, b, Morand-Prieur *et al.* 2002) and amplification fragment length polymorphisms (AFLP markers) (Vos *et al.* 1995). In order to correlate genotypical and phenotypical variations, phenological and floral-ecological data from the master thesis by O. Tal (2003) were included.

MATERIALS AND METHODS

Plant material

In order to establish microsatellite and AFLP markers for population genetic estimations of the ash trees in the LAK, a total of 25 leaf samples were collected from September until November 2003. This set comprises 11 individuals of *F. excelsior* from the Leipzig floodplain forest experimental plot, as well as one individual of *F. pennsylvanica* from the LAK plot. In order to check whether the populations from various regions can be distinguished using this marker type, five individuals from the Hamburg area were included in this set. This involved two adult trees and three young trees from a presumably planted private garden in Hamburg Othmarschen. In addition, the reproducibility of the markers was checked

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[2] `www.cites.org/eng/cop/12/prop/E12-P51.pdf`

via double sampling from 8 ash individuals from the LAK. The characteristics (dbh, tree height, position coordinates, origin, etc.) of the sampled individuals are indicated in Table 1. From this set, the four *F. excelsior* 2312/j, HHd, 1101/b and 2101/j2 were used for establishing the AFLP method for estimations of *Fraxinus* populations (see Table 1).

Genetic analyses

The molecular marker method for population analyses on *Fraxinus* was established at the Plön Max-Planck-Institute for Limnology and at the Biocenter Klein Flottbek at the University of Hamburg. A time-consuming development of microsatellite markers was avoided, since microsatellite primers for analyses on *Fraxinus* have already been published (Lefort *et al.* 1999a, b; Morand-Prieur *et al.* 2002). The methods for the outstanding investigations were optimised according to Rudolph 2001. For the AFLP analyses, suitable combinations of restriction enzymes and primers were selected. Here, various primer combinations first had to be tested for their usability. In order to optimise the SSR marker analysis, initial molecular biological examinations of the ash tree population were carried out on the basis of a set of 25 leaf samples (Table 1).

DNA isolation

Fresh ash leaves were dried using silica gel. The DNA isolation was carried out according to Dumolin *et al.* (1995) with some modifications. This protocol based on the CTAB method by Doyle & Doyle (1990). For the extraction, approx. 50 mg of leaf material was used. Each sample was ground to a fine powder in a Retsch mill at a frequence of 30/sec for 2 min.

The samples were lysed at 55 °C for 1 h, shaken gently, in 1 ml extraction buffer (2% (w/v) ATMAB, 1% (v/w) PVP 40 000, 20 mM EDTA pH 8.0, 100 mM Tris-HCl pH 8.0, 1.4 M NaCl) with 50 mM DTT. After cooling for approx. 10 min at room temperature, a precipitation in 400 μl dichloromethane and adjacent centrifugation at 13 000 rpm, (17949 rzb, Eppendorf centrifuge 5804R) for 10 min took place. To the upper phase 400 μl ice-cold isopropanol was added and centrifuged for 10 min at 13 000 rpm. The pellet was washed with 1 ml 76% ethanol and centrifuged (see above). The cleaned DNA was dried and resuspended overnight at 4 °C in TE buffer containing RNase A (10 μg RNase A/ml TE). RNA was digested at 37 °C for 30 min. The concentration of the extracted DNA was measured via OD determination in a biophotometer (Eppendorf). Working solutions were diluted to 100 ng/μl DNA.

Table 1 – Analysed *Fraxinus excelsior* from the LAK plot and from Hamburg, and one *F. pennsylvanica* in the LAK plot.

No.	Tree	DBH	Tree height	Sample height	Direction	Comment	Date	Site
1	2312/j	76,4	30,50	—	—	—	12.09.2003	LAK
2	3007/b2	43,9	29,40	—	—	—	12.09.2003	LAK
3	3309/p1	37,6	27,00	—	—	*F. pennsylvanica*	12.09.2003	LAK
4	2701/f	70,0	30,40	—	—	—	12.09.2003	LAK
5	HHa	—	—	—	—	old growth	20.10.2003	Hamburg
6	HHb	—	—	—	—	old growth	20.10.2003	Hamburg
7	HHc	—	—	—	—	young 1	20.10.2003	Hamburg
8	HHd	—	—	—	—	young 2	20.10.2003	Hamburg
9	HHe	—	—	—	—	young 3	24.10.2003	Hamburg
10	3208/r1	38,2	30,40	20 m	W	—	03.11.2003	LAK
11	3208/r1	38,2	30,40	29 m	O	—	03.11.2003	LAK
12	4310/l	64,0	28,80	26 m	S	—	03.11.2003	LAK
13	4310/l	64,0	28,80	27 m	NO	1. twig	03.11.2003	LAK
14	2322/i	89,1	32,60	30 m	NW	—	03.11.2003	LAK
15	3210/t	60,5	30,40	30 m	O	—	03.11.2003	LAK
16	1101/b	53,2	31,00	29 m	S	main branch	03.11.2003	LAK
17	1101/b	53,2	31,00	29 m	NO	—	03.11.2003	LAK
18	2101/j2	48,1	29,00	25 m	SO	main branch	03.11.2003	LAK
19	1206/a	79,6	32,50	26 m	SO	side branch	03.11.2003	LAK
20	1206/a	79,6	32,50	29 m	SW	main branch	03.11.2003	LAK
21	2312/j	76,4	30,50	25 m	central	—	03.11.2003	LAK
22	3007/b2	70,0	33,70	30 m	cental	—	03.11.2003	LAK
23	2101/j2	48,1	29,00	20 m	S	twig S	03.11.2003	LAK
24	3219/t3	63,7	31,40	27 m	W	—	03.11.2003	LAK
25	3219/t3	63,7	31,40	27 m	W	fruits	04.11.2003	LAK

SSR screening

The PCR reaction took place in a 10 μl total volume containing 25 ng DNA, 1.5 mM $MgCl_2$, 1x buffer, 2% DMSO, 0.2 mM dNTPs, 0.5 μM Cy-5 labelled forward primer, (Metabion), 0.5 μM reverse primer (Metabion), 2.5 U Biotherm DNA polymerase (Invitek). The sequences of the primers used are described in Table 2. A touchdown PCR was carried out in a PTC 200 gradient cycler (Biozym) with the following program: an initial denaturation at 94 °C for 2 min; followed by cycles of denaturation at 94 °C for 1 min, annealing at 65 °C for 30 sec, elongation at 72 °C for 45 sec. The annealing temperature was reduced by 1 °C every second cycle. On reaching the annealing temperature of 55 °C, 20 repetitions were carried out. The reaction was completed with a 10-minute elongation at 72 °C (Rudolph *et al.* 1999, Rudolph 2001). The PCR products were separated on an ALFexpress II (GE Healthcare) using a Reprogel High Resolution Gel (GE Healthcare) in 0.5x TBE. As an internal standard, 71 bp, 140 bp and 300 bp PCR products (Rudolph 2001) were added to the loading buffer (5 mg dextran blue/ml deionised formamide). The samples were mixed 1 : 1 with the loading buffer containing the internal standard and denatured at 94 °C (4 min). From each sample 0.8 to 2 μl were analysed on the automated sequencing gel.

AFLP analyses

For the establishment of AFLP analyses for ash populations, samples from four different ash trees were used. This DNA was applied in four different concentrations. The AFLP analyses were carried out with 100 ng, 250 ng, 500 ng and 1 000 ng DNA respectively. Double restriction was effected in 25 μl total volume with 5 U Pst I and 5 U Tru I (Mse I) (MBI Fermentas) and 1x tango buffer. The samples were incubated for 2 h at 37 °C. For the adapter ligation, adapter mix PstI (Adapter 1 CTCGTAGACTGCGTACATGCA and 20 pM PstI Adapter 2 CATCTGACGCATGT) (Metabion) together with 20 pM Tru I (MseI) (Adapter 1 GACGATGAGTCCTGAG) and TruI (MseI) (Adapter 2 TACTCAGGACTCAT) (Metabion), 5 U T4 ligase (MBI Fermentas) and 1x ligase buffer were used in a total volume of 25 μl. The ligation was incubated at 16 °C for 12 h. For the preamplification, the adapter ligations were diluted 1 : 10 using HPLC water. For the PCR, 5 μl of the adapter ligation was used. The pre-amplification itself was carried in a total volume of 50 μl with the following components: 5 μl template, 1 U Biotherm DNA polymerase (Invitek). 1x PCR buffer, 3 mM $MgCl_2$, 0.1 mM dNTP (Roche); 0.3 μM primer-mix (PstI + X: GACTGCGTACATGCAGX and TruI (MseI) + X: GACGATGAGTCCTGAGTAAX) (Metabion). The PCR was carried out in a PTC 200 gradient cycler (Biozym) as follows: an initial denaturation step at 94 °C for 5 min, followed by 20 cycles with denaturing at 94 °C for 30 sec, annealing at 60 °C for 30 sec, elongation at 72 °C and 1 min, followed by a final elongation step at 72 °C for 10 min. The samples were likewise diluted 1 : 10 using HPLC water and 5 μl was used for the selective PCR. The reaction conditions were: 20 μl total volume with 5 μl template, 0.5 U Biotherm DNA polymerase (Invitek), 1x PCR buffer, 3 mM $MgCl_2$, 0.25 mM dNTP (Roche), 0.6 μM primer mix: PstI + XXX (GACTGCGTACATGCAGXXX) and TruI (MseI) + XX (GACGATGAGTCCTGAGTAAXX) (Metabion). The PCR was carried out in the gradient cycler according to the following touchdown program: an initial denaturation at 94 °C for 5 min, followed by 3 cycles: denaturation at 94 °C for 30 sec, annealing at 65 °C for 30 sec and an elongation at 72 °C for 1 min. The annealing temperature was then reduced for one degree every four cycles, until a final temperature of 56 °C was reached. This cycle was repeated 24 times. The reaction was completed by a 10-minute elongation step at 72 °C. The samples were separated on the ALFexpress, as described for the SSR analyses.

Data analysis

Size determination of the fragment lengths of the AFLPs and microsatellites was carried out using ALFwin Fragment Analyser Version 1.03 (GE Healthcare). The fragment lengths obtained were transferred manually into a binary matrix, whereas the presence of a PCR product was coded as 1 and the absence of a PCR product as 0. In so doing, the assumption was that fragments of identical size correspond to homologous sequences and are not of the same size by coincidence. Dubious PCR products were not taken into account. Although SSR analyses enable a co-dominant evaluation and these should also be evaluated co-dominantly in future, in the initial analyses of these markers a dominant evaluation method was chosen during which every allele of a locus is evaluated as an independent marker.

In order to check the reliability of the SSR markers, for 8 examined individuals, two samples per individual were examined in parallel and distances or, respectively, similarities were calculated in pairs. This matrix was used for cluster algorithms such as UPGMA (unweighted pair group method) were used. For these calculations, the PAUP program, version 4.0b10 for Macintosh (Swofford, D.L. 2002, Sinauer Associated Inc. Publishers, Sunderland, MA, USA) was used in order to produce distance trees.

Relations with the phenological variation

In order to compare the phenotypical and the genetic variation within the ash population of the LAK, the trees were grouped according to phenotypical features. Subsequently these are compared with the genotypical evaluations.

RESULTS

Establishment of SSR markers for analysis of the LAK ash population

In total, 10 microsatellite markers were tested. Seven of these resulted in reproducible PCR products. These microsatellites showed the typical profile of two alleles each per locus. However, more than two bands per marker were also identified.

The number of alleles per SSR locus was between 11 and 19, with an allele diversity (A) of 13.9 (Table 2). Allele frequencies were between 0.016 and 0.319 with an average value of 0.076. Average heterozygocity was 0.54. In a separate analysis of the LAK populations – excluding the Hamburg population and *F. pennsylvanica* – 9 and 19 alleles per locus were scored. A total of 310 polymorphic markers were identified, which could be used for an initial calculation of genetic distances.

Initial population analyses using SSR markers

The UPGMA distance analysis showed that all double samples cluster with one another (Fig. 5, 6). The Hamburg population, however, can be separated from the LAK population only partially. One ash tree from the Leipzig floodplain forest is integrated in the Hamburg cluster, while one ash tree from the Hamburg population shows a smaller distance to the LAK population than to the rest of the Hamburg population. The *F. pennsylvanica* of the LAK is also integrated in the Hamburg population. It cannot be genetically separated from the *F. excelsior* population as a basic group. In total, four clades can be differentiated within this examined set, where the Hamburg ash trees are integrated within the overall population and were not divided basally.

Table 2 – Overview of the SSR primer pairs used. Forward primer was labelled with Cy5 for the detection on an the ALFexpress sequencer. – no reproducible PCR-products (these primer pairs were not analysed further). A: allele diversity, H: mean heterozygosity.

Primer name	Sequence	Reference	A	H
FEMSATL1	forward: 5’ AGC AGC ATT TAT GAA TGT TC 3’ reverse: 5’ATC AAC TGA AGA TGA CGA CG	Lefort *et al.* 1999a, b	19	0,72
FEMASTL2	forward: 5’ TCT TTA TCA TCA AAA AAT AA 3’ reverse: 5 TAC AAG GTG ATA TCA CTT CT 3	Lefort *et al.* 1999a, b	12	0,48
FEMSATL4	froward: 5’ TTC ATG CTT CTC CGT GTC TC 3’ reverse: 5’ GCT GTT TCA GGC GTA ATG TG 3’	Lefort *et al.* 1999a, b	13	0,68
FEMSATL5	forward: 5’ GGA TTG AGA TTC AAT TTG CA. 3’ reverse: 5’ TCC GAG TGA TGC CTA CTC TA 3’	Lefort *et al.* 1999a, b	11	0,24
FEMSATL8	forward: 5’ TGT AGC TCA GGA TTG GCA AT 3’ reverse: 5’ AGC GTT GTC CTT AAC CTT TT 3’	Lefort *et al.* 1999a, b	–	–
FEMSATL10	forward: 5’ TTG AGC AAC ATG TAA TTA TG 3’ reverse: 5’ AAA TAT CCG GTG CTT GTG TA 3’	Lefort *et al.* 1999a, b	14	0,16
FEMSATL11	forward: 5’ GAT AGC ACT ATG AAC ACA GC 3’ reverse: 5’ TAG TTC TAC TAC TTC AAG AA 3’	Lefort *et al.* 1999a, b	–	–
FEMSATL12	forward 5’ TTT TTG GAA CCC TTG ATT TT 3’ reverse: 5’ GAT GGA CGG GCA TTC TTA AT 3’	Lefort *et al.* 1999a, b	–	–
FEMSATL16	forward: 5’ TTT AAC AGT TAA CTC CCT TC 3’ reverse: 5’ CAA CAT ACA GCT ACT AAT CA. 3’	Lefort *et al.* 1999a, b	11	0,64
FEMSATL19	forward: 5’ CTG TTC AAT CAA AGA TCT CA. 3’ reverse: 5’ TGC TCG CAT ATG TGC AGA TA 3’	Lefort *et al.* 1999a, b	17	0,88
			Ø 13,86	Ø 0,54

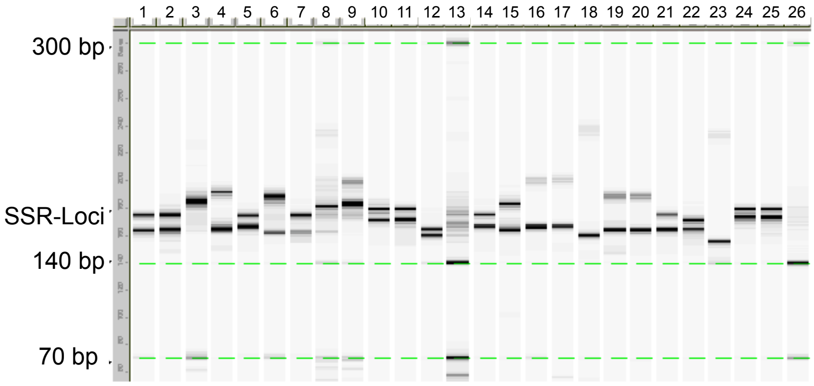

Figure 5 – Cut-out of one microsatellite analysis on an ALFexpress. Samples 1 to 25 see Table 1, green: internal standard 300 bp, 140 bp und 71 bp.

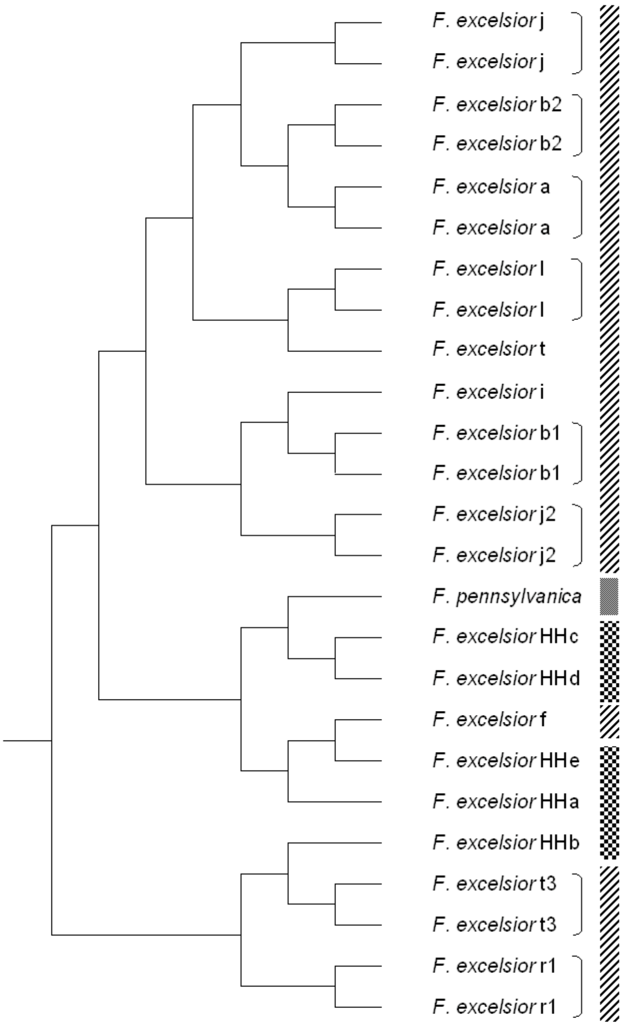

Figure 6 – UPGMA tree calculated using 310 SSR markers: 16 individual trees of *F. excelsior*, fasciated: population of the LAK plot, checkered: samples from Hamburg, black: *F. pennsylvanica*, parentheses show dual samples from one individual.

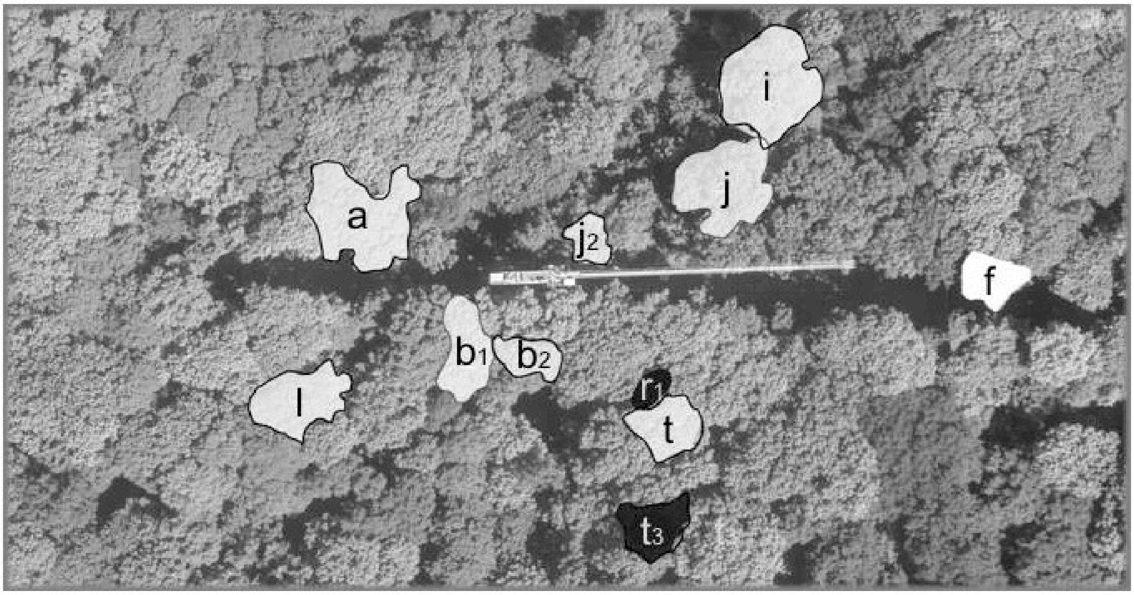

Figure 7 – LAK plot with 64 adult ash trees with more than 22 m height (Tal 2003) combined with results of the UPGMA analysis.

DNA fingerprint

Due to the high genetic variability of the SSR markers in the LAK ash tree population, all trees examined in this set could be identified by individual alleles of one or two SSR primer combinations and thereby were provided with a genetic fingerprint.

Establishment of the AFLP analyses

Since the establishment of AFLP marker analyses for various taxa is, by our experience, more time consuming, a test set consisting of 16 samples was used. This set comprised four individuals (three from the LAK plot and one individual from the Hamburg population) in four different concentrations to identify the optimal template composition and to test the reproducibility and variability of the AFLP marker method within certain parameters. Initial analyses in this test set indicate the same high extent of polymorphism as was already demonstrated in the SSR analyses. Due to the low number of individuals in this test, a population-genetic evaluation of the AFLP markers has been omitted so far.

Connections with phenological variation

Due to the low sample number, no statements concerning the comparison of genotypical and phenotypical groupings could be made so far. Also, no geographical division of the clusters could be found yet (Fig. 7). In this connection, an analysis of a total of 77 ash trees using 130 leaf samples from the LAK plot with microsatellite and AFLP primers is currently underway at the MPI Plön.

DISCUSSION

Genetic variability of the LAK ash tree population

The main questions – a) genetic differences within the overall adult population, b) relations between the genotypical and phenotypical variations, i.e. are there similarities between phenotypical and genetic characteristics of individuals, are there genetic/phenological similarities between the two planting phases – cannot yet be answered using the database examined so far. Only the establishment of two different marker types for the analyses is described here, and the reproducibility of these markers proven via double sampling. All examined ash trees in the LAK could also be provided with a DNA fingerprint by means of SSR markers.

The results presented here, however, provide an initial insight into the astonishingly high genetic variability of the adult semi-natural ash tree population of the LAK. The high genetic diversity can be seen clearly from the high allele diversity as well as from the high value of the average heterozygocity of the SSR markers. More than half of the individuals examined show heterozygous microsatellite loci.

The intention is to examine the overall population, including the regeneration occurring naturally in the forest as well. Here, evidence of paternity and maternity will be aspired to (Wagner 1996, Rudolph 2001, Ziegenhagen *et al.* 2003). The comparison of adult trees with the regeneration should deliver further information concerning the dispersal strategy of domestic trees. To this end, a combined evaluation of relatedness analyses of young and adult trees, of genetic distances, of geographical data and, in particular, of floral phenology is also to be carried out. For this purpose, a total of 130 leaf samples were collected between September and November 2003, and August and September 2004. Molecular biological analyses are currently being carried out using this sample set.

Influence of invasive species

Furthermore, the significance of the introduced ash species is to be examined. Therefore, 6 individuals from *F. pennsylvanica / F. americana* from the LAK plot were integrated into the sample set described above.

The intention is to investigate the possibility of spreading out of *F. pennsylvanica / F. americana* or even hybridising *F. excelsior* with *F. pennsylvanica* and/or *F. americana*. This should clarify the potential endangering of the species *F. excelsior* by the introduction of putatively invasive species (see also Volk 2002). The spread out of the introduced species and possible displace of *F. excelsior*, or cross-breed with it, is to be investigated. There are no larger-scale plantings of *F. pennsylvanica* to be found in Germany, only in parks and botanic gardens, meaning that supersession by this species appears to have been of no significance so far. On the other hand, in the case of *F. angustifolia* near Darmstadt, repression of *F. excelsior* (C. Niers, pers. comm.) resulted after seed was obtained from southern Europe. Later on it was noticed that it was a different species. With the establishment set of 25 samples used up to now, the integrated *F. pennsylvanica* could not be basally separated from *F. excelsior*. In this case, further investigations with a larger number of individuals need to be described.

Planning comparison of the LAK with natural populations

The plan is to complete a comparison with a natural ash tree population, in view of genetic diversity in planted and natural tree populations. Suitable locations for natural stands exist, for example, in the Storman and Lauenburg regions (Poppendieck, pers. comm.). Analyses using the establishment set have so far been unable to separate the Hamburg population from the LAK population completely; this could also not be expected due to the low sample number. 20 to 40 individuals therefore need to be sampled when further natural locations are analysed.

Do somatic mutations increase the genetic variability of the ash tree population?

Leipzig Canopy Crane Project provides us with a golden opportunity to take samples at any random point within the canopy. Particularly in the case of older trees, this makes it possible to investigate genetic differences within a tree and discover somatic mutations. Whitham & Slobodchikoff were able to detect somatic mutations in plants as early as 1981. Moreover, it could be demonstrated that somatic mutations occur more frequently in plants than in animals. Klekowski Jr. & Godfrey (1989) even mention an accumulation of mutations in perennial, long-lived plants and demonstrated this in mangroves. This accumulation of mutations, particularly in the apical meristems, result from an open growth system of plants where most of the mutations within the plant do not directly threaten the plant's life, and are therefore fatal, or necessarily lead to reduced fitness of the plant. Moreover, plants do not have – and this is also not the case with animals – a fixed germline. Flowers, which are responsible for sexual reproduction, develop on the apical meristems. Particularly in plants which predominantly reproduce via inbreeding, or reproduce more or less vegetatively, this higher variability appears to have benefits, for example during adaptation between shoots of one individual (Whitham & Slobodchikoff 1981), in the changing of a population's allele frequencies (Orive 2001) or in plants' defence system and evolution (O'Connell & Ritland 2004).

For morphological mutations of an individual, the mutation rate in this context is about 1×10^{-5} per locus. Similar rates are also expected for AFLP markers. The mutation speed of microsatellites is higher by one decimal power, because they tend to cause so-called hot spots of spontaneous mutations due to their repetitive motifs in the DNA sequence. The mutation rate is 1×10^{-4} (Frankham *et al.* 2004).

Ash trees live approx. 150 years long and it can be expected that somatic mutations will occur during these periods and therefore accumulate at the apical points. The mutation rate in ash trees during their lifetime is to be calculated in this additional study. On the one hand, it is interesting to see the extent to which these somatic mutations have an effect on the reproducibility of the AFLP and microsatellite markers as marker system for relatedness analyses and DNA fingerprinting. On the other hand, the intention is to use these investigations to clarify whether the high genetic and phenotypical variability can be explained by additional accumulation of somatic mutations. For this reason, in August to September 2004, ten further old trees were sampled with ten leaves each at principal branches located as far apart as possible (the order of branches was noted) within the tree canopy. Somatic mutations within the trees are to be investigated using these samples.

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2.3 Leaf fall in the Leipzig riparian forest

Anja Homscheid & Peter J. Horchler[1]

SHORT COMMUNICATION

All trees shed their leaves or needles in order to rejuvenate photosynthetic tissue. In temperate deciduous forest this process is cyclic and strongly linked to the seasonal climate change. Collecting falling leaves in a systematic way allows to calculate a rough estimate of the forests annual net primary production of leaf mass. From October 2003 to February 2004 we collected litter fall (leaves, fruits and twigs) in an area of 5 500 m^2 by means of 79 litter traps (buckets) with an total area of 5.58 m^2. The collected material was air-dried at 35 °C for two days. All leaves and fruits were sorted according to the species they belonged and were counted and weighed subsequently.

The overall leaf mass we obtained was 2.32 kg which corresponds to 4.16 tons per hectare. The number of collected leaves amounted for 9 467 (16 965 950 / ha). Fruit mass was 160 g (0.3 t / ha). Most leaves fell between mid October and mid November with some differences between species. The sequence was *Tilia cordata*, *Fraxinus excelsior*, followed by *Carpinus betulus*, and finally *Quercus robur.*

The value obtained for the overall leaf mass is similar to other values. But we believe that it has been underestimated because a notable number of leaves were shed during the extraordinarily dry and warm summer 2003. Hence, the relatively high leaf mass of supposedly more than 4.2 tons per ha reflects the high productivity of the Leipzig forest.

Since it is known that the net primary production of plant biomass changes from year to year, more litter collections would be useful.

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Table 1 – Comparison of leaf mass from different forest sites.

Source	LAK (this study)	Sitte *et al.* (2002)	Ellenberg (1986)	Körner (pers. comm)
Forest type	Mixed deciduous	Mixed deciduous	Beech	Mixed deciduous
Leaf mass (t/ha)	4.16 +	4.0	3.72 (S.D. 0.4)	3.0

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[1] corresponding author

2.4 Spatial patterns of folivory at Acer pseudoplatanus L. in the Leipzig forest canopy

Jan Mitscherling & Peter J. Horchler[1]

Herbivory is a key process in most ecosystems and is functionally linking ecosystem compartments and trophic levels across space and time. Yet, this process is insufficiently understood. We conducted two studies addressing folivory, i.e. leaf tissue 'eaten' by herbivorous insects, in a temperate, mixed deciduous forest. One study aimed to assess stand-level folivory, i.e. the overall proportion of herbivory in a forest, the second, more intensive study, dealt with spatial aspects of folivory at Sycamore Maple (*Acer pseudoplatanus* L.). In both studies leaves (n = 570/2 913) were collected in October 2002/2003, using a canopy crane system. Folivory was measured by scanning the leaves and 'counting' the pixels of the leaf area removed by herbivorous insects using a graphical software. The results are: *First study*: Stand-level folivory in 2002 amounted for 1.13% (Median = 0.21%) with a very high variation (SD = 2.55%). The distribution of folivory rates to area classes revealed an extremely right-skewed distribution, i.e. most leaves did not show any or only minor damage by folivory. *Second study*: The overall degree of folivory was 1.71% (Median = 0.59%, SD = 2.84%). The frequency distribution of the degree of folivory to area classes is also extremely right-skewed. The degree of folivory was significantly different between most (73%) of the individual trees. Significant overall differences of folivory could be detected (tested by GLM) between understorey and canopy as well as between midstorey and canopy. The differences between understorey and midstorey were not significant. The highest degrees of folivory were found at upper canopy leaves. However analysing individual trees resulted in highly contrasting patterns. The results are discussed.

INTRODUCTION

Herbivory is a key process in almost all ecosystems (e.g. Schowalter 2000) but its controlling factors are still poorly understood. Herbivores are primary consumers that feed on the primary food resource, green organic matter. At the same time herbivores serve as prey for higher order consumers like spiders, parasites, birds, and bats. But they also nourish the forest soil and its organisms by dropping leaves, green frass and faeces (Rinker & Lowman 2004). Hence, the process herbivory links ecosystem compartments as well as trophic levels across space and time. Especially in forests where the access to the biggest part, the canopy, is strongly restricted, herbivory is insufficiently studied. Most studies performed so far were case studies with a sampling at one moment in time (Rinker & Lowman 2004). Yet, it is known that herbivory varies considerably in space and time (Lowman 1992). Hence, clearly long-term studies are needed for a better understanding of this process. Herbivory studies also offer a peculiar chance because they easily enable to gain insight to an important ecosystem process while many other processes remain difficult to study because patience and/or expensive equipment is needed.

We conducted a study on the herbivory in a central European mixed deciduous forest using a crane system to access the canopy (Morawetz & Horchler 2003). In two different approaches we studied **(1)** stand-level herbivory and **(2)** herbivory at one tree species. We selected *Acer pseudoplatanus* L. since this is the most frequent and abundant tree species in the study area. We decided to study folivory, i.e. leaf damages by herbivorous insects since this can easily be done in a quantitative way.

Besides addressing the question of the overall, so called stand-level folivory, we concentrated on its spatial distribution. The research question were: **(1)** What is the overall degree of folivory in the forest? **(2)** Are there differences in the degree of folivory between different woody species? **(3)** Are there differences in the degree of folivory at different heights in the canopy? **(4)** What is the overall degree of folivory at *Acer pseudoplatanus*? **(5)** Are there differences in the degree of folivory between the individuals of *A. pseudoplatanus*? **(6)** Are there differences in the

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[1] corresponding author

degree of folivory at *A. pseudoplatanus* at different heights in the canopy?

MATERIALS AND METHODS

Field work

To study stand-level folivory, we followed a proposal for a standard protocol developed by K. Ernest and collaborators (Ernest 2004). We took advantage of the existing canopy crane, which enables to access almost all parts of the forest canopy (Morawetz & Horchler 2003). For spatial reference the area accessible by the crane was subdivided using a three-dimensional coordinate system. This allowed us to assign 100 sampling sites completely at random. Based on this design we collected 570 leaves at 57 sites in the canopy in late summer 2002. Since many sites that had been chosen were empty spaces only collections at 57 sites could be realised. At each collection site 10 leaves were randomly harvested.

For the second study we randomly selected 10 trees of *Acer pseudoplatanus* in the study area. At these trees ca. 100 leaves were collected each at three heights in the canopy (0–3 m, 12–16 m, 25–30 m) summing up to a total of 2 913 leaves. The leaves were collected in October 2003. Light conditions at each collection site were estimated subjectively using a five-score ordinal scale ranging from very shady to very sunny.

Data processing

The collected leaves were scanned with a flatbed scanner in black/white mode (300 dpi) and stored to files readable by a graphical software (Adobe Photoshop™). Thus, the leaf area appears as black area, the area removed by herbivorous insects as white dots. In case of area removed at leaf margins we tried to reconstruct and outline the original margin with a thin black line. With the help of the 'histogram' function of Adobe Photoshop it was possible to count black and white pixels and compare them to the number of pixels of an area (square) with a known size. In this way leaf area and folivory area were measured for each leaf and the percentage of folivory was calculated. Note that only a complete removal of the leaf tissue can be detected by this method. Damages like leaf stippling (German: Fensterfraß), which only comprises a part of the leaf's cross section (parenchyma), cannot be detected in that way.

Data analysis

The data of the first study were analysed taking all 570 samples as one sample supposedly representative for the whole forest stand. For this sample the mean, standard deviation and median of the area removed by herbivores (in cm^2 and %) were calculated. Furthermore the distribution of those values to area classes was represented as histogram.

The same procedure was carried out for all leaf collections specific to the woody species. A graphic representation of folivory at different heights in the forest was done for *Acer pseudoplatanus* since only for this species sufficient leaves were collected. To check for a correlation of folivory at this species to light levels, we could use height specific data of light (PAR) measurements (Horchler, this volume). We plotted folivory rates against relative PAR values and performed a regression analysis.

The data of the second study focussing on *Acer pseudoplatanus* were analysed in a similar way. Additionally, the samples of the 10 tree individuals were analysed separately. For those, as well as for the complete sample, differences in folivory at the three different heights were tested for significance in pair wise comparisons using a Mann-Whitney test as well as a Generalised Linear Model (GLM). Most data were also represented graphically. All analyses were carried out with the software MS Excel™, Analyse-It™(`www.analyse-it.com`) and R (`www.r-project.org`).

RESULTS

The results are presented separately for the two studies.

Study of stand-level folivory

The total area of the collected leaves summed up to 4.74 m^2. The leaf area removed by herbivorous insects was 531.2 cm^2 (0.053 m^2), resulting in an average stand-level degree of herbivory of 1.13% (Median 0.21%) with a very high variation (SD = 2.55%). The most striking feature of the folivory data is that its distribution to area classes was extremely right-skewed, i.e. most leaves did not show any or only minor damage by folivory. There were notable differences between the leaves of different species. *Tilia cordata*, *Fraxinus excelsior*, and *Ulmus* sp. for example showed higher degrees of folivory than *Carpinus betulus* and *Acer pseudoplatanus*.

Only for the most abundant tree species (*Acer pseudoplatanus*) sufficient leaves (194) were collected to analyse differences in folivory at different heights. The result showed higher degrees of folivory at upper canopy leaves except the uppermost outer canopy leafs. Regression analysis (Fig. 1) of these average values of folivory and the average percentage of light showed a rather close and significant positive correlation, except the uppermost outer leaves. This sample consisted of just 10 leaves of one tree and is regarded as statistical outlier since further studies mostly showed high degrees of folivory at canopy leaves of *Acer pseudoplatanus*.

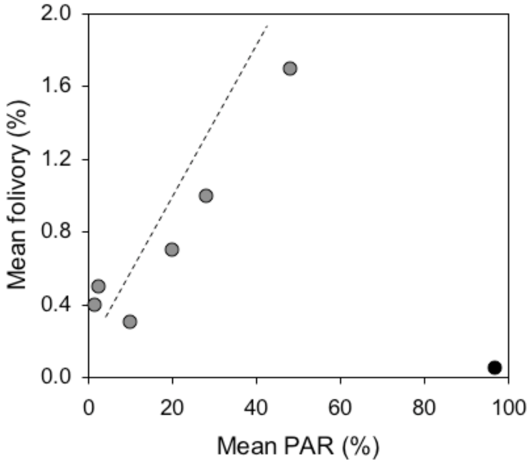

Figure 1 – Mean folivory [%] at leaves of *Acer pseudoplatanus* L. plotted against the mean values of photosynthetically active radiation (PAR) at different heights in the Leipzig Canopy Crane plot (n = 194). The average folivory rates linearly increase up to a medium rate of PAR. The data point at ca. 100% PAR is likely to be a statistical outlier.

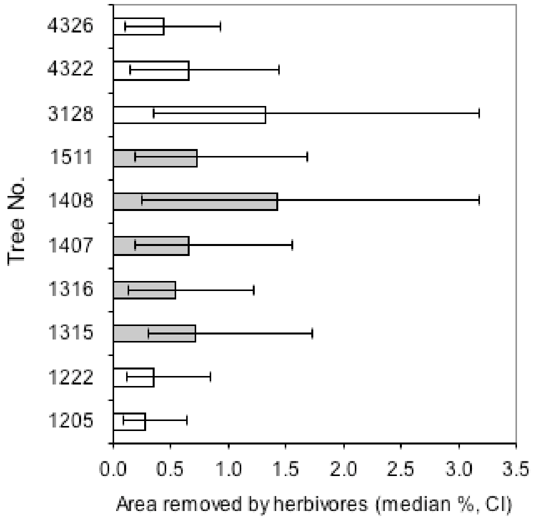

Figure 2 – Folivory rates (median and 95% confidence intervals) at leaves (n = ca. 300) at 10 trees. Note the high variation (CI lines). The grey shaded bars represent the adjacent trees shown in Fig. 4 (see below).

The overall degree of folivory is on average 1.71% (Median = 0.59%). Again the variation is high (SD = 2.84%). The frequency distribution of the degree of folivory to area classes is also extremely right-skewed. The degree of folivory as tested by a Mann-Whitney test was significantly different between most (73%) of the individual trees (Fig. 2). Taking all leaves as one sample supposedly representative for the whole forest plot, significant differences of folivory could be detected (tested by GLM) between the understorey and canopy as well as between the midstorey and canopy. The differences between understorey and midstorey were not significant. The highest degrees of folivory were found at upper canopy leaves (Fig. 3).

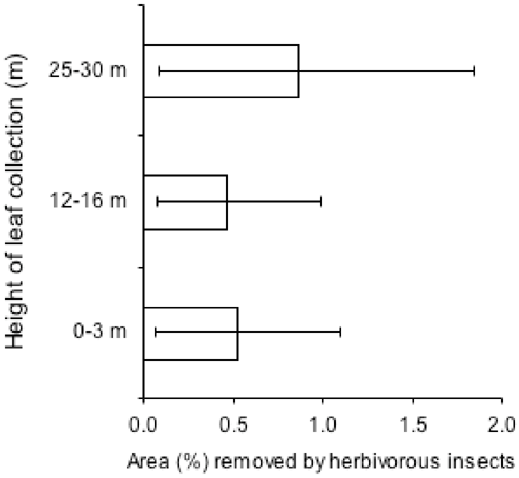

Figure 3 – Folivory rates (% removed area, median and 95% confidence intervals) at leaves (n = ca. 1 000 for each level) from different heights in the canopy. A test (GLM) revealed significant differences in folivory rates between understorey and canopy, and midstorey and canopy but no significant difference between understorey and midstorey.

However analysing individual trees resulted in highly contrasting patterns even for trees standing next to each other (Fig. 4). Estimates of light conditions at the sites of leaf collections did not show any correlation to the observed patterns.

DISCUSSION

Stand-level herbivory

Most studies on herbivory in forests were carried out in the understorey. If data from the forest canopy were taken into account they often originated from litter trap collections. Visual estimates of stand-level herbivory in temperate deciduous forests range from 7–10% (e.g. Nielson 1978). Exact measurements by Schowalter *et al.* (1981) lowered the range to 1–5%. Near ground level Bray (1964) found 3–10% of annual losses by herbivore defoliation.

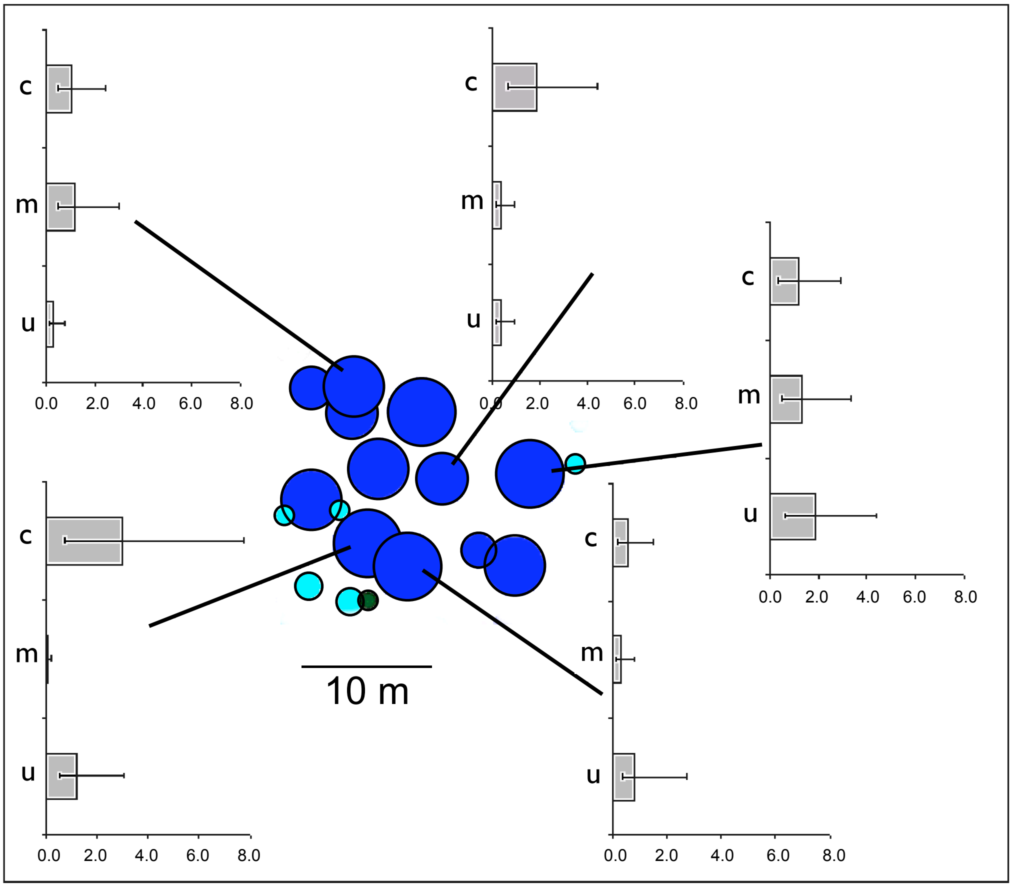

Figure 4 – Folivory rates (% removed area, median and 95% confidence intervals) at leaves (n = ca. 100 for tree at each height level) from different heights in the canopy (c = canopy, m = mid storey, u = under storey) and from five trees which are situated very close to each other. Note the striking differences. Dark blue dots represent trees of *Acer pseudoplatanus*. The diameter corresponds roughly to the stem diameter. Light blue dots represent tress of *Acer platanoides* and the green dot a tree of *Ulmus* cf. *laevis*.

For evergreen tropical forests LOWMAN & HEATWOLE (1992) and SCHOWALTER (1994) reported values ranging from 2–15% or higher. The value obtained for the Leipzig forest of 1.13% is quite low and in the range of coniferous forests (SCHOWALTER 1989). Of course 570 leaves might be too low to provide a good estimate, but a similar study of leaves of three tree species in the forest under storey at the same site in 2003 also revealed a low overall level of herbivory (unpublished). The large sample of almost 2 913 leaves of *Acer pseudoplatanus* obtained by the second study also showed a fairly low level of 1.7%. It is known that herbivory rates can differ considerably between sites (LOWMAN 1995, SCHOWALTER 2000). Among the potential causes for this RINKER & LOWMAN (2004) lists variation in phenology, leaf age, vegetation stratum, forest type, as well as differences in natural history and demography among local arthropods including predators and parasites of the herbivores.

In conclusion, the low degree of folivory might be normal for the Leipzig forest. But there are also various facts that may explain this low value.

As stated above we may have missed the 'right time' to detect higher degrees of folivory. Given that we always sampled leaves by the end of summer, we might have missed bigger folivory damages in early summer. In early June 2003 for instance, we observed a notable degree of folivory at leaves of *Quercus robur*, with a subsequent dropping of those leaves, followed by a second leaf flush. Therefore we may have underestimated the 'true' degree of folivory at least for the annual calculation.

The climatic situation, especially a fairly wet summer 2002 followed by an extremely dry summer 2003 may have caused a considerably lower abundance of Lepidopteran herbivores than 'normal', which in turn caused less folivory (FRÖHLICH 2004 and FRÖHLICH *et al.* this volume). The same unusual climatic factors might have led to a shift in herbivore/predator and/or herbivore/parasite ratio causing a higher pressure on herbivores.

Finally, the forest, situated in close vicinity to the city, may still suffer of the decades of environmental pollution in GDR times, which ended just a decade ago. This also might have led to a rather unbalanced situation of ecological processes.

Clearly, more long-term studies at all seasons are needed to get further insight to this process.

Folivory at different heights

The trend for the average folivory was similar in both studies and revealed a higher percentage of removed plant tissue in the upper canopy. In the first study one sample of 10 leaves from the upper canopy did not show a notable damage. This is surely due to a sampling outlier. In the second study most of the upper canopy leaves did show high degrees of folivory, which led to the general trend mentioned above. These findings suggest a general herbivores' preference of *Acer pseudoplatanus* leaves in the upper canopy with higher light levels. This might be due to a higher photosynthetic activity and hence a better food quality (e.g. higher sugar content) of leaves of *Acer pseudoplatanus* in the upper canopy. The most interesting finding in this study appears to be the striking differences in folivory between individual trees and at different canopy heights. There are various potential reasons for this observation.

Microclimatic preferences of the herbivorous insects along with predation avoidance may lead to a preference of certain sites in the canopy with higher feeding intensities.

The trees may differ genetically in their resistance or defence to herbivore attacks, just like humans differing in the performance of their immune system.

A varying biochemical composition of the leaf tissue due to slight differences in the tree's growing sites (soil chemicals, light conditions) might also be responsible for these patterns.

Finally the scale of the studies may have simply been inappropriate, i.e. the sampling area might be to small to detect clearer patterns or trends.

Again it can be concluded that only more and long-term studies including the whole forest space enable to get more insight in this complex ecosystem. Such studies accompanied by detailed surveys of the spatial and temporal distribution of herbivores and other important organisms of the food web (e.g. birds, bats, arthropods, parasites) may lead to a much better understanding of the forest ecosystem. This is essential to deal with future requirements and developments for a sustainable forest management and conservation.

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2.5 Plant-animal interactions in the canopy: intraspecific variability in herbivory on sycamore (Acer pseudoplatanus L.)

Haike Ruhnke[1], Martin Brändle, Stefan Klotz, Roland Brandl & Martin Schädler

The quality of leaf tissue differs not only among plant species, but may also show considerable variability among and within individuals of a given species. Insect populations may respond to this resource heterogeneity by forming ecologically and genetically distinct groups (adaptive deme formation; ADF, Edmunds & Alstad 1978). To evaluate central assumptions of the ADF-hypothesis, we analysed variability in herbivore attack, palatability and leaf utilization in a feeding experiment as well as leaf traits among and within three sycamore individuals in two consecutive years on the crane plot in Leipzig. Herbivore attack in the field, palatability and leaf utilization by a generalist herbivore as well as leaf traits differed among the investigated individuals of sycamore. Only in 2003 did herbivore attack differ significantly between the upper and the lower tree layer. In the feeding experiments, larvae of *Spodoptera littoralis* showed differences between tree layers only in terms of conversion efficiency in the first year of our study. All measured variables point to considerable heterogeneity of leaf quality among the investigated individuals, with only little variation within trees. Palatability, the relative growth rate and the conversion efficiency of the larvae of *S. littoralis* correlated negatively with the carbon/nitrogen-ratio of the leaf tissue. Herbivore attack in the field, however, was not related to palatability, relative growth rate and conversion efficiency of *S. littoralis* or to the measured leaf traits. Due to confounding environmental effects, levels of herbivory do not always follow the patterns of palatability and leaf traits in space and time. Overall, our analyses support two basic assumptions of the ADF-hypothesis. Firstly, there is considerable variability of quality among individual trees and, secondly, the variability is to some extent predictable across time.

INTRODUCTION

Leaves of trees may differ in palatability to insect herbivores. Several authors showed that concentration of leaf nitrogen and secondary compounds may vary among individual trees within species (Howard 1990; Suomela & Ayres 1994; Laitinen *et al.* 2000; Osier *et al.* 2000b) as well as between sun and shade leaves within individuals (Hollinger 1989; Dudt & Shure 1994). These variations may affect attack, feeding behaviour and development of associated insect herbivores (Ayres *et al.* 1987; Howard 1990; Strauss 1990; Osier & Lindroth 2001; Fortin & Mauffette 2002). Ultimately, differences in the quality of leaves may translate into genetic differentiation between populations of phytophagous insects living on different individuals. The adaptive deme formation hypothesis (hereafter called ADF-hypothesis) predicts the evolution of distinct groups (demes) within species of herbivorous insects in response to differences of resource quality among individuals. Demes are adapted to a particular individual (Edmunds & Alstad 1978). Although some studies have demonstrated genetic variation among populations of phytophagous insects, the underlying mechanisms are still poorly understood (Mopper 1996).

In our study, we investigated the intraspecific variability of herbivore attack, of palatability and leaf utilization as well as of leaf traits among and within individuals of sycamore (*Acer pseudoplatanus* L.) in two consecutive years. We approached the following questions: **(1)** Is there any difference in herbivore attack, palatability and leaf utilization as well as of leaf traits among and within individual trees? **(2)** If such differences exist, is there any correlation between herbivore attack in the field and palatability as well as of leaf traits? **(3)** Do the differences among individual trees show a consistent pattern across the two consecutive years?

MATERIALS AND METHODS

We estimated herbivore attack in the field. Palatability and related variables of leaves were measured with

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[1] corresponding author

laboratory experiments using a polyphagous moth. Furthermore, we measured two leaf traits known to be important for herbivores. For our work we sampled three mature sycamore trees (*Acer pseudoplatanus* L.) in two consecutive years. The maximum distance between individual trees was about 90 m. Within trees we distinguished between an upper (sun leaves) and a lower layer (shade leaves).

Herbivore attack in the field

At the end of growing season in August 2002 and 2003, we quantified the levels of herbivory by estimating the amount of removed leaf material. From each tree individual we selected four branches in each layer. We collected 25 leaves from each branch (200 leaves per tree). Consumed leaf area [mm^2] was estimated after digitising and measuring leaf area (SigmaScan-Pro5). The specific weight of leaf material differed between the two layers. Therefore, we corrected the consumed leaf area of the upper layer by tree-specific correction factors. These correction factors were the ratio of leaf fresh mass to dry mass of 20 samples from each tree layer collected in July of 2002 and 2003.

Feeding experiments

For our feeding experiments we used larvae of the African cotton leafworm (*Spodoptera littoralis* (Boisduval), Lepidoptera: Noctuidae) a polyphagous herbivore. Larvae originated from a laboratory stock and were reared on artificial diet.

The experiments were carried out in July 2002 and July 2003, when the foliage was fully mature. In every experiment, we used different branches within each tree layer to avoid possible confounding effects of induced plant defence. The branches selected for the feeding experiments were near to those selected to estimate herbivore attack in the field. We collected leaves from short shoots of each branch. Leaves were sprayed with deionised water to keep them turgescent and leaves were stored at 4 °C. The experiments started a few hours after sampling. From six leaves of each branch we punched leaf discs (diameter 23 mm). Discs were weighed and placed individually in Petri dishes lined with moist filter paper. For each Petri dish we used one larva of *S. littoralis* (third instar). Prior to the experiments, larvae were weighed. The Petri dishes were placed in a climate chamber (26 °C and 12 h light) for 24 h. At the end of the experiment larvae were killed by freezing. Dead larvae and remaining leaf material were dried at 60 °C to weight constancy. Initial larval mass was converted to dry mass using a linear regression equation for each year (30 larvae in each year). The initial fresh mass of leaf discs was converted to dry mass by using the mean water content of leaves for each selected branch (see below). Leaf consumption was expressed as mg consumed leaf dry mass in 24 h.

Osier *et al.* (2000a) showed that the growth of caterpillars reared in bags on trees was highly correlated to the growth of larvae reared in the laboratory on leaves of the same tree. Hence, we expect that the feeding experiments in the lab reflect leaf quality in the field (see also Kleiner 1991). Lab experiments have the advantage that all experiments are performed under identical climatic conditions. In the field microclimatic differences between trees and layers may influence the results.

Leaf traits

Leaf water, nitrogen and carbon contents are known to be closely related to functional leaf traits and to palatability (Schädler *et al.* 2003). Therefore, we measured these traits for the foliage of each branch used during the feeding experiments and to the same time as in the bioassays. Water content was determined by the ratio of leaf dry mass to fresh mass of five leaf discs per branch. To estimate the carbon/nitrogen-ratio a sample of leaves from every branch was vacuum-dried for 48 h, milled with a high-speed rotor mill and analysed for carbon and nitrogen with an element analyzer (Vario EL, Elementar Analysensysteme GmbH, Hanau, Germany).

Data analyses

For the analysis of consumed leaf area in the field we averaged the 25 individual values of each branch. These means were square-root transformed to normalize the distribution of residuals. The effects of year, tree individual and tree layer were tested using a three-way ANOVA (Proc GLM [Version 8.02]; SAS Institute).

In the analyses of the feeding experiments, for every trait we used the average across the six values of each branch. The effects of year, tree individual and tree layer on consumed leaf material, final larval dry mass, and increase of larval mass during the experiment were analysed using an ANCOVA (see Raubenheimer & Simpson 1992, Horton & Redak 1993). For the analysis of consumed leaf material and final larval dry mass, initial larval dry mass was used as a covariate. By using type I sums of squares, we analysed the effects after removing confounding effects of initial larval dry mass from the analysis. Thereby, we standardized leaf consumption to herbivore mass, and adjusted means are a measure of palatability. Similarly, adjusted means of final larval dry mass measure relative growth rates of larvae; for this analysis we log-transformed initial and final larval dry mass. For the analysis of increase in mass, the consumed leaf material was used as covariate. Thereby, we estimated an equivalent to the efficiency of conversion of ingested food into body substance (see Waldbauer 1968).

Effects of year, tree individual and tree layer on leaf C/N-ratio and water content were analysed using a three-way ANOVA. The relationships between variables measured during the feeding experiments (adjusted means from the ANCOVA for every layer of each tree individual), the herbivore attack in the field, and leaf traits were tested by a Spearman's rank correlation using the mean of every trait per layer, tree and year.

RESULTS

Herbivore attack in the field

In the field, the consumed leaf area differed significantly between the two consecutive years (Table 1). We observed a significant interaction between year and tree individual indicating different levels of herbivory on the individuals between years (Fig. 1a). Separate statistical analyses for the two years showed, however, significant differences among individual trees only in 2003 (Fig. 1a, ANOVA results not shown). Herbivore attack was larger in the upper tree layer in the second year only (significant year x tree layer interaction, Table 1, Fig. 1b). Furthermore, the effect of tree layer varied among individual trees (significant tree individual x tree layer interaction, Table 1).

Table 1 – Results of the ANOVA of effects of year, tree individual, and tree layer on the consumed leaf area by herbivores (herbivore attack). *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$, df: degrees of freedom, MS: Mean square.

Source	df	F values
Year	1	15.37 ***
Tree individual	2	1.56
Tree layer	1	15.08 ***
Year x tree individual	2	3.73 *
Year x tree layer	1	25.10 ***
Tree individual x tree layer	2	4.82 *
Year x tree individual x tree layer	2	1.89
Residual	36	[MS = 8.26]

Feeding experiments

Palatability, relative growth rate, and conversion efficiency of *Spodoptera littoralis* differed significantly between the two years (Table 2). All traits differed among individual trees (Fig. 2). We found no general difference between the upper and lower tree layer for all three variables. Overall, we found few significant interactions between factors. For the conversion efficiency we found a significant interaction between year and tree layer; in 2002 we found higher conversion efficiency for the lower layer (Fig. 3). For the growth rate we found a three-way interaction.

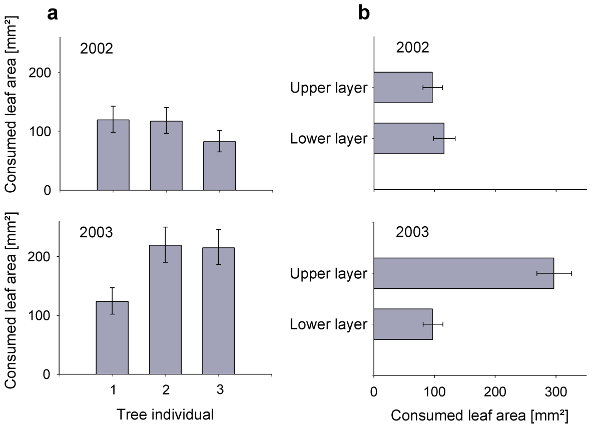

Figure 1 – Herbivore attack measured by the consumed leaf area on sycamore by herbivores in the field. The graphs present means of tree individuals (a) and tree layer (b) for each year (back-transformed means ± 1 SE).

Leaf traits

The C/N-ratio of leaves differed between the two years as well as among individual trees (Table 3). We found a significant interaction of year and tree individual as well as a significant three-way interaction (Table 3). The water content of leaf tissue was similar in the two years but differed among individual trees and between tree layers. Generally, water content was significantly lower in leaves of the upper tree layer. However, the strength of this effect differed between years and individual trees (significant year x tree layer and tree individual x tree layer interaction, Table 3). Palatability ($P = 0.052$), relative growth rate ($P = 0.019$), and the conversion efficiency ($P = 0.003$) of larvae of *S. littoralis* were all negatively correlated to the C/N-ratio of the leaf tissue, although we could only use the mean of the trait per layer and tree and year. In contrast, we could not detect correlations with the water content of leaves (all $P > 0.3$). We found no relationship between herbivore attack in the field and variables measured during the feeding experiments as well as with the measured leaf traits (all $P > 0.3$).

Table 2 – Results of an ANCOVA of effects of year, tree individual, and tree layer on palatability, growth rate and conversion efficiency of the larvae of *S. littoralis.* *: P < 0.05, **: P < 0.01, ***: P < 0.001, df: degrees of freedom, MS: Mean square.

Source	**df**	**F values**		
		Palatability	**Growth rate**	**Conversion efficiency**
Covariate	1	52.16 ***	204.23 ***	424.69 ***
Year	1	6.65 *	76.03 ***	52.07 ***
Tree individual	2	23.94 ***	41.98 ***	15.55 ***
Tree layer	1	3.02	0.93	3.48
Year x tree individual	2	0.62	1.19	1.35
Year x tree layer	1	0.88	0.17	6.59 *
Tree individual x tree layer	2	0.76	1.65	1.19
Year x tree individual x tree layer	2	2.58	3.48 *	0.98
Residual	35	[MS = 3.27]	[MS < 0.01]	[MS = 0.06]

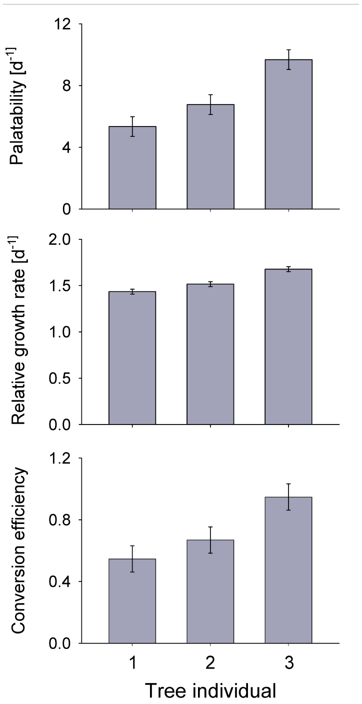

Figure 2 – Effects of tree individual on palatability, relative growth rate, and conversion efficiency of larvae of *S. littoralis* on sycamore (adjusted means of both years ± 1 SE).

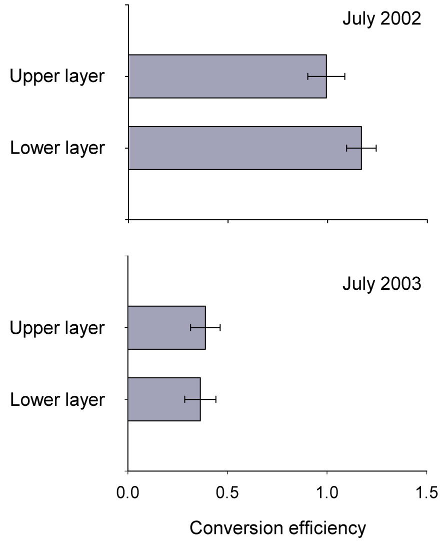

Figure 3 – Effects of tree layer on the conversion efficiency of larvae of *S. littoralis* for 2002 and 2003 (adjusted means ± 1 SE).

Table 3 – Results of an ANOVA of effects of year, tree individual, and tree layer on the carbon/nitrogen-ratio and water content of leaves. *: P < 0.05, **: P < 0.01, ***: P < 0.001, df: degrees of freedom, MS: Mean square.

Source	**df**	**F values**	
		C/N-ratio	**Water content**
Year	1	235.26 ***	1.07
Tree individual	2	17.00 ***	19.83 ***
Tree layer	1	2.86	411.99 ***
Year x tree individual	2	6.97 **	1.72
Year x tree layer	1	0.50	19.85 ***
Tree individual x tree layer	2	0.95	3.93 *
Year x tree individual x tree layer	2	8.38 **	1.00
Residual	36	[MS = 0.908]	[MS = 0.001]

DISCUSSION

One may answer the three questions posed in the introduction as following: **(1)** We found significant differences among individual trees in herbivore attack in the field, variables derived from feeding experiments as well as measured leaf traits. **(2)** We found no correlation between herbivore attack in the field and variables derived from the feeding experiments or measured leaf traits. However, variables derived from the feeding experiments and leaf traits were correlated **(3)**. Although we found significant interactions for the leaf traits, the results from the feeding experiments provided a consistent ranking of tree individuals across the two years.

A number of studies have shown that the content of certain compounds differs among tree individuals (Howard 1990; Suomela & Ayres 1994; Laitinen *et al.* 2000; Osier *et al.* 2000b). Further, their utilization by herbivores varied among host-plant individuals (Ayres *et al.* 1987; Howard 1990; Strauss 1990; Osier & Lindroth 2001). We found significant differences in herbivore attack, palatability and related variables as well as simple leaf traits among three sycamore individuals. Note that these individuals grow close to each other. However, the variation in herbivore attack in the field was not correlated to the results of the feeding experiments and measured leaf traits. This lack of correlation between field patterns and lab experiments has been reported by a few other authors (Rowe & Potter 1996; van Nouhuys *et al.* 2003). Rowe & Potter noticed "...there is no a priori expectation for whether leaves in the upper or lower canopy will be preferred on the basis of foliar chemistry". This points to fundamental differences between patterns of herbivory in the field and lab studies. In the field the variation in herbivore pressure within and among trees is not only influenced by leaf quality but by a plethora of factors such as microclimate (Stamp & Bowers 1990), predation, parasites (Stamp & Bowers 1988) or migration (Batzer *et al.* 1995; Magalhães *et al.* 2002).

Leaf traits like water content, C/N-ratio, or concentration of secondary compounds influence leaf palatability (Mattson 1980; Scriber & Slansky 1981; Hartley & Jones 1997; Schädler *et al.* 2003). Nevertheless, several studies found that palatability is sometimes not affected by those traits (Dudt & Shure 1994; Rowe & Potter 1996; Osier & Lindroth 2001; Shibata *et al.* 2001). Furthermore, the details of the relationship may depend on the specific plant-insect species combination considered (Howard 1990; Hemming & Lindroth 1995), and the relationship may change with environmental factors (Jansen & Stamp 1997). In our study, palatability, relative growth rate and the conversion efficiency measured with the larvae of *S.littoralis* showed the expected negative relationship to the C/N-ratio of the leaf tissue.

We found significant differences in herbivore attack as well as water content of leaves between tree layers. However, we were not able to demonstrate general differences in palatability, growth rate and conversion efficiency between layers. Fortin & Mauffette (2002) found that leaves from the upper layer of sugar maple were more palatable to larvae of a generalist moth, with positive effects on pupal mass and number of eggs. In addition, these leaves were preferred in feeding tests. Only our results from the second year support these findings. In general, little information is available on the variability of herbivore attack as well as leaf palatability within individual trees (Howard 1990; Rowe & Potter 1996; Kause *et al.* 1999; Fortin & Mauffette 2002). Some authors suggested that differences in leaf quality within plants are directly or indirectly related to the effects of solar irradiation (references in Fortin & Mauffette 2002). However, many published experiments used sun and shade leaves from different plants respectively. Our finding of considerable differences among individuals suggests that results in the literature are confounded by those differences.

The ADF-hypothesis suggests that monophagous herbivorous insects may form distinct adaptive groups in response to resource heterogeneity among host individuals. However, the formation of demes requires temporal predictability of host plant quality for the insects. Mopper *et al.* (2000) showed for a leafminer that ten generations may be necessary to form demes. At least across such temporal scales host individuals should have predictable properties to which the insect can respond. Leaf traits, however, show considerable seasonality (McKinnon *et al.* 1998; Osier *et al.* 2000b; Riipi *et al.* 2004) and leaf traits differ between years (Laitinen *et al.* 2000; Covelo & Gallaro 2001). Thus, insect herbivores have to deal with considerable variability in leaf quality within (Kause *et al.* 1999; Haukioja *et al.* 2002) and between years (McPheron *et al.* 1988; Cronin *et al.* 2001). Cronin *et al.* (2001) even showed fluctuations in host-plant preferences and performance between successive years. Although in our study we found significant interactions between tree individuals and year in their effect on leaf traits, few interaction terms were significant for variables measured during the feeding experiments. The relative ranking among individuals was the same in the two years (see also Riipi *et al.* 2004). Leaves of some tree individuals may be in general a better food source than leaves of other individuals. Hence, our study suggests that resource heterogeneity is predictable between years. But remember that about ten or even more generations are required to form demes. Hence more long-term studies are badly needed to draw safe conclusions (see also Cronin *et al.* 2001).

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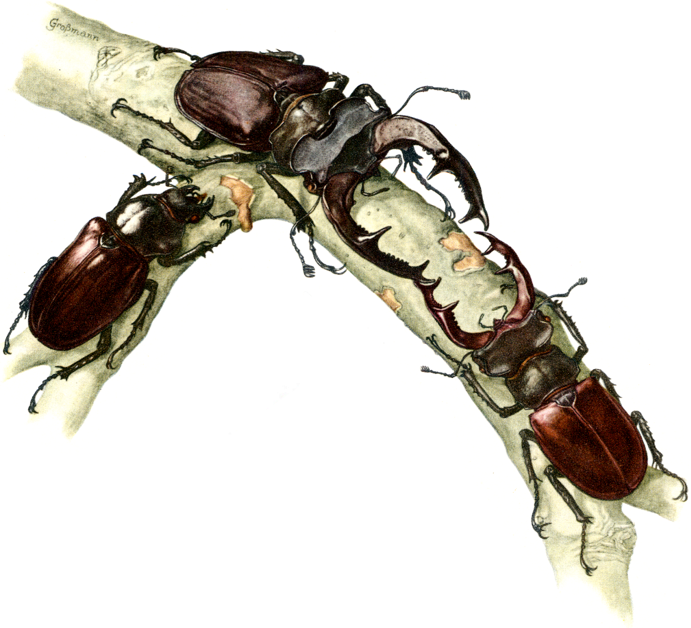
Part II

Studies of organismical biodiversity

3 Animal diversity and ecology of wood decay fungi



Contents

3.1 Methods of sampling arthropods in the canopy of the Leipzig floodplain forest

Erik Arndt[1], Martin Unterseher & Peter J. Horchler

SHORT COMMUNICATION

Intensive entomological investigations have been carried out at the Leipzig crane site in the years 2001 to 2003, to evaluate the diversity and distribution of both flying and non-flying arthropods in its canopy region (see contributions in this volume). Besides hand collections from aerial inflorescenses of *Acer*, *Tilia*, *Fraxinus*, and *Quercus* trees (Tal, this volume) and tree fogging (Floren & Sprick, this volume), several trap types were used to investigate the arthropod fauna in tree crowns. The forest floor was also investigated using pitfall traps (Carabidae; Arndt & Hielscher, this volume).

Figure 1 – Window trap in a tree crown of the Leipzig crane site. The handrail of the orange coloured gondola is visible in the front.

Window trap (Flight interception traps)

Composite flight-interception traps (Basset *et al.* 1997, Schubert 1998) were used to catch flying insects (e.g. wasps, gnats, aphids, beetles). The insect flight is interrupted when it hits the acrylic glass pane. Good and light flyers try to overcome the obstacle by flying upwards. They are conducted then into the container partly filled with diethylene glycol. Bad and heavy flyers plump down through the funnel into a second vessel (Fig. 1).

Branch eclectors

The full range of crawling arthropods can be recorded with this trap type. The tubular shaped trap is installed around a branch, fixed and closed on one side. Animals moving on the branch surface are conducted through the only opening and are trapped either in the upper or lower vessel (Fig. 2). Construction and use of branch eclectors followed Simon (1995).

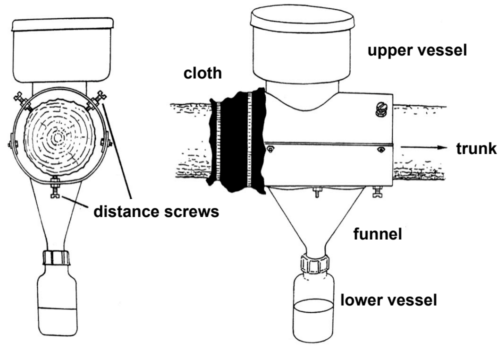


Figure 2 – Branch eclector fixed to a branch in the canopy (left); schenatic drawing (right; from Simon, 1995).

Stem eclectors

Stem eclectors following the method of Funke (1971) and Behre (1989) were installed on one tree each of *Quercus robur*, *Tilia cordata*, and *Fraxinus excelsior*,

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[1] corresponding author

to get an impression of the activity of climbing invertebrates in the years 2002 and 2003 (Fig. 3). Stem eclectors measure ground-canopy-interactions of the invertebrate fauna. They are installed using a steel ring under which the mounts carrying the white sampling tins are clamped. The black cloths are also clamped under a steel ring. The type of branch eclectors described here is a variant to sample the fauna that moves from ground to the tree top.

Figure 3 – Stem eclector fixed around a large *Tilia cordata* tree in about 3 m in height.

Sampling design

The arthropod fauna of the tree crowns at the crane site was examined using 50 window traps with two in each of 25 trees and 48 branch eclectors with four in each of 12 trees (Fig. 4, Appendix Table 1).

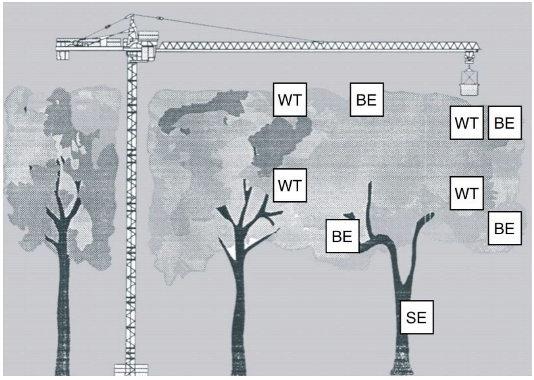

Figure 4 – Schematic view of the sampling design used for flight interception traps (WT) and branch eclectors (BE).

The window traps were fixed at two levels (26 m average [light crown] and 22 m average [shadow crown] respectively), and sampled at two weekly intervals from the beginning of May to the end of Oktober 2002 and from early April to late October 2003. The branch eclectors were sampled at four weekly intervals in the same periods. Fig. 5 shows the exact positions of the trees selected for installing the traps whereas Appendix Table 1 depicts the exact locations of every individual trap in metres above ground in the years 2002 and 2003. Six trees each of *Q. robur*, *T. cordata*, *F. excelsior*, four trees of *Acer pseudoplatanus*, two of *Q. rubra*, and one tree each of *F. pennsylvanica* and *Robinia pseudacacia* where prepared with window traps.

Twelve of these trees were also used for branch eclectors. In 2002: Four trees each of *Q. robur*, *T. cordata*, and *F. excelsior*, two per tree in the lower crown (ø 20 m in height) and two in the upper crown (ø 27 m). In 2003: Three trees each of *Q. robur*, *T. cordata*, and *F. excelsior*, two of *A. pseudoplatanus* and one *Q. rubra* tree (Appendix Table 1). This sample design made possible a statistical analysis of the main trees on side but also trends of species composition in neophytic trees on the other side.

Additionally, stem eclectors were installed on one tree individual of *Q. robur*, *T. cordata*, and *F. excelsior*, respectively, to get an impression of the activity of climbing invertebrates (compare Stenchly *et al.*, this volume).

This sample design made possible a statistical analysis of the main trees on side but also trends of species composition in neophytic trees on the other side. In contrast to most of the formerly used methods of studying temperate canopies (e.g. cutting of trees, cutting of branches, fogging with pyrethrum), the use of a crane and the mentioned trap types are little destructive and allowed continuous and comparable research of the tree crowns.

In contrast to most of the formerly used methods of studying temperate canopies (e.g. cutting of trees, cutting of branches, fogging with pyrethrum), the use of a crane and the mentioned trap types are little destructive and allowed continuous research of the tree crowns.

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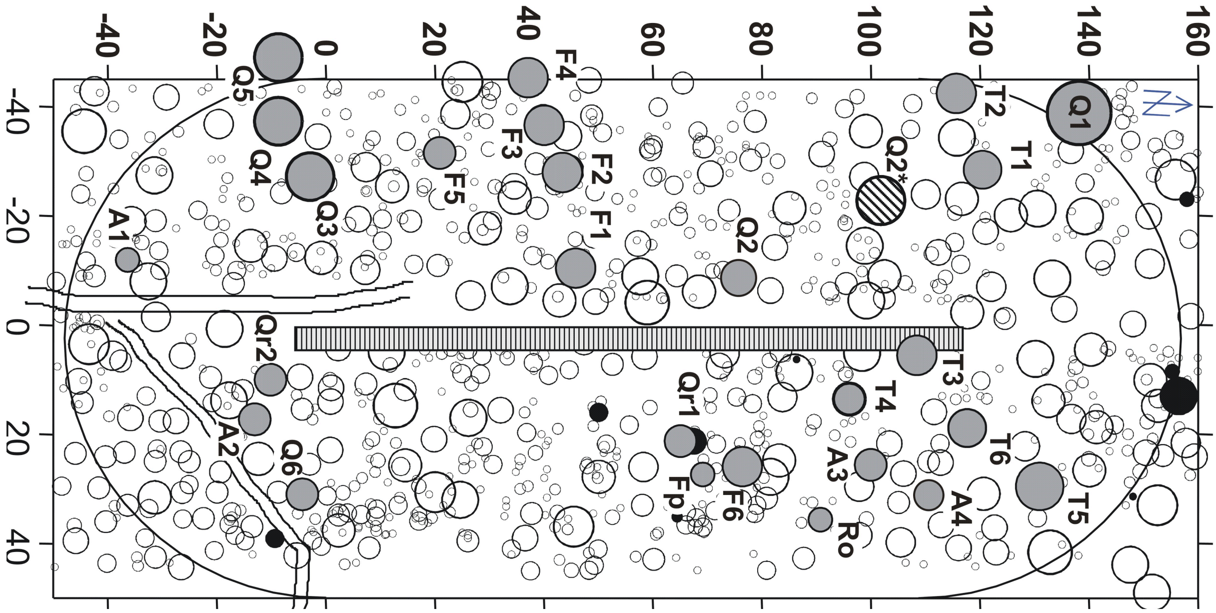

Figure 5 – Exact position of the trees selected for the different trap types in the investigation site (redrawn from ARNDT & HIELSCHER, 2006). A: Acer pseudoplatanus; F: Fraxinus excelsior; Fp: Fraxinus pennsylvanica; Q: Quercus robur; Qr: Quercus rubra; T: Tilia cordata.

Appendix Table 1 – Positions of window traps (WT) and branch eclectors (BE) in the tree crowns of the investigation site; N: northern part of the tree crown; W: western part; S: southern part; E: eastern part.

Tree	Trap	2002		2003	
		Height in m	Exposition	Height in m	Exposition
Quercus robur 1	WT 1	27.8	–	27.4	–
	WT 2	24.2	–	20.1	–
Quercus robur 2	WT 3	27.8	–	29	–
	WT 4	24	–	20.5	–
	BE 1	25.3	N	–	–
	BE 2	29.7	SW	–	–
	BE 3	20.3	N	–	–
	BE 4	24	NW	–	–
Quercus robur 3	WT 5	28.4	–	28.1	–
	WT 6	23	–	20	–
	BE 5	27.6	N	27.6	N
	BE 6	27.8	W	27.8	W
	BE 7	16.2	NE	16.2	NE
	BE 8	19	W	19	W
Quercus robur 4	WT 7	27.7	–	27.7	–
	WT 8	20.5	–	20.4	–
	BE 9	27.3	NW	27.3	NW
	BE 10	27.8	W	26.9	S
	BE 11	20	W	22.7	NW
	BE 12	21.5	S	21.5	S
Quercus robur 5	WT 9	25.4	–	26.5	–
	WT 10	18.1	–	20.1	–
Quercus robur 6	WT 11	23.7	–	27.1	–
	WT 12	19.3	–	18.4	–
	BE 13	22	E	22	E
	BE 14	15.6	E	15.6	E
	BE 15	22.5	S	15.6	E
	BE 16	13.7	E	18.6	N
Tilia cordata 1	WT 13	26.6	–	26.2	–
	WT 14	22.8	–	19.2	–
	BE 17	24.7	N	26	N
	BE 18	26.6	W	25.8	W
	BE 19	20	W	20	W
	BE 20	17.1	N	21.8	E
Tilia cordata 2	WT 15	26.3	–	25.8	–
	WT 16	22.5	–	19.3	–
Tilia cordata 3	WT 17	26.3	–	26.7	–
	WT 18	22	–	19.4	–
	BE 21	26.5	E	–	–
	BE 22	25.2	SE	–	–
	BE 23	18	NW	–	–
	BE 24	20.5	W	–	–

Appenidx Table 1 continued – Positions of window traps (WT) and branch eclectors (BE) in the tree crowns of the investigation site.

Tree	**Trap**	**2002**		**2003**	
		Height in m	**Exposition**	**Height in m**	**Exposition**
Tilia cordata 4	WT 19	28.2	–	27.4	–
	WT 20	24	–	19	–
	BE 25	26.3	N	27	NE
	BE 26	26.3	E	27.6	W
	BE 27	17.8	N	17.6	N
	BE 28	18.2	S	18.2	S
Tilia cordata 5	WT 21	28.5	–	27.8	–
	WT 22	24.3	–	21.1	–
	BE 29	27.5	E	26.7	N
	BE 30	27.2	S	25.9	W
	BE 31	20.9	E	19.4	E
	BE 32	20.9	S	19.5	W
Tilia cordata 6	WT 23	25	–	27.7	–
	WT 24	20.6	–	20.3	–
Fraxinus excelsior 1	WT 25	29.2	–	29	–
	WT 26	23.8	–	20.3	–
	BE 33	28.1	S	28.1	S
	BE 34	29.2	W	29.2	W
	BE 35	22.4	S	22.4	S
	BE 36	23.8	SW	22.5	W
Fraxinus excelsior 2	WT 27	26.7	–	26.8	–
	WT 28	21	–	19.8	–
	BE 37	27	N	27	E
	BE 38	27.5	N	27.5	N
	BE 39	22.4	NE	22.3	E
	BE 40	22.5	NE	22.5	NW
Fraxinus excelsior 3	WT 29	28.9	–	26.9	–
	WT 30	24.6	–	20.1	–
Fraxinus excelsior 4	WT 31	29.1	–	27.4	–
	WT 32	23.2	–	20.9	–
	BE 41	30.6	W	–	–
	BE 42	29.1	SE	–	–
	BE 43	24.7	N	–	–
	BE 44	21.4	S	–	–
Fraxinus excelsior 5	WT 33	26.6	–	26.5	–
	WT 34	23.8	–	20.8	–
Fraxinus excelsior 6	WT 35	28	–	27.1	–
	WT 36	24.9	–	20.1	–
	BE 45	28.6	SE	27	E
	BE 46	28	W	26.7	W
	BE 47	20.1	SE	19.3	E
	BE 48	18.1	SW	22.2	NW

Appenidx Table 1 continued – Positions of window traps (WT) and branch eclectors (BE) in the tree crowns of the investigation site.

Tree	**Trap**	**2002**		**2003**	
		Height in m	**Exposition**	**Height in m**	**Exposition**
Acer pseudoplatanus 1	WT 37	27.7	–	24.1	–
	WT 38	23.2	–	16.8	–
Acer pseudoplatanus 2	WT 39	24.2	–	25.1	–
	WT 40	21.1	–	17.8	–
	BE 49	–	–	21.4	SW
	BE 50	–	–	25.3	NW
	BE 51	–	–	17	SW
	BE 52	–	–	16.8	NW
Acer pseudoplatanus 3	WT 41	22.8	–	27.3	–
	WT 42	18.1	–	20.2	–
Acer pseudoplatanus 4	BE 53	–		27.7	NW
	BE 54	–	–	27	W
	BE 55	–	–	20.1	NE
	BE 56	–	–	22.5	N
Robinia pseudacacia	WT 43	24.8	–	27	–
	WT 44	20.4	–	19.9	–
Fraxinus pennsylvanica	WT 45	25.2	–	25.4	–
	WT 46	20.1	–	19.3	–
Quercus rubra 1	WT 47	24.4	–	25	–
	WT 48	18.7	–	17.9	–
Quercus rubra 2	WT 49	26.8	–	27.1	–
	WT 50	19.5	–	20.3	–
	BE 57	–	–	26	S
	BE 58	–	–	26.2	N
	BE 59	–	–	18.4	SW
	BE 60	–	–	19.1	NW

3.2 Arboricolous spiders (Arachnida, Araneae) of the Leipzig floodplain forest – first results

KATHRIN STENCHLY[1], DETLEF BERNHARD & OLIVER-D. FINCH

During 2002 and 2003 an extensive study of the arthropod fauna, including the spider fauna, was carried out within the research plot of the Leipzig Canopy Crane Project. Bark-inhabiting spiders were collected using five upwards-directed stem eclectors installed at three autochthonous and abundant tree species: *Fraxinus excelsior*, *Quercus robur*, and *Tilia cordata*. Branch traps were used to sample arboricolous spiders that dwell in the canopy. For each investigated tree, two branch traps were arranged at the lower and at the upper canopy areas, resulting in a total of 48 traps. Additionally, 50 flight-interception traps at two different heights were used to investigate the ballooning activity of spiders in the canopy. Using the combination of different trap types a comprehensive analysis of the diversity of spiders was realised. Thus, on the one hand, comparisons of the spider fauna between different tree species were possible. On the other hand, investigations of different elevations enabled us to compare two strata of the canopy. The presented results refer to samples of the year 2002. A total of 4 289 spiders belonging to 71 species (15 families) were recorded. Clubionidae were dominant in both strata (trunk zone and canopy). Amaurobiidae, Linyphiidae, and Theridiidae were abundant on the trunks, whereas Anyphaenidae, Philodromidae, and also Theridiidae were common groups in the canopy. The most active species were *Coelotes terrestris* (trunks) and *Anyphaena accentuata* (canopy). The spider fauna of the stems comprised 52% web-builders and 48% free living hunters, however, more hunters than web-builders occurred in the canopy. Trunks of *Quercus robur* showed the most abundant spider fauna with highest species richness compared to both other tree species. In the *Quercus* canopies spider species richness was also high, but activity was low. Preferences of certain spider species for single tree species were not detected. Further data from 2003 will strengthen these preliminary results.

INTRODUCTION

Concerning the tree canopies of tropical forests, it is known that they hold an extremely high animal diversity (e.g. ERWIN 1988; LOWMAN & NADKARNI 1995; STORK, ADIS & DIDHAM 1997; ADIS 2001; FLOREN & LINSENMAIR 2001; BASSET 2001; ADIS & JUNK 2002). It has not yet been clarified whether a comparably high biodiversity can be found in the canopy of temperate forests, since only a small number of investigations exist so far (e.g. BARNARD, BROOKS & STORK 1986; BARBOSA & WAGNER 1989; REYNOLDS & CROSSLEY 1997; STORK & HAMMOND 1997; STORK *et al.* 2001; THUNES, SKARVEIT & GJERDE 2003). Due to the small number of projects, which mostly have been started recently, knowledge about the canopy-specific fauna, including that of central Europe, is still limited (e.g. KLOMP & TEERINK 1973; AMMER & SCHUBERT 1999; FLOREN & SCHMIDL 1999). Species adaptations, e.g. to certain heights within the canopies or to different tree species, have been the subject of little research so far.

Spiders from the canopy region of central European tree species have been studied to varying degrees (e.g. HESSE 1939; ENGELHARDT 1958; SIMON 1995; GUTBERLET 1997; SCHUBERT 1998), yet overall the canopy stratum is among the least commonly investigated habitats of forests for this animal group. Detailed knowledge concerning the requirements of the species, together with for example the abundance and ecological function of spiders in tree canopies, is almost completely lacking.

So far, investigations of the fauna of central European tree canopies have mostly been carried out using highly destructive methods that make a continuous investigation impossible (including tree felling, e.g. ENGELHARDT 1958; HESSE 1939; sawing off branches, e.g. KLOMP & TEERINK 1973), or the entire fauna was removed at a time by fogging (e.g. FLOREN & SCHMIDL 1999; FLOREN & OTTO 2002). As part of the Leipzig Canopy Crane Project in the

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[1] corresponding author

Burgaue nature reserve a non-destructive trap system was set up in the tree canopies with the aid of a crane, enabling almost unlimited access to all tree regions. It was therefore possible to provide continuous analysis throughout the vegetation period. Analyses of bark-inhabiting and canopy-active arthropod fauna, in which spiders were also condsidered, took place in 2002 and 2003. In the present article, results concerning spiders caught during the year 2002 are presented, while an evaluation of the results from 2003 remains to be done. The following questions are in focus: **(1)** What is the community structure of spiders in the canopies or, respectively, on trunks and how large is their species richness? **(2)** Do spiders living on trunks or in the canopies show a preference for certain tree species and are there differences between different tree species? **(3)** Are certain canopy regions preferred by spiders? **(4)** What is the phenology of spiders in the canopy area?

MATERIALS AND METHODS

Open, upwards-directed stem-eclectors (tree photoeclectors; e.g. Funke & Sammer 1980; Simon 1995), branch traps and flight-interception traps (e.g. Winter *et al.* 1999) were used to analyse the spider fauna. (Arndt & Unterseher, this volume). In total, stem-eclectors were installed at five living trees, of which two stood at respectively in a gap. Thus the intention was to search for potential differences in the range of species as a result of altered parameters such as light intensity and temperature in the trunk region. In the closed forest stand, an oak (*Quercus robur*), ash (*Fraxinus excelsior*), and lime (*Tilia cordata*) were each equipped with a stem-eclector, in the vicinity of the gap, one ash and one lime tree.

Of the branch traps, two in each case were installed in the upper canopy regions (27.0 m ± 2.0 m) and in the lower canopy regions (20.0 m ± 2.8 m). In total, 12 trees were equipped with branch traps ($\sum = 48$). The three tree species *Q. robur*, *F. excelsior* and *T. cordata* were likewise taken into account and four trees in each case equipped with four branch traps.

The free-hanging flight-interception traps were attached at an average height of 27.0 m (± 1.8 m) and 22.0 m (± 2.2 m). Of the three main tree species mentioned above, six trees in each case were fitted with one trap in the upper, and one trap in the lower canopy region ($\sum = 36$). The tree species *Acer pseudoplatanus* (6 traps), *Robina pseudoacacia* (2 traps), *Fraxinus pennsylvanica* (2 traps) and *Quercus rubra* (4 traps), also equipped with fligth-interception traps, had a lower number of traps. The killing-preserving agent was H_2O dest. diluted diethylenglycol (ratio 1 : 1). After emptying, the animals were transferred to 70% ethanol. The investigation period under consideration in this article was 22/4/-21/10/2002 for both eclector types and for the flight-interception traps 9/5/-21/10/2002.

RESULTS

Species numbers and numbers of individuals

During the first year of the investigation, 2002, a total of 4 289 spider individuals were caught with all the traps used. So far 71 species belonging to 15 families were recorded (Table 1). *Pachygnatha*-, *Pholcus*-, *Scotophaeus*- and *Zelotes*-species were caught only as juveniles. More than 80% of the species were characteristic for dry or humid mixed deciduous forests. 40 species were classified as arboricolous spiders, of which 11 were stenotopic bark-inhabiting spiders.

Diaea livens (on *Q. robur* and *T. cordata*), *Philodromus albidus* (on *F. excelsior*, *Q. robur*, and *T. cordata* as well as in flight-interception traps) and *P. praedatus* (on *F. excelsior* and *Q. robur* as well as in flight-interception traps) were recorded for the first time in Saxony (Tolke & Hiebsch 1995). *P. buxi* (on *T. cordata* and in flight-interception traps) has only rarely been found in Germany so far. There is only one record of this species for the federal state of Saxony (Martin 1973 in Tolke & Hiebsch 1995). The rare Theridiidae *Theridion blackwalli* (in flight-interception traps) was likewise only recorded once in Saxony (Heimer 1982). *Entelecara congenera* is classified in Saxony's Red List in the "highly endangered" risk category; *Gibbaranea gibbosa*, *Lathys humilis* and *Micaria subopaca* are deemed "at risk" (Hiebsch & Tolke 1996).

Stem-eclectors

In total, only 234 individuals were recorded in the stem region using the five trunk eclectors. 200 of them were identified down to the species, genus or family level, respectively. The 111 adult spiders belonged to 23 species (Table 2).

With a total of 62 individuals (31%, Fig. 1) the Clubionidae were the dominant family. Further abundant families were the Amaurobiidae (16%) together with the Theridiidae and the Linyphiidae, each with a proportion of around 15% of the total catch. The Salticidae represented 11% of the bark-inhabiting spiders. Both the Agelenidae and Gnaphosidae appeared subdominantly, each at 5%. The families Anyphaenidae, Dictynidae, Philodromidae and Thomisidae were present with less than four individuals. Web-builders represented 52% of the total catch, of which 18% were funnel-web-builders. The remaining 48% were free living hunters. Of these 37% were nocturnal hunters (e.g. Clubionidae), the remaining 11% were day-active (e.g. Salticidae).

Table 1 – List of spider species that were recorded with different trap types during 2002 (*: new to Saxony, trap types: A: branch trap, F: flight-interception trap, S: stem-eclector).

	A	**F**	**S**
Agelenidae			
Tegenaria ferruginea			S
Tegenaria silvestris	A		
Amaurobiidae			
Coelotes terrestris	A		S
Anyphaenidae			
Anyphaena accentuata	A	F	S
Araneidae			
Araneus diadematus	A		
Araneus sturmi		F	
Araneus triguttatus		F	
Araniella cucurbitina		F	
Cyclosa conica		F	
Gibbaranea gibbosa	A		
Larinioides patagiatus	A	F	
Nuctenea umbratica	A	F	
Clubionidae			
Clubiona brevipes	A	F	S
Clubiona corticalis	A	F	S
Clubiona pallidula	A	F	
Clubiona reclusa	A		
Dictynidae			
Dictyna pusilla	A	F	
Lathys humilis	A	F	
Nigma flavescens		F	
Gnaphosidae			
Scotophaeus spec. juv.	A		
Micaria subopaca	A	F	S
Zelotes spec. juv.			S
Linyphiidae			
Araeoncus humilis		F	
Bathyphantes nigrinus		F	
Ceratinella brevis		F	
Diplocephalus latifrons		F	
Diplocephalus picinus		F	
Drapetisca socialis			S
Entelecara acuminata	A	F	
Entelecara congenera			S
Entelecara erythropus			S
Entelecara flavipes		F	
Erigone atra		F	
Erigone dentipalpis		F	
Lepthyphantes minutus	A		S
Lepthyphantes tenuis		F	S
Linyphia triangularis	A		S
Maso sundevalli			S
Meioneta rurestris		F	S
Moebelia penicilata	A		S
Neriene montana	A		S
Oedothorax apicatus		F	S
Trematocephalus cristatus		F	
Metidae			
Metellina segmentata	A	F	
Philodromidae			
*Philodromus albidus**	A	F	
Philodromus aureolus	A		
Philodromus buxi	A	F	
*Philodromus praedatus**	A	F	
Philodromus rufus	A	F	
Pholcidae			
Pholcus spec. juv.	A		
Salticidae			
Ballus chalybeius	A	F	
Salticus zebraneus	A	F	S
Tetragnathidae			
Pachygnatha spec. juv.		F	
Tetragnatha montana	A		
Tetragnatha obtusa	A	F	
Theridiidae			
Achaearanea lunata	A	F	
Achaearanea simulans		F	
Anelosimus vittatus	A	F	
Dipoena melanogaster	A		
Enoplognatha ovata	A	F	S
Paidiscura pallens		F	
Theridion blackwalli		F	
Theridion melanurum	A	F	
Theridion mystaceum	A	F	S
Theridion pictum	A		
Theridion pinastri	A	F	
Theridion tinctum	A	F	S
Theridion varians		F	
Thomisidae			
Diaea dorsata	A		S
*Diaea livens**	A		
Xysticus lanio	A	F	S

Table 2 – Abundance of spiders at tree trunks (only adult specimen).

Species	Family	Individuals
Coelotes terrestris	Amaurobiidae	21
Salticus zebraneus	Salticidae	16
Enoplognatha ovata	Theridiidae	16
Drapetisca socialis	Linyphiidae	8
Clubiona corticalis	Clubionidae	8
Tegenaria ferruginea	Agelenidae	7
Theridion mystaceum	Theridiidae	7
Leptyphantes minutus	Linyphiidae	5
Entelecara congenera	Linyphiidae	3
Theridion tinctum	Theridiidae	3
Anyphaena accentuata	Anyphaenidae	2
Clubiona brevipes	Clubionidae	2
Entelcara erythropus	Linyphiidae	2
Moebelia penicillata	Linyphiidae	2
Micaria subopaca	Gnaphosidae	1
Leptyphantes tenuis	Linyphiidae	1
Linyphia triangularis	Linyphiidae	1
Maso sundevalli	Linyphiidae	1
Meioneta rurestris	Linyphiidae	1
Neriene montana	Linyphiidae	1
Oedothorax apicatus	Linyphiidae	1
Diaea dorsata	Thomisidae	1
Xysticus lanio	Thomisidae	1
total		111

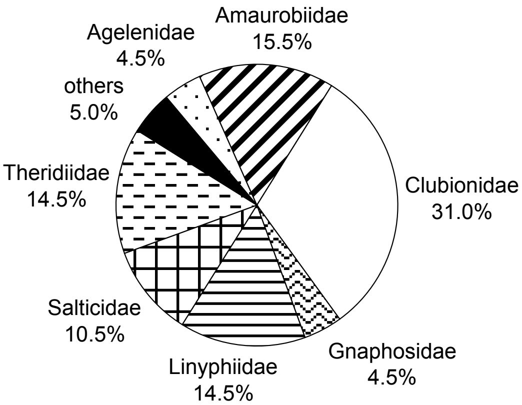

Figure 1 – Proportion of single spider families in the total catch of the stem-eclectors (n = 200 ind.; without unidentified immature spiders).

The Linyphiidae (11 species) were the most species-rich family. The Theridiidae were represented with three species characteristic for the lower trunk zone. Among the trunk inhabiting Clubionidae were the typical bark spiders *Clubiona corticalis* and *C. brevipes*. *Coelotes terrestris* (Amaurobiidae) was predominantly recorded on trunks of *Q. robur*. *Tegenaria ferruginea* (Agelenidae) was identified as a further common species in the trunk area, likewise preferring stems of *Q. robur*. From the Salticidae only *Salticus zebraneus* was recorded. It was present with a higher number of individuals (n = 15) on the free-standing stem of *F. excelsior*. Of the Gnaphosidae and Dictynidae predominantly juvenile and sub-adult individuals were caught.

Taking into account the overall small total catch in the stem eclectors, the trunk area of *Q. robur* produced the highest diversity of species and families (Table 3). The highest numbers of individuals were also recorded on this tree species. The high proportion of epigeic spiders (mainly Agelenidae and Amaurobiidae) was striking. Theridiidae, Linyphiidae and Clubionidae were also common. The catches on *T. cordata* and *F. excelsior* in the closed forest stand produced similar results to those on *Q. robur*. *F. excelsior* in the forest gap, by contrast, showed a different family range due to the appearance of Salticidae and Gnaphosidae. The trunk of the free-standing lime tree showed the lowest diversity. Only three species of three families were recorded. Here, too, the Clubionidae dominated.

Table 3 – Number of spider families, species and individuals collected with stem-eclectors at the five tree trunks.

Tree	Families	Species	Individuals
Fraxinus excelsior (forest stand)	5	12	24
Fraxinus excelsior (gap)	7	15	44
Quercus robur (forest stand)	9	22	67
Tilia cordata (forest stand)	8	17	57
Tilia cordata (gap)	3	3	8

Branch traps

In 2002 a total of 2 436 individuals were recorded in the branch traps. 977 juveniles were determined only to a higher taxonomic level; the 1 316 adults belonged to 42 species.

As in the trunk area, the Clubionidae family was also dominant in the tree canopies (33%, Fig. 2). The Theridiidae too, with approx. 16%, showed similarly high proportions in the total catch as in the trunk region. The Anyphaenidae were encountered considerably more often in the canopies (21%). Further, considerably higher catch numbers of the Philodromidae (13%) were registered in the canopy area. The most abundant guild within the canopy-active spider community recorded with branch traps were the hunters (76%). Spaceweaving species made up to 17% and orbweavers 5%.

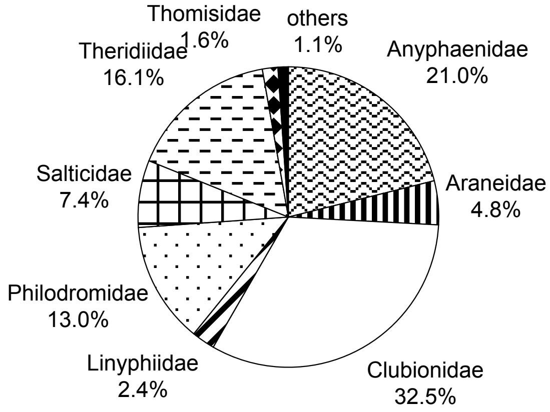

Figure 2 – Proportion of single spider families in the total catch of the branch traps (n = 2 436 ind.).

Among the 1 316 adult spiders, *Anyphaena accentuata* (Anyphaenidae) was eudominant at 34%. *Clubionia brevipes* (19%) and *Theridion tinctum* (11%) were dominant, *Salticus zebraneus* (8%), *Clubiona pallens* (6%), *Clubiona corticalis* (5%), and *Nuctenea umbratica* (3%) subdominant species. Thus the proportion of main species in the total catch was 86%.

An analysis of the preference behaviour of the individual families with respect to height revealed that the Salticidae and Clubionidae were concentrated in the upper canopy region (27.0 m±2.0 m) (Table 4); by contrast, Linyphiids were recorded in the lower canopy region (20.0 m±2.8 m).

Table 4 – Most dominant spider families in the lower and the upper canopy.

Family	Lower canopy	Upper canopy
Anyphaenidae	53%	47%
Philodromidae	49%	51%
Theridiidae	54%	46%
Clubionidae	39%	61%
Salticidae	20%	80%
Linyphiidae	75%	25%

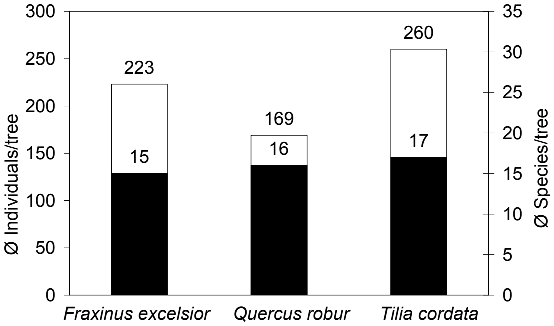

Figure 3 – Mean total catch of individuals and species per investigated tree species.

Table 5 – Mean number of individuals (SD: standard deviation) of dominant spider families in the canopies of the investigated tree species.

Family	*Fraxinus excelsior*		*Quercus robur*		*Tilia cordata*	
	Ø ind./tree	SD	Ø ind./tree	SD	Ø ind./tree	SD
Anyphaenidae	41	±10	36	±15	52	±5
Clubionidae	81	±17	49	±11	69	±24
Philodromidae	20	±2	24	±17	37	±31
Salticidae	14	±3	14	±9	18	±18
Araneidae	9	±4	9	±5	12	±6
Theridiidae	33	±6	25	±12	42	± 20

Table 6 – Most dominant spider species in the lower and the upper canopy.

Species	Lower canopy	Species	Upper canopy
Anypaena accentuata	45.8%	*A. accentuata*	25.6%
Clubiona brevipes	11.3%	*C. brevipes*	23.2%
Theridion tinctum	10.0%	*T. tinctum*	10.9%
Clubiona corticals	6.5%	*S. zebraneus*	9.7%
Clubiona pallidula	4.9%	*C. pallidula*	7.4%
Salticus zebraneus	4.9%	*Gibbaranea gibbosa*	4.5%
Nuctenea umbratica	3.8%	*Theridion pinastri*	4.1%
Moebelia penicillata	3.3%	*Clubiona corticals*	3.4%

No clear pattern for either of the two canopy regions could be observed for any of the remaining families.

Comparisons of the three tree species investigated using the results from the branch traps in respect of their inventory of individuals or species showed that the highest numbers of individuals and species appeared on *T. cordata* (Fig. 3). 16 spider species on average were recorded on *Q. robur*, even though the fewest individuals were caught on this tree species. On average, the second-highest number of individuals per tree was recorded on *F. excelsior* (15 species). There was no recognisable preference for any of the three investigated tree species (*F. excelsior*, *Q. robur* and *T. cordata*) for any spider family so far. A consideration of individual species so far has also not revealed any clear preference for a particular tree species (Table 5). Slight differences became evident between the upper and lower canopy area (Table 6). For example, *Anyphaena accentuata* was eudominant in the lower canopy area, while the proportion of this species was smaller in the spider community in the upper canopy area. There, proportions of *Clubiona brevipes* increased.

The highest activity of adult spiders appeared during the early summer (Fig. 4), the activity phenology of sexually mature spiders differing considerably from that of the juvenile animals. Thus, the adult spiders were most active at the beginning of June. At this time, the recorded number of males was more than double that of females. During the vegetation period the number of recorded adults declined continuously, while the number of juveniles increased steadily until the end of October.

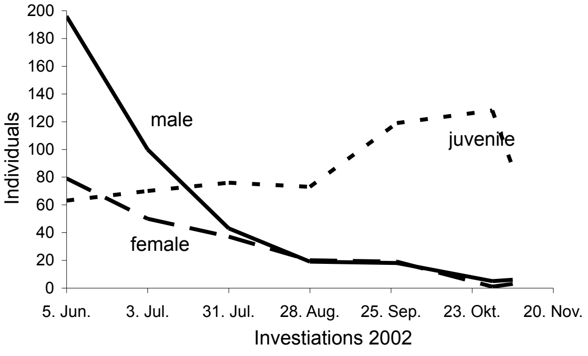

Figure 4 – Activity phenology of adult and immature spiders during 2002.

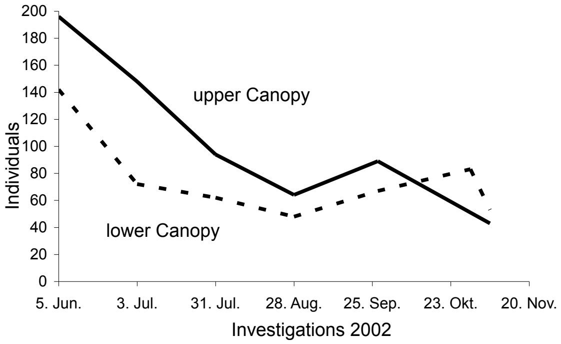

Figure 5 – Activity phenology of spiders in branch traps of the lower and the upper canopy during the year 2002.

The peak of the juveniles' activity came at the end of October, at the close of the investigations. While upper and lower canopy area differed in respect of their spider communities (see above), only slight differences could be seen in the spiders' activity phenology (Fig. 5). Of the two activity peaks observed, the second peak was only achieved in the lower canopy region about one month later than in the upper.

Flight-interception traps

A total of 1 618 individual spiders were recorded in the flight-interception traps. These were predominantly juvenile. The proportion of adult animals was only 27% (n = 434 ind.), and they belonged to 47 species and 12 families. Theridiidae, Clubionidae, Philodromidae and Anyphaenidae were predominantly recorded (Fig. 6).

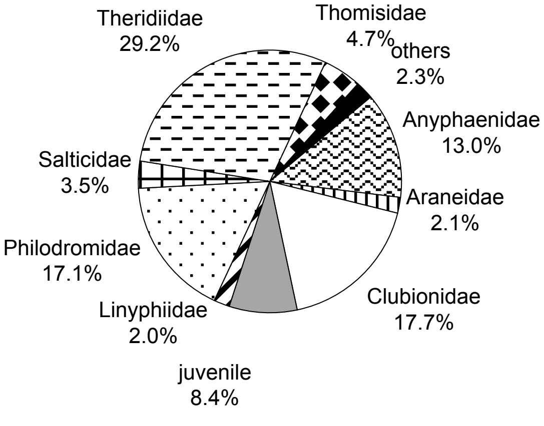

Figure 6 – Proportion of single spider families in the total catch of the flight-interception traps (n = 1 618 ind.).

The Theridiidae were the most abundant family (29%). The Clubionidae and Philodromidae were similarly abundant (18% resp. 17%), followed by the Anyphaenidae, which achieved a proportion of 13%.

Clubionia brevipes (18%), *Anyphaena accentuata* (14%) and *Theridion tinctum* (14%) were common. *Salticus zebraneus* (9%), *Philodromus albidus* 6%, *Theridion blackwalli* 4% and *T. pinastri* 4% were subdominant. The proportion of main species was 70%. With reference to their hunting behaviour, 61% of the individuals were hunters, and 36% were web-building spiders.

The highest numbers of adults appeared from mid-May to mid-June (Fig. 7); thereafter their number declined considerably, while the number of juveniles increased sharply and reached its maximum at the end of September.

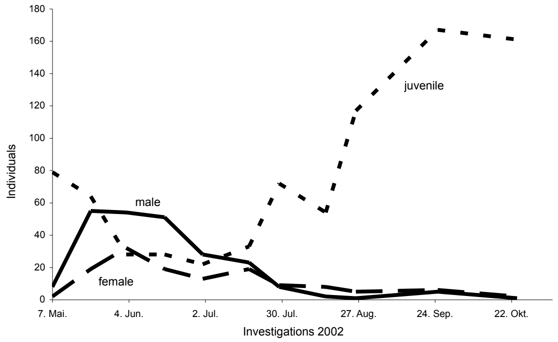

Figure 7 – Activity phenology of adult and immature spiders in flight-interception traps during 2002.

So far, a number of species have been recorded exclusively in flight-interception traps. Among these many Linyphiids, such as *Diplocephalus picinus*, *D. latifrons*, *Ceratinella brevis* and *Trematocephalus cristatus*. A number of other species, such as *Theridion blackwalli* (Theridiidae) and *Cyclosa conica*, *Araneus sturmi* and *A. triguttatus* (Araneidae), so far have likewise only been recorded using this method.

DISCUSSION

Bark and canopy spiders

Although several central-European spider species were described as stenotopic bark-inhabiting spiders (e.g. Wunderlich 1982), they are mostly only present in the trunk area during certain phases of their life cycle. Many spiders hibernate, for example, in the litter layer of the forest floor and then dwell to higher strata during the vegetation period. They may remain in the trunk area or simply migrate through it in order to reach the canopy (e.g. Funke & Sammer 1980, Simon 2002). Therefore, on trees, two groups of spiders can be distinguished with reference to their preferred habitat: on the one hand, species which reproduce in the canopy and on the other, species which are associated with tree trunks and in particular with bark (Kubcová & Schlaghamersky 2002). So, although *Anyphaena accentuata* (Anyphaenidae), belongs to the first group, it appeared occasionally on the trunks particularly at the start of our investigations. This species was principally recorded in the tree canopies and counts among the dominant spiders there. The trunk is used by this species predominantly as a transitional area, since according to our data mainly juveniles migrate to the canopy. Furthermore, *Clubionia brevipes*, *Theridion tinctum* and *Salticus zebraneus* count among the characteristic elements of the spider fauna active in the canopy of the Leipzig floodplain forest. *Drapetisca socialis*, by contrast, was in our investigations only recorded in the trunk area, but not in the canopy. This is confirmed by the results of Simon (2002), who, in contrast to Ellenberg *et al.* (1986), classifies this species as being stenotopic on trunks, but not as an inhabitant of high tree canopies.

In the Leipzig floodplain forest, among the spiders defined as characteristic for tree barks according to Wunderlich (1982) are *Clubiona corticalis*, *Drapetisca socialis*, *Micaria subopaca*, *Moebelia penicillata* and *Theridion mystaceum.* However, species of the field layer (e.g. *Enoplognatha ovata*), as well as epigeic species, were also recorded (see also Braun 1992). The former include for example *Coelotes terrestris*, which occurred during other investigations also with a high abundance in stem eclectors (e.g. Finch 2001). This species evidently leaves the forest floor from time to time, for example on its search for a mate.

The influence of various parameters on the spider cenosis

Evidence as to the influence of bark structure arise from the comparative investigations of the three tree species with varying bark structures using stem eclectors. According to this, the bark of *Q. robur* represents a particularly suitable habitat for spiders. Its deep and wide bark furrowing appears to provide a well structured habitat for web-building as well as good opportunities for hiding. Web-building spider families (Linyphiidae, Theridiidae) therefore were well established at the oak stem. For the Theridiidae in particular, bark structure may be the limiting factor for web-building, since they were recorded on *Q. robur* with a high abundance in comparison with the catches on *F. excelsior* and *T. cordata.* In general, highest numbers of spider species can be found on trunk areas of tree species with a particularly richly-structured bark (e.g. Nicolai 1994). Overall, it can be assumed that tree species with a similar bark texture are also inhabited by similar spider coenoses and that there are no tree species-specific communities (cf. Curtis & Morton 1973, Wunderlich 1982). In addition to bark texture, microclimatic conditions may also considerably influence the qualitative and quantitative composition of spider communities. If the dominance structure of the spider community of *F. excelsior*, situated in the gap, is considered in comparison with the trunks of this tree species situated in the forest stand, it becomes evident that *Salticus zebraneus* preferred the trunk area which received plenty of sun light. Representatives of the Gnaphosidae, too, appeared exclusively on this free-standing trunk.

While there seems to be a preference for particular bark structures by some species, the data assessed so far delivers no clues as to a preference of spiders for the canopy area of certain tree species. It is possible that the spider communities in the canopy area are predominantly determined by microclimatic conditions. Thus, a preference for the upper canopy strata by Salticidae and Clubionidae would be explainable by the exposure to sun light and the associated increased temperatures. Work on the material from 2003, which remains to be done, will provide the results obtained so far with a broader database.

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3.3 Species diversity and tree association of Heteroptera (Insecta) in the canopy of a Quercus-Fraxinus-Tilia floodplain forest

Erik Arndt[1], Detlef Bernhard, Claudia Jesche, Sven Kupillas & Winfried Voigt

The canopy bug fauna (Heteroptera) was examined in the mesophilic floodplain forest area "Burgaue" north of Leipzig in the scope of the LAK project. All arthropods were collected by window traps and branch eclectors in the canopy of 25 trees (*Quercus robur, Tilia cordata, Fraxinus excelsior*, and some neophytic trees) using a mobile tower crane during two seasons. A total of 67 species with 7 315 adult bugs (7 065 in window traps, 250 in branch eclectors) was collected. *Deraeocoris lutescens* was the most common species representing 30.5% of the entire sample. Further dominant species were *Rhabdomiris striatellus, Campyloneura virgula, Dryophilocoris flavoquadrimaculatus, Harpocera thoracica, Orius* cf. *minutes*, and *Pentatoma rufipes*, therefore only one phytophagous bug (*H. thoracica*) reached high abundances. We could not detect differences in the species numbers on different trees. However, significant differences between different trees appeared with regard to the individual numbers of phytophagous and omnivorous Heteroptera, while the species richness of carnivorous bugs did not show significant differences on various tree species. Most of the phytophagous bugs live on *Quercus* (*Q. robur* as well as the neophytic *Q. rubra*). The lowest species numbers appear on *Tilia cordata.* Similar results were found for omnivorous species . A total of 14 bug species show a preference for a certain tree species or *Quercus* as genus (including *Q. rubra*). Only two phytophagous Heteroptera occur among these specialists. These results indicate a stronger preference for specific tree species by carnivorous than by phytophagous Heteroptera.

INTRODUCTION

Considering species diversity, habitat requirements and feeding type bugs (Heteroptera) are quite an ecologically heterogeneous group. Members of terrestrial families, however, are predominantly associated with vegetation structures, to a considerable extent living on bushes or trees. So far in middle Europe, only a small number of examinations concerning the ecology of woodland-dwelling Heteroptera have been carried out, and refer predominantly to forest edges or comparisons of natural with cultivated forests (Achtziger 1991; 1995; Schubert 1998; Gossner 2002). One focus of these studies is the distribution of bug species on individual tree species or in various strata.

Our project contributes to and proceeds with the objectives and results of the studies mentioned above. We analysed the vertical and horizontal distribution of Heteroptera in the canopy stratum of a dried-out oak-ash-winter lime tree floodplain forest. The aim of the project was to (a) check whether there are differences between individual tree species with respect to bug fauna and to (b) detect if there are bug species associated with certain tree species. To this end the Heteroptera were recorded during two vegetation periods in a sample of all major tree species of the floodplain forest and then assessed both specifically and grouped according to several"feeding types". In particular by analysing ecological types we expected new insights into species composition of the community as well as into structural aspects of the canopy-dwelling fauna. We used this approach to test the two following hypotheses: (a) species diversity between individual types of woodland varies significantly, (i.e. oak as an autochthonous species has the highest, neophytic woodland introduced by forestry, in contrast, the lowest species diversity); (b) there is a close association of phytophagous species with certain types of woodland but no association of zoophagous species generally to a particular tree species.

MATERIALS AND METHODS

Data were gathered during a two-year examination of the canopy area of the Burgaue nature reserve in the Leipzig floodplain forest (vegetation periods 2002 and 2003) by using a 40 m high mobile tower crane in

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[1] corresponding author

conjunction with window traps and branch eclectors. Details of sampling design are described earlier in this volume.

The sampling design we used enables us **(1)** to test our hypotheses for the principal tree species and **(2)** it also reveals trends in species composition on the neophytes introduced by forestry (*Quercus rubra, Fraxinus pennsylvanica*). Multivariate analyses (PCA; calculated using CANOCO, Ter Braak & Šmilauer 2002, Lepš & Šmilauer 2003), together with the Species Indicator Analysis according to Dufrêne & Legendre (1997) by means of PC-Ord 4 (McCune & Mefford 1999) were used for the statistical evaluation. The Species Indicator Analysis was originally developed by Dufrene and Legendre in order to ascertain the indicator value of certain animal species for a habitat type or (in the case of nature conservation purposes) a certain usage or preservation status. This method is therefore suitable for testing the preference of species in relation to a certain locality (here: tree species).

Differences in species and individual numbers in the colonisation of individual trees or tree species, respectively, were tested using ANOVA.

Identification of species

All bugs recorded during the examination were identified to species level. Some species (e.g. among Anthocoridae) were unable to be identified beyond doubt; their names are therefore prefixed with 'cf.'. Voucher specimens of all species are available for inspection in the institutional collections of the Anhalt University (Bernburg) and the Friedrich Schiller University (Jena), Institute of Ecology. The nomenclature follows Hoffmann & Melber (2003).

In the genera *Orthotylus* Fieber and *Psallus* Fieber (Miridae) only males can be identified absolutely certainly with the aid of their genital appendage. However, since the majority of specimens collected in both genera were females, these genera can only be included into the analysis summarily as *Orthotylus* sp, respectively, *Psallus* sp. In the genus *Orthotylus* males of the following species were detected: *O. nassatus* (Fabricius), *O. tenellus* (Fallén), *O. viridinervis* (Kirschbaum) (in the ratio 7 : 4 : 1).

In the genus *Psallus*, seven species were identified based on their male genitals: *P. variabilis* (Fallén), *P. lepidus* Fieber, *P. perrisi* (Mulsant & Rey), *P. albicinctus* (Kirschbaum), *P. mollis* (Mulsant) *P.* cf. *assimilis* Stichel, *P. varians* (Herrich-Schaeffer) (in the ratio 9 : 9 : 6 : 3 : 2 : 2 : 1). A problem in the allocation of feeding types results from the grouping of *Psallus* species into one complex: *P. perrisi* is classified as zoophagous (Wagner 1955), while all other species are regarded as polyphagous (= omnivorous). We therefore listed this genus in both feeding groups while doing numerical analyses.

Abbreviations used: (Ac) - Sycamore, *Acer pseudoplatanus*; (ET) - Feeding type; (F) - Common ash, *Fraxinus excelsior*; (Fp) - Red ash, *Fraxinus pennsylvanica*; (OV) - omnivorous, polyphagous; (PCA) - Principal Component Analysis (see Lepš & Šmilauer 2003); (PP) - phytophagous; (Q) - Common oak, *Quercus robur*; (Qr) - Red oak, *Quercus rubra*; (T) - Winter lime tree, *Tilia cordata*; (ZP) - zoophagous.

RESULTS

With the aid of the crane, a total of 7 315 adult individuals of Heteroptera in 67 species were recorded in the canopy area of the Leipzig floodplain forest. The majority of individuals (7 065) were caught in the window traps (WT; Appendix Table 1) but only 250 specimens in the branch eclectors (BE; Appendix Table 2). The results of both examination years differ considerably, 4 458 bugs were collected in 2002, only 2 857 in 2003. These differences are probably due to weather differences (temperature progression, precipitation totals) between the two years.

Of the total of 67 species, at least 30 species (excluding *Psallus* sp. and *Orthotylus* sp.) were only detected in the window traps (while flying through the canopy area) and not by branch eclectors (while crawling on branches). At least 18 species were caught in 2002 alone, 12 species only in 2003. The dominant species in the canopy area (abundances > 3.2% of the total collection) were, in decreasing frequency, *Deraeocoris lutescens* (Schilling) (ZP), *Harpocera thoracica* (Fallén) (PP), *Pentatoma rufipes* (Linné) (OV), *Orius* cf. *minutus* (Linné) (ZP), *Campyloneura virgula* (Herrich-Schaeffer) (ZP), *Rhabdomiris striatellus* (Fabricius) (OV), and *Dryophilocoris flavoquadrimaculatus* DeGeer (OV). 30.5% of the entire catch fell to *Deraeocoris lutescens* alone.

Differences between the tree species with regard to the structure of their bug fauna

In order to analyse differences between the tree species, the recorded bugs were allocated to three ecological groups (Fig. 1): phytophagous, polyphagous (= omnivorous) or zoophagous feeding type (see Appendix Table 1 for classification). Species distribution across the three groups is in the same order of magnitude. In 2002 the PP : OV : ZP ratio was 14 : 14 : 19, in the following year 16 : 11 : 14, while both *Psallus* sp. and *Orthotylus* sp. are included as a summary species. Ratios of individuals from the three feeding types also level out in the window trap catches of examination year 2003. By contrast, the zoophagous bugs, with 2 736 specimens (incl. *Psallus* sp.), exceed the total of the other two gropus in 2002 (OV 1 040 and PP 774 individuals). All three groups and both years were analysed separately using, however, only data obtained from window trap catches for statistical reasons. There were no detectable differences between feeding types or years regarding the species numbers in relation to individual trees.

The analysis of individuals (not differentiated according to species, but lumped across feeding types, see Table 1) delivered more differentiated results (Fig. 2). The distribution of individuals varies significantly on individual tree species, even highly significantly in 2003 for phytophagous and omnivorous species, while no differences are detectable in the zoophagous species. By far most phytophagous bugs live on *Quercus* species (both on common oak as well as on the neophytic red oak), the fewest live on *Tilia cordata*. A similar result was found for omnivorous bugs, but the differences between the individual trees are not so marked there.

Table 1 – Results of the distribution of Heteroptera individuals in the main trees of the flood plain forest of Leipzig (*Quercus robur, Tilia cordata, Fraxinus excelsior*; sampled with window trap samples in the years 2002, 2003). Samples of both years were listed in the ecological groups "zoophagous (carnivorous)", "phytophagous", and "omnivorous (polyphagous)" as a first step, and the differences between trees were tested using an ANOVA in a second step. Except for omnivorous individuals of 2002, the significance increases if neophytic trees are included.

	2002					**2003**				
	D.f.	**SS**	**MS**	**F**	**p**	**D.f.**	**SS**	**MS**	**F**	**p**
Zoophage	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Phytophage	2	1411.4	705.7	4.84	0.023	2	10981.4	5490.7	7.022	0.007
Omnivore	2	2357.4	1178.7	4.12	0.037	2	9439	4719.5	13.4	0.0004

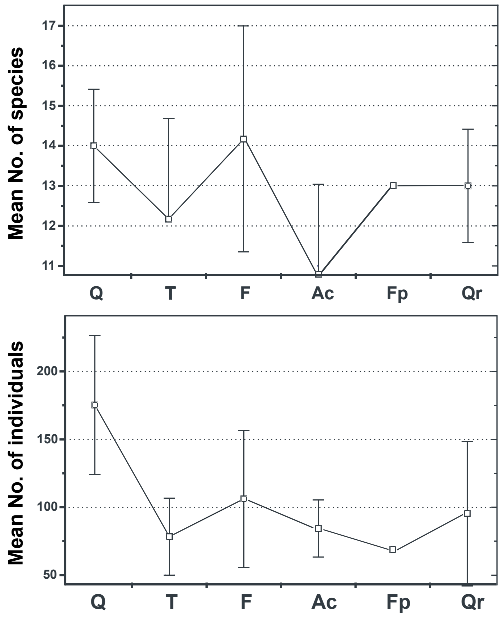

Figure 1 – Average numbers and standard deviation of species and individuals of Heteroptera sampled in window traps on the examined trees in 2003.

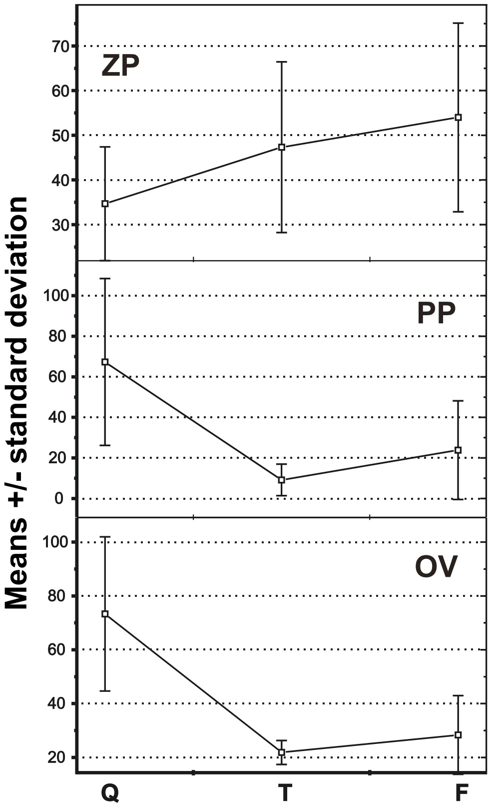

Figure 2 – Average numbers and standard deviation of Heteroptera individuals sampled in window traps on the main trees in 2003 – according to their feeding types. OV: omnivorous; PP: phytophygous; ZP: zoophagous.

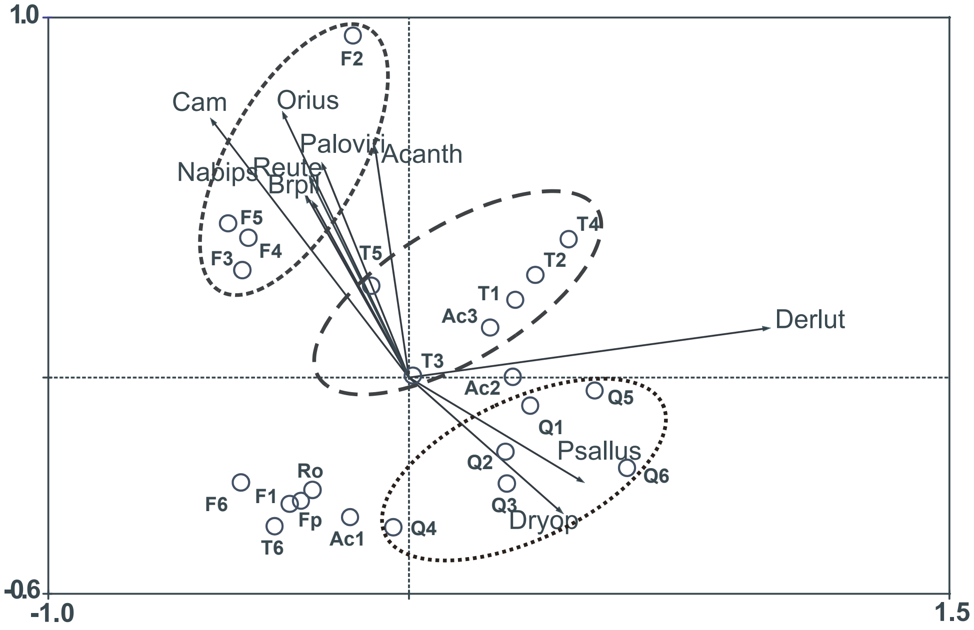

Figure 3 – Non-standardised PCA of Heteroptera sampled in window traps in 2002 (axis 1 vs. axis 2; eigenvalues axis 1: 0.6561, axis 2: 0.1348) . Except for *Quercus rubra* (which was excluded from the analysis because of its unduly influence on axis 1 caused by the dominating huge abundance of *Harpocera thoracica*) all trees and species with species fits ≥ 30% are shown. The figured species may be suitable indicators or tree specialists. The three main tree species are well separated on both the first and the second axis.

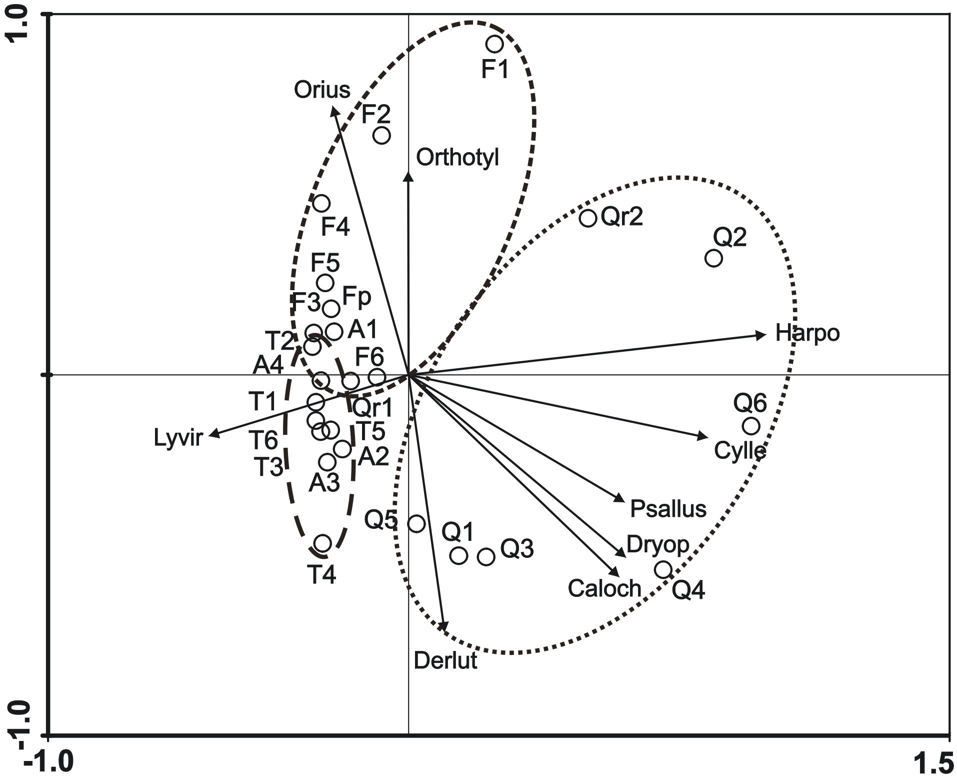

Figure 4 – Non-standardised PCA of Heteroptera sampled in window traps in 2003 (axis 1 vs. axis 2, eigenvalues: axis 1: 0.6364, axis 2: 0.1565). All trees and Heteroptera species with species fits ≥ 30% are shown. The figured species may be suitable indicators or tree specialists. The main tree species are surrounded by circles.

Preferences of canopy-dwelling bug species with reference to certain tree species

In order to ascertain bug species preferences in terms of tree species, a "Species Indicator Analysis" was first carried out (Appendix Table 1).

Seven species turned out to be significant specialists for one tree species or one tree genus in both years: **(1)** *Quercus robur*: *Psallus* sp., *Cyllecoris histrionicus* (Linné) **(2)** *Quercus* spp: *Dryophilocoris flavoquadrimaculatus* DeGeer, *Harpocera thoracica* (Fallén) **(3)** *Tilia cordata*: *Phytocoris tiliae* (Fabricius) **(4)** *Fraxinus excelsior*: *Temnostethus reduvinus* (Herrich-Schaeffer), *Orius* cf. *minutus* (Linné).

Seven other species only achieve significance in one of the two years and must therefore be classified as indicators of little value in respect of tree species preference. *Phylus* cf. *melanocephalus* (Linné) (on *Q. robur*) could only be detected in 2002, this species shows a low abundance, but high tree specificity.

Six species were caught in both years; but their tree specificity is only significant in one of the two years: **(1)** *Rhabdomiris striatellus* (Fabricius) has the highest number of individuals on *Quercus robur* in both years, but only in 2003 this specificity of host plant is significant, since in 2002, 39 individuals were also caught on *Acer pseudoplatanus.* **(2)** *Brachyocoleus pilicornis* (Panzer) and *Campyloneura virgula* (Herrich-Schaeffer) show by the far the highest abundance in both years on *Fraxinus excelsior.* However, *B. pilicornis* was not caught in 2003 in sufficient number of individuals to achieve significance. *C. virgula* also achieves a high abundance on lime tree in 2003 in contrast to the previous year. **(3)** *Lygus viridis* (Fallén) has, in both years, the highest abundance on *Tilia cordata*, but only achieves significant results in 2003, since in 2002, 21 individuals were also caught on an *Acer pseudoplatanus. Pinalitus cervinus* (Herrich-Schaeffer) and *Orthotylus* cf. *nassatus* (Fabricius) achieve significance in 2002 on *Tilia cordata*, but were detected in the second year in one or two specimens only.

We produced a comparable result performing a multivariate analysis (PCA, Figs. 3, 4). If only bug species with a PCA-declared variance of ± 30% are taken into consideration, *Quercus robur* is associated with the same six species in 2003 as in the Species Indicator Analysis (see above). For the winter lime tree, this is *Lygus viridis*, and for the oak, *Orius* cf. *minutus* (Fig. 4). For 2002, in contrast to the Species Indicator Analysis, the PCA graphic (Fig. 3) shows seven species as characteristic for *Fraxinus excelsior.* Only *Phytocoris tiliae* and *Temnostethus reduvinus* show significance associations in the Species Indicator Analysis in both years, with a relatively low fraction of shared variance as explained by the PCA.

The surprise during analysis of these indicators is that among the species which were significant for both years, there is one phytophagous species to three omnivores (including *Psallus* sp.) or three zoophagous species, respectively. Within the seven indicator species with a low indication weight we find an equally low proportion of phytophagous species: one phytophagous species to five omnivores and one zoophagous species.

This result means that predatory or partially predatory species show a much larger tree specificity than is the case with phytophagous bugs.

DISCUSSION

As an exceedingly species-rich order of insects, bugs colonise the widest variety of aquatic and terrestrial habitats and are characterised by different adaptations in respect of their micro-habitats (in the canopy area for example, to living under bark) and feeding type (phytophagous, zoophagous, polyphagous).

The examination evaluated here in the canopies of various tree species covers only a small part of the bug fauna to be expected in floodplains. The use of standardised trapping technology, however, enables a targeted analysis of ecological questions and statements concerning the colonisation of individual tree species to be made which so far have not been possible from the ground.

So far, robust middle-European comparisons of the bug fauna of various tree species have been available concerning common oak vs. red beech or, respectively, common oak + red beech vs. spruce or larch (Schubert 1998) as well as common oak vs. red oak+red beech (Gossner 2002). Schubert (1998) arrives at the conclusion that numbers of species and individuals differ significantly between the examined tree species. According to his analyses, bug species numbers are "ranked" *Quercus* > *Larix* > *Picea* > *Fagus* and numbers of individuals *Quercus* >> *Larix* > *Fagus* > *Picea.* Gossner (2002) sees significant differences in the number of species between common oak and the other tree species, and there was an identical trend among the numbers of individuals. On the basis of these findings from southern German low mountain range forests, it was an aim of our examinations to check whether the results can also be confirmed in a floodplain in a completely different natural area. Against the background of the studies cited above, the result of our examinations is no doubt surprising: no differences in the colonisation of tree species in respect of species numbers of Heteroptera, but significant differences in phytophagous and omnivorous individuals. The significances are lost in one of the two years if the species of all feeding types are considered summarily. Therefore, hypothesis (a), which was expressed at the start, must be rejected; neither the species diversity is significantly varied among the individual tree species, nor does the neophytic *Quercus rubra* show the lowest species diversity. In respect of numbers of individuals, the two *Quercus* species dominate for the phytophagous species, while the fewest phytophagous bugs live on *Tilia* and *Acer*.

Omnivorous species are the most common on *Quercus robur*, and the least numerous on *Tilia* or *Fraxinus*. By contrast, *Tilia* and *Fraxinus* show the highest numbers of zoophagous Heteroptera, but the differences for this feeding type are not significant.

A second aim of our work was to investigate tree preferences while taking account of the various feeding types. For plant suckers, which are adapted to certain plant constituents, a closer association to tree species or genera should be detectable than is the case for zoophagous species, which feed for example on butterfly caterpillars or leaf lice and can potentially find suitable food on any one of the autochthonous deciduous trees (hypothesis b).

In order to test tree species specificity, the Species Indicator Analysis (Dufrêne & Legendre 1997) was used. The results obtained were tested by means of a PCA. When the examined bug species were roughly evenly distributed among the three feeding types, we could not detect a particularly close association of phytophagous species to one tree species or genus: two significant specialists among the phytophagous bugs for 8, respectively 4 of the other two feeding types. This means that hypothesis (b) must also be rejected.

With reference to tree species / genera, we were able to detect two specialists for *Quercus* sp. as a genus as well as four specialists each for *Quercus robur*, *Tilia cordata* and *Fraxinus excelsior* in the canopy area of the floodplain forest. Among these specialists are 12 taxa of the Miridae, which are all named by Wagner (1955) for the same tree genus, together with two Anthocoridae, which Wagner (1967) classifies as ubiquitous.

In middle European woodland flora, the common oak is regarded as particularly species-rich in Heteroptera, which has also been confirmed in various studies concerning bugs (Kennedy & Southwood 1984, Dorow 2002, Gossner 2002). So far, 51 species are known to dwell in common oaks; 15 of these are specialists for *Quercus robur* (Dorow 2002). At the genus level, our results confirm a higher number of oak specialists compared with *Fraxinus* or *Tilia*, particularly since eight different *Psallus* species were recorded by us, all of which Wagner (1952), with the exception of *P. lepidus* (on *Fraxinus*), identifies as *Quercus* dwellers. A higher number of bugs dwelling on oaks is, however, not surprising, since *Quercus* is a widespread genus in Europe and, compared with *Tilia* or *Fraxinus*, it is also species-rich with endemites in the Mediterranean biodiversity centres and glacial refuge areas.

Two of the specialists detected by us on *Quercus robur* (*Psallus* sp.; *Cyllecoris histrionicus*) are also indicated by Gossner (2002), who conducted the same indicator analysis during his examinations on common oak, red oak and red beech. For two other species, however, the preferences calculated by us differ from the results that Gossner (2002) obtained. Thus, *Harpocera thoracica* in Gossner (l.c.) significantly prefers the common oak, while this species in our examination is a specialist for *Quercus* overall. On average, this species was more commonly caught on red oak (114 individuals in window traps per individual tree) than on common oak (44 individuals per individual tree). *Orthotylus tenellus* is likewise indicated as significantly associated with common oak by Gossner (2002). In our examination, the *Orthotylus* group (*O. nassatus*, *O. tenellus* and *O. viridinervis*; only significant in one year) prefers *Tilia cordata*. However, this tree species was not investigated by Gossner (2002). Existing differences between the two studies in respect of indicator species cannot, however, really be estimated using the Species Indicator Analysis. The calculated indicator values are a combination of the information concerning the relative abundance of bug species on various tree species (specificity) and their presence (fidelity) on all individual trees of one and the same species. They therefore only refer to the variation in the data included in the calculation and cannot be compared among different studies straight away.

The results concerning bug fauna obtained on the crane show that there are species-rich guilds in the canopy area of floodplain forests and many flight-active species can be recorded using window traps. Furthermore, dominance structures (numbers of individuals) of individual tree species differ clearly from one another and there are differences in respect of ecological types - we investigated feeding types - among the tree species. A number of interesting questions could not be clarified with the aid of the present evaluation. For example, there are still no answers as to whether interactions or niche separation occur among individual species. There are different findings from the same examination area concerning other animal groups in this respect (e.g. Schmidt *et al.* in this volume and Arndt *et al.* in press). Microclimatic dependencies and vertical zonation have not yet been analysed. The guild of bark dwellers (Aradidae, Aneuridae) could also not be reached using flight traps and branch eclectors. These gaps of knowledge should form the subject of future studies on canopy-dwelling Heteroptera.

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Appendix Table 1 – Heteroptera of the LAK-project sampled with window traps in 2002 and 2003. Feeding type (ET), average numbers of individuals per individual tree, significant values of the species-indicator-analysis (species-IVS; genera-IVG), as well as average numbers of bug species per tree species (last row) are given. Species of the genera *Psallus* and *Orthotylus* are combined.

WT 2002	**ET**	**Q**	**T**	**F**	**Ac**	**Ro**	**Fp**	**Qr**	**IVS**	**IVG**
Acanthosoma haemorrhoidale (Linné)	pp	0.33	0.5	1.33	0.33	0	2	0	-	-
Aelia acuminata (Linné)	pp	0.17	0.17	0	0	0	0	1	-	-
Alloeotomus germanicus Wagner	pp	0	0.33	0.17	0	1	0	0	-	-
Anthocoris amplicollis Horvath	zp	0.17	0	0	0.33	0	0	0	66.7	66.7
Anthocoris cf. *visci* Douglas	zp	0.17	0	0	0	0	0	0	-	-
Anthocoris minki Dohrn	zp	0	0	0.17	0	0	0	0	-	-
Anthocoris nemorum (Linné)	zp	0	0	0	0.33	0	0	0	-	-
Blepharidopterus cf. *angulatus* (Fallén)	zp	0	0.17	0.17	0	0	0	0	-	-
Brachyocoleus pilicornis (Panzer)	pp	0.33	2.67	4.5	0.33	2	1	0.5	50.9	54.2
Campyloneura virgula (Herrich-Schaeffer)	zp	1.5	5.83	39.83	0.67	2	3	0	81.2	81.9
Chilacis typhae (Perris)	pp	0.17	0	0	0	0	0	0	-	-
Cyllecoris histrionicus (Linné)	ov	1.17	0	0	0	0	0	0	50	-
Deraeocoris lutescens Schilling	zp	109.3	89.3	35.17	83.33	41	37	25.5	-	-
Dryophilocoris flavoquadrimaculatus DeGeer	ov	6.33	0.5	1	0	0	7	20	-	80.5
Elasmostethus interstinctus (Linné)	pp	0.5	0	0.33	0.33	1	0	1	-	-
Elasmucha grisea (Linné)	pp	0.17	0	0	0	0	0	0	-	-
Harpocera thoracica (Fallén)	pp	23.5	0.33	11.33	1.67	1	3	186.5	-	84.1
Himacerus apterus (Fabricius)	zp	0.17	1.5	1.33	0.67	2	1	1	-	-
Isometopus intrusus (Herrich-Schaeffer)	zp	0.17	0.17	0.17	0	0	0	0	-	-
Kleidocerys resedae (Panzer)	pp	1.5	1	2.33	0	0	3	1	-	-
Loricola cf. *elegantula* (Baerensprung)	zp	0.17	0	0.33	0	0	0	0	-	-
Lygus pratensis (Linné)	ov	0.33	0.33	0.5	0.67	0	1	0.5	-	-
Lygus viridis (Fallén)	ov	0.83	11.5	1.33	10.67	4	1	1	-	-
Miris striatus Linné	zp	0	0.33	0.17	0.33	0	0	0	-	-
Nabis pseudoferus Remane	zp	0.33	1.33	1.67	0	0	1	1	-	-
Orius cf. *minutus* (Linné)	zp	4.5	15.8	21.67	8	3	1	5	51.8	-
Orthotylus sp.	ov	1.67	9.5	1.67	0.67	0	0	0.5	57.6	61
Palomena prasina (Linné)	pp	0.5	1.83	0.5	1.67	0	1	2.5	-	-
Palomena viridissima (Poda)	pp	0	0	3.5	0	1	1	0.5	-	-
Pantilius tunicatus (Fabricius)	pp	0	0.17	0	0	0	0	0	-	-
Pentatoma rufipes (Linné)	ov	8.5	11	15.5	12.33	16	23	8	-	-
Phylus cf. *melanocephalus* (Linné)	ov	1	0	0	0	0	0	0	66.7	50
Phytocoris dimidiatus Kirschbaum	ov	0.33	0.83	0.5	0	1	0	0.5	-	-
Phytocoris longipennis Flor	ov	0	0.83	0.17	0	0	0	0	-	-
Phytocoris populi (Linné)	ov	0	0.83	0.5	0.33	0	0	0	-	-
Phytocoris tiliae (Fabricius)	zp	0	2.33	0.33	1	0	0	0	50.7	51.7
Pilophorus clavatus (Linné)	zp	0	0.5	0	0	0	0	0	-	-
Pinalitus cervinus (Herrich-Schaeffer)	ov	0	5	1.17	0	0	2	0	75	79.5
Psallus sp.	zp/ov	28	2.17	7	3.33	1	0	2	67.1	57
Reuteria marqueti Puton	ov	0	0	0.33	0	0	0	0	-	-
Rhabdomiris striatellus (Fabricius)	ov	9.5	0.17	0.17	13	1	0	6.5	-	-
Rhopalus parumpunctatus (Schilling)	pp	0	0	0	0.33	0	0	0	-	-
Stenodema laevigata (Linné)	pp	0.33	0.33	0.33	0.33	0	0	0.5	-	-
Temnostethus reduvinus (Herrich-Schaeffer)	zp	1	1.17	3.17	0	0	1	0	56.7	59.9
Tingis crispata Herrich-Schaeffer	zp	0.17	0	0	0	0	0	0	-	-
Troilus luridus (Fabricius)	zp	0	0.17	0	0	0	0	0	-	-
Sum of individuals		1217	1012	951	436	77	89	530		
Species per tree		16.5	18.5	19.17	13	14	17	14.5		

Appendix Table 1 – continued.

WT 2003									
	ET	**Q**	**T**	**F**	**A**	**Fp**	**Qr**	**IVS**	**IVG**
Acanthosoma haemorrhoidale (Linné)	pp	0.5	0.5	1	0	1	0.5	-	-
Aelia acuminata (Linné)	pp	0	0	0.17	0	0	0.5	-	-
Alloeotomus germanicus Wagner	pp	1.17	2.83	1.33	3	0	0	-	-
Brachycarenus tigrinus (Schilling)	pp	0.17	0	0	0	0	0	-	-
Brachyocoleus pilicornis (Panzer)	pp	0.33	0.33	1.83	0.5	0	1.5	-	-
Campyloneura virgula (Herrich-Schaeffer)	zp	1.83	4	6.33	0.25	1	0.5	-	-
Chilacis typhae (Perris)	pp	0	0	0	0.25	0	0	-	-
Cyllecoris histrionicus (Linné)	ov	1.33	0	0	0	0	0	50	-
Deraeocoris lutescens Schilling	zp	24.33	23.3	7	22.75	3	5	-	-
Deraeocoris olivaceus (Fabricius)	zp	0	0	0.17	0	0	0	-	-
Deraeocoris trifasciatus (Linné)	zp	0.33	0	0	0	0	0	-	-
Dryophilocoris flavoquadrimaculatus DeGeer	ov	23.17	0.83	0.5	0	2	2	87.4	92
Eurydema oleracea (Linné)	ov	0.17	0.17	0	0	0	0.5	-	-
Gastrodes grossipes (DeGeer)	zp	0	0	0.17	0	0	0	-	-
Harpocera thoracica (Fallén)	pp	63.67	1	16.67	3.5	4	42	55.8	75.1
Himacerus apterus (Fabricius)	zp	0.17	0.83	0.5	1.5	1	0	-	-
Isometopus intrusus (Herrich-Schaeffer)	zp	0	0.17	0	0	0	0	-	-
Kleidocerys resedae (Panzer)	pp	0.67	0.33	0.83	0.25	0	1.5	-	-
Lygus rugulipennis Poppius	ov	0	0.17	0	0	0	0	-	-
Lygus viridis (Fallén)	ov	1.17	8.83	2.67	4.5	2	3	44.5	50.4
Megacoelum infusum (Herrich-Schaeffer)	zp	0	0	0.17	0.25	0	0	-	-
Megalonotus chiragra (Fabricius)	pp	0.17	0	0	0	0	0	-	-
Miris striatus Linné	zp	0.33	0.17	0.33	0	0	0	-	-
Nabis pseudoferus Remane	zp	0.67	1.33	0.83	0.5	0	0.5	-	-
Nysius thymi (Wolff)	pp	0	0	0.17	0	0	0	-	-
Orius cf. *minutus* (Linné)	zp	5.17	13.33	32.8	10	11	11.5	45.2	49.7
Orthotylus sp	ov	0	0	0.33	0	0	0	-	-
Palomena prasina (Linné)	pp	0.5	3.83	1.67	1.75	5	2	-	-
Pentatoma rufipes (Linné)	ov	15.17	10.83	21.5	28.25	34	17	-	-
Phytocoris populi (Linné)	ov	0.17	0	0	0	0	0	-	-
Phytocoris tiliae Fabricius	zp	1.5	3.83	4.17	1.75	0	0.5	36	-
Pinalitus cervinus (Herrich-Schaeffer)	ov	0.17	0	0	0	0	0	-	-
Psallus sp.	zp/ov	8	0.67	2.5	2.25	2	1	54.2	-
Rhabdomiris striatellus (Fabricius)	ov	24	0.33	0.83	1.25	0	5.5	79.8	89.4
Rhopalus parumpunctatus (Schilling)	pp	0	0.17	0	0	0	0	-	-
Scoloposthetus affinis (Schilling)	pp	0.17	0	0	0	0	0	-	-
Stenodema laevigata (Linné)	pp	0	0	0	0	1	0.5	-	-
Stictopleurus abutilon (Rossi)	pp	0	0	0.17	0	0	0	-	-
Temnostethus reduvinus (Herrich-Schaeffer)	zp	0.33	0.33	1.5	0.25	2	0	-	56
Tritomegas sexmaculatus (Rambur)	pp	0	0	0	0.25	0	0	-	-
Sum of individuals		1052	470	637	332	69	191		
Species per tree		14.17	13	15.17	11	14	13		

Appendix Table 2 – Heteroptera of the LAK-project sampled with branch eclectors in 2002 and 2003. The table shows feeding type (ET) and numbers of collected specimens of the different trees.

BE2002

	ET	**Q3**	**Q4**	**Q6**	**T1**	**T3**	**T4**	**T5**	**F1**	**F2**	**F4**	**F6**
Acanthosoma haemorrhoidale (Linné)	pp	0	0	0	1	0	0	0	1	1	1	3
Anthocoris minki Dohrn	zp	0	0	0	0	0	0	0	1	0	0	0
Brachyocoleus pilicornis Panzer	pp	1	0	0	0	0	0	0	0	0	0	1
Campyloneura virgula Herrich-Schaeffer	zp	0	0	0	1	0	1	0	1	0	0	1
Deraeocoris lutescens Schilling	zp	0	1	0	2	0	0	0	0	0	0	0
Dryophilocoris flavoquadrimaculatus DeGeer	ov	0	0	0	0	0	0	0	0	0	0	1
Elasmostethus interstinctus (Linné)	pp	0	0	0	0	0	0	0	1	0	0	0
Harpocera thoracica (Fallén)	pp	0	1	2	0	0	0	0	0	0	0	0
Himacerus apterus (Fabricius)	zp	4	1	1	6	3	7	15	2	7	3	4
Isometopus intrusus (Herrich-Schaeffer)	zp	0	0	0	0	0	0	0	1	0	0	0
Lygus viridis (Fallén)	ov	0	0	1	1	0	0	0	0	0	1	0
Nabis pseudoferus Remane	zp	0	0	0	0	0	0	0	0	0	1	0
Orius cf. *minutus* (Linné)	zp	0	0	0	2	2	0	5	1	0	6	1
Orthotylus sp.	ov	0	0	0	0	5	0	0	0	0	0	0
Palomena prasina (Linné)	pp	0	0	0	1	0	0	1	0	0	0	0
Pentatoma rufipes (Linné)	ov	0	2	1	1	1	1	3	5	7	1	2
*Phytocoris dimidiatus*Kirschbaum	ov	1	0	0	0	0	0	0	0	0	0	2
Phytocoris longipennis Flor	ov	0	0	0	0	0	0	0	0	1	0	0
Phytocoris populi (Linné)	ov	0	0	0	0	0	0	0	0	1	0	0
Phytocoris tiliae (Fabricius)	zp	1	0	0	2	0	0	1	0	1	0	0
Pinalitus cervinus (Herrich-Schaeffer)	ov	0	0	1	0	0	0	1	0	0	0	0
Psallus sp.	ov	0	0	0	1	0	0	0	0	0	0	0
Stenodema laevigata (Linné)	pp	0	0	0	0	0	0	0	1	0	0	0
Temnostethus reduvinus (Herrich-Schaeffer)	zp	0	0	0	0	0	0	0	0	0	2	0
Individuals		7	5	6	18	11	9	26	14	18	15	15
Species		4	4	5	10	4	4	5	9	6	7	8

BE2003

	ET	**Q3**	**Q4**	**Q6**	**T1**	**T4**	**T5**	**F1**	**F2**	**F6**	**A2**	**A4**	**Qr2**
Acanthosoma haemorrhoidale (Linné)	pp	0	0	0	0	0	0	0	1	0	0	0	0
Alloeotomus germanicus Wagner	pp	0	1	0	0	0	0	0	0	0	0	0	0
Brachycarenus tigrinus (Schilling)	pp	0	0	0	0	0	0	0	1	1	0	0	0
Cyllecoris histrionicus (Linné)	ov	0	0	1	0	0	0	0	0	0	0	0	0
Deraeocoris lutescens Schilling	zp	0	0	0	1	0	0	0	0	0	0	0	1
Dryophilocoris flavoquadrimaculatus DeGeer	ov	0	0	0	0	0	1	0	0	0	0	0	1
Harpocera thoracica (Fallén)	pp	0	0	0	0	0	0	1	0	0	0	0	0
Himacerus apterus (Fabricius)	zp	0	1	1	0	4	7	2	0	0	4	1	1
Isometopus intrusus (Herrich-Schaeffer)	zp	0	0	0	1	0	0	0	1	0	0	0	0
Nabis pseudoferus Remane	zp	0	0	2	1	0	2	0	0	0	0	0	0
Orius cf. *minutus* (Linné)	zp	0	0	0	1	0	0	8	2	0	0	0	0
Palomena prasina (Linné)	pp	1	0	0	0	0	0	0	1	0	0	0	0
Pentatoma rufipes (Linné)	ov	2	3	1	4	1	2	4	8	2	1	1	1
Phytocoris tiliae (Fabricius)	zp	0	0	0	4	0	1	0	1	1	3	0	0
Pilophorus clavatus (Linné)	zp	0	0	0	1	0	0	0	0	0	0	0	0
Psallus sp.	zp	0	2	2	0	0	0	0	3	0	1	0	0
Rhabdomiris striatellus (Fabricius)	ov	0	1	3	0	0	0	0	0	0	0	0	0
Temnostethus reduvinus (Herrich-Schaeffer)	zp	0	0	1	1	0	0	0	0	0	0	0	0
Individuals		3	8	11	14	5	13	15	18	4	9	2	4
Species		2	5	7	8	2	5	5	8	3	4	2	4

3.4 Spatial distribution of Neuropterida in the LAK stand: significance of host tree specificity

Axel Gruppe

The insect material caught in flight interception and branch traps which were exposed in tree crowns of the LAK plot contained 306 adult Neuropterida of 24 species (3 Raphidioptera; 21 Neuroptera) in the year 2002. The number of specimens and species caught on the three main tree species *Fraxinus excelsior* (ash), *Quercus robur* (oak), and *Tilia cordata* (lime) differed between 80 (ash) and 96 (lime) specimens and 11 (ash) and 17 (oak) species. Although, the differences are not statistically significant, a DCA revealed a separation of the neuropterid communities on the three tree species. These numbers of species are low compared to the results of other studies on the same tree species in Central Europe. The occurrence and distribution of some species was unexpected compared to literature. Requirements of larvae and adults of the neuropterid species for specific nutritional qualities are more likely the reason for the host tree preference than the tree species itself.

INTRODUCTION

The Neuropterida are one of the poorly studied insect taxa in faunistical studies. This applies also to studies of arthropod assemblages in tree crowns but there are some publications already recently dealing with lacewings in this stratum (Czechowska 1994, 1997, 2002; Gruppe & Schubert 2001; Gruppe, Gossner & Simon 2004; Gossner, Gruppe & Simon 2005). Eventhough the autecology and ecological demands of most of the Central European species of Neuropterida are assumed to be known (New 1998), these informations are derived from samplings in strata close to the ground level and from light trapping (Aspöck *et al.* 1980; Gepp 1999; Saure & Gruppe 1999). Therefore, conspicious differences might appear between the assemblages close to the ground level and in the tree crowns of closed forest stands. 'Rare species' might be very abundand in the crown stratum.

The abundance and spatial distribution of species in a diverse environment like the canopy of forests is determined by the demands of each particular species, like food, mating and oviposition sites, and structures which match the particular camouflage behavour etc. The natural food ressource of many species, particularly of Coniopterygidae, is unknown, but Raphidioptera, Hemerobiidae and Coniopterygidae are assumed to be zoophagous in all developmental stages. In green lacewings (Chrysopidae) the food ressource of larvae and adults may be different, because adults of many species feed on nectar or pollen whereas larvae are zoophagous (Canard 2001). This makes it difficult to analyse host tree specificity from sampling by flight interception traps in which mostly adults are caught.

In this paper I discuss the spatial distribution patterns of adult lacewings which were caught with flight interception traps and branch traps in tree crowns of different tree species in the flood plain forest of Leipzig.

MATERIALS AND METHODS

In the year 2002, the flight interception traps (window traps; WT) (Winter *et al.* 1999) and branch traps (branch eclector; BE) (Simon 1995) provided by the LAK research facility were used to investigate neuropterid species (for a detailed description of sampling design refer to Arndt & Unterseher, this volume). Dominant tree species in the plot were *Quercus robur* (oak), *Tilia cordata* (lime) and *Fraxinus excelsior* (ash) with six individual trees each and *Acer pseudoplatanus* with three trees. In addition, two trees of the neophytic tree species *Quercus rubra*, and one tree of *Robinia pseudoacacia* and *Fraxinus pennsilvanica* were sampled. The traps were purged in regular intervals of 2–4 weeks. The captured arthropods were sorted down to the order level and all adult Neuropterida (orders Raphidioptera, Neuroptera) were further determined to the species level. Females of the genus *Coniopteryx* (Neuroptera, Coniopterygidae) were determined to the genus level only since species determintion is uncertain even after mazeration of the internal genitalia. At least three species of the genus *Chrysoperla* occure in Germany (Tröger 2000; Gruppe 2002) but since morphologicla characters are highly variable (Henry *et al.* 2002) several specimens were determined to the genus level only. Some specimens could not be determined to the species level due to damages and/or discoloration.

Abundance and host tree preference were analysed using data from flight interception traps of *Quercus robur*, *Tilia cordata* and *Fraxinus excelsior* only. These tree species were sampled in similar numbers. Statistical tests were done by SPSS 12 (SPSS Inc. 2003) and PC-ORD 4.10 for Windows (McCune & Mefford 1999).

RESULTS AND DISCUSSION

A total number of 306 specimens of 21 species of Neuroptera and 3 species of Raphidioptera was caught in the year 2002 (Appendix Tab. 1).

All species were reported to occur in Saxonia by Kleinsteuber (1994) except of *Chrysoperla pallida*. This species was separated from the *C. carnea* group and described as a valid species by Henry *et al.* (2002). It has been found all over Germany in arboreal habitats in the meantime (Tröger 2000; Gruppe 2002). This suggests that the species is also present in older collections from the region but this was not yet verified. The Raphidioptera *Subilla confinis* was known to occur in Saxonia from the literature earlier than 1956 only. Its high abundance characterizes it as a typical species of the tree crown fauna as it was also shown by Gruppe & Schubert (2001) and Gruppe, Gossner & Simon (2004) in different forest stands in southern Bavaria especially for oak.

Statistical analysis of the abundance of neuropterid species was done using data of flight interception traps of the three dominant tree species. Similar numbers of specimens were caught on lime (83 specimens) and oak (82) but less on ash (52) with this trap type. The same appeared for the numbers of species (lime 15 species, oak 15, ash 9). However, differences between average number of specimens as well as species were not statistically significant (specimens: K-W-test $p = 0.053$; species: K-W-test $p = 0.220$) (Fig. 1).

A correspondence analysis revealed a large variability between the communities of single trees either along axis 1 (oak) or along axis 2 (oak, lime, ash), respectively. However, there was a separation of neuropterid communities in tree crowns along the first two axes. A high β-diversity particular in oak is indicated by the high range along axis 1 and 2. Although no distinct borderlines were found between the assemblages of respective data points communities of Neuroptera can be separated in regard to all three abundant tree species. In ash and oak a high variability between neuropterid assemblages are obvious. Lime trees seem to be peculiar due to their low variability along along axis 1 (Fig. 2).

The captured neuropterid community in the Leipzig flood plain forest comprised 24 species, a relatively low number compared to the assemblages in other forest types in Central Europe (Table 1).

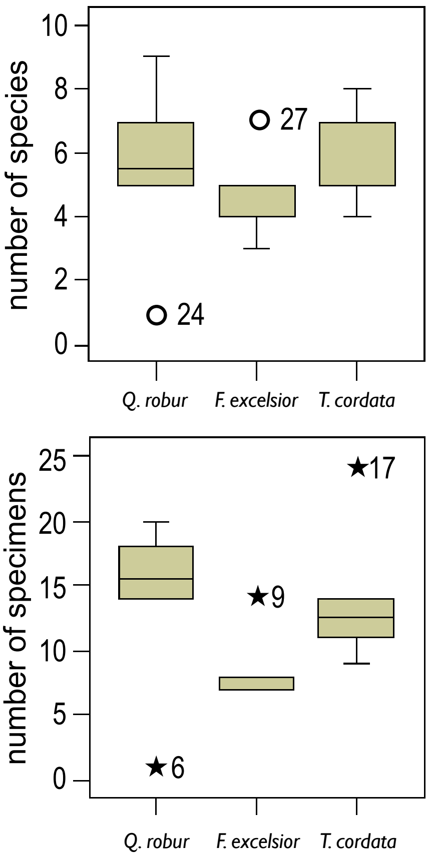

Figure 1 – Average number of Neuropterida (species top, specimens bottom) caught on different tree species at the LAK plot.

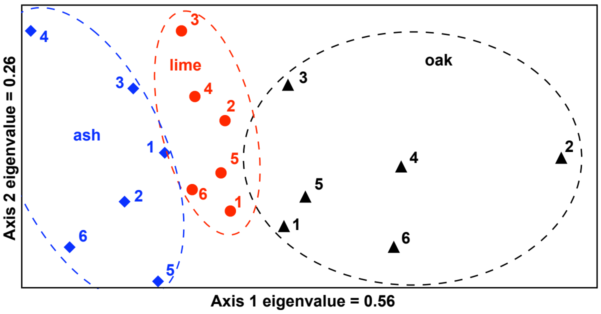

Figure 2 – DCA ordination of the neuropterid communities in the tree corwon of oak, ash, and lime at the LAK plot.

Table 1 – Number of neuropterid species in tree crowns in different Central European forest stands caught with several trap types. *yellow pan traps, **total number of species in the studied stand. [1]Gruppe, Gossner & Simon 2004; [2]Gruppe & Schubert 2001; [3]Czechowska 1997; [4]Gossner 2004. Raph: Raphidioptera, Chrys: Chrysopidae, Hem: Hemerobiidae, Coni: Conioterygidae.

		No. traps	No. years	Raph	Chrys	Hem	Coni	sum	total**
Quercus petrea/robur									
D-Krumbach[1]	Luzulo-Fagetum	6	2	0	9	7	5	21	31
D-Freising[1]	Luzulo-Fagetum	6	2	5	12	4	3	20	30
D-Hienheim[2]	Asperulo-Fagetum	9	3	5	11	9	8	33	44
D-Leipzig	Querco-Ulmetum minoris	12	1	3	5	5	4	17	24
D-Berlin[4]	Pino-Quercetum	6	2	0	3	2	3	8	10
Poland[3]	Tilio-Carpinetum	3*	2	1	8	4	3	16	28
Poland[3]	Pot.albae-Quercetum	3*	2	2	9	3	2	16	26
Poland[3]	Qu.roboris-Pinetum	3*	2	3	8	5	4	20	31
Tilia cordata									
D-Leipzig	Querco-Ulmetum minoris	12	1	2	8	3	2	15	24
Poland[3]	Tilio-Carpinetum	3*	2	2	8	5	3	18	28
Poland[3]	Pot.albae-Quercetum	3*	2	2	8	5	2	17	26

One reason for this discrepancy is probably the different type and numbers of traps in these studies. However, these data are the first systematic study of flood plain forests in that region. All others were done in stands of more diversity, i.e. in mixed forest stands with both, decidous and conifer tree species (Czechowska 1994, 1997, 2002; Gruppe & Schubert 2001; Gruppe, Gossner & Simon 2004). According to Engelmann's system (Engelmann 1978) we could find eight 'Hauptarten' defined as species the percentage of which is more than 3.2% of all caught specimens. These are discussed more detailed as follows.

About 75% of all *Subilla confinis* and *Coniopteryx borealis* were caught on oak. This suggests that they belong to the neuropterid community typically for oak crowns. Both species occurred also on lime but *C. borealis* was missing on ash. *S. confinis* seems to be a real oak specialist. It was captured in oak crowns, rarely but exclusively, in studies in southern Bavaria and, more important, it was reared in high numbers from dead wood from oak crowns (Gruppe & Schubert 2001; Gruppe *et al.* 2004). In contrast, *C. borealis* is more euryoecious and was reported by the same authors for huge number of host tree species, broad leaved trees and conifers as well. The second group of species was represented by two thirds of their specimens on ash: *Hypochrysa elegans*, *Chrysopidia ciliata* and *Sympherobius elegans*. These species show very different ecological requirements which might be responsible for their occurrence on ash. Adults of *H. elegans* are specialized pollen feeders (Canard 2001) but they seem to be strongly associated with *Fagus sylvatica* in almost all forest types (Szentkiralyi 2001). More than 60% of all specimens occurred in the sample derived at Mai 21st, when ash was still blooming but oak trees had just started to bloom. This suggests that the availability of pollen seems to be responsible for the high abundance of adult *H. elegans* in particular tree species. *S. elegans* is aphidophagous during adult and larval stage with the larvae specialized for galling aphids (Szentkiralyi 2001). Many Pemphigidae species (Homoptera) live on ash and most of these Homopterans are gall forming species which may serve as food ressource for *S. elegans* larvae. Galling Homoptera are missing on lime and oak although free living species are common on the leaves. No particular specialisation is known for *Chrysopidia ciliata* neither for adults nor for larvae. It is one of the most abundant chrysopid species in decidous forests with dense undergrowth in Central Europe (Aspöck *et al.* 1980). The reason for its high abundance on ash however is not yet clear.

Three neuropterid species were found with about 50% of their specimens on lime but also frequently on the other tree species. These were the euryoecious species *Phaeostigma notata, Chrysoperla carnea* and *C. pallida.* It seems that the distribution of the food resource, aphids and honeydew, might be responsible for the occurrence on lime.

Most lacewing species are assumed to have a more or less intense host tree preference, and therefore, it should be possible to define characteristic lacewing assemblages for several tree species (Szentkiralyi 2001), a context which is probably questionable at least for some species. The results from the LAK show that *Hypochrysa elegans* which might be strongly associated with *Fagus sylvatica* (Montserrat & Marin 1994; Szentkiralyi 2001), occurs in the flood plain forest predominantly on ash. Thus, not only the tree species seems to be the clue for host tree preference but also the tree composition of any particular forest stand.

One important factor regarding host tree preference is the nutritional requirement of a particular species. Neuropterida like other holometabolic insects often use different food ressources as larvae and adult insects. In discussion about host tree preference temporal food availability and prey community has to be considered. All terrestrial larvae of Neuropterida in Central Europe are zoophagous but due to their behaviour and morphology of the mouthparts some species are restricted to more or less motionless arthropods like Coccidae, Aleyrodidae, mites, insect eggs or galling aphids. The nutritional ecology of adult insects is more diverse. Species can roughly be subdivided to be zoophagous, glycophagous or palynophagous, but for many species, even in Central Europe, the natural food is not well known. Notably palynophagous species need a close coincidence to blooming plant species and, thus, might show a high seasonality in host plant preference.

The neuropterid community in a Central European flood plain forest which typically consists of broad leafed trees seems to have a low degree of tree species specialisation. The differences in the number of specimens indicate that oak offers the most suitable habitat to Neuropterida whereas ash does less. However, some species prefer even ash when the occurrence of adult insects coincides with food. This suggests that the association of Neuropterida with particular host tree species is more likely to be influenced by the tree as a resource-carrying structure than as an individual of a particular species.

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Appendix Table 1 – Total number af Neuropterida caught in the crowns of different tree species at the LAK plot (Sum of all trap types). *specimens collected by hand from various tree species.

	Quercus robur	***Fraxinus excelsior***	***Tilia cordata***	***Acer pseudoplatanus***	***Quercus rubra***	***Robinia pseudacacia***	***Fraxinus pennsilvanica***	**Unknown***	**no. of specimens**
no. of WT	6	6	6	3	2	1	1	–	–
no. of BE	16	16	16	–	–	–	–	–	–
Raphidioptera									
Phaeostigma notata	4	1	6	–	–	–	–	18	29
Subilla confinis	12	2	2	–	–	–	–	5	21
Xanthostigma xanthostigma	1	–	–	–	–	–	–	2	3
Neuroptera, Chrysopidae									
Hypochrysa elegans	–	13	8	3	–	–	–	–	24
Nineta flava	–	6	3	–	–	–	–	–	9
Chrysopa viridana	–	–	1	–	–	–	–	–	1
Chrysopa sp.	1	1	–	–	–	–	–	–	2
Dichochrysa abdominalis	–	1	1	–	–	–	–	–	2
Dichochrysa prasina	1	–	–	–	–	–	–	–	1
Cunctochrysa albolineata	–	1	1	–	–	–	1	–	3
Chrysopidia ciliata	2	7	2	–	1	1	1	–	14
Chrysoperla carnea	19	19	37	6	3	–	–	–	84
Chrysoperla pallida	3	6	10	–	–	–	–	–	19
Chrysoperla sp.		7	4	1	–	–	–	–	12
Neuroptera, Hemerobiidae									
Drepanepteryx phalaenoides	1	–	–	–	–	–	–	–	1
Hemerobius humulinus	4	–	3	–	1	–	–	–	8
Hemerobius stigma	–	–	–	1	–	–	–	–	1
Hemerobius micans	–	–	–	1	–	–	–	–	1
Hemerobius lutescens	–	–	2	–	–	–	–	–	2
Hemerobius marginatus	1	–	–	–	–	–	–	–	1
Wesmaelius nervosus	–	–	–	–	1	–	–	–	1
Wesmaelius sp.	1	–	–	–	–	–	–	–	1
Sympherobius elegans	1	14	6	2	–	–	–	–	23
Neuroptera, Coniopterygidae									
Coniopteryx borealis	13	–	4	–	–	–	–	–	17
Coniopteryx haematica	6	–	2	–	–	–	–	–	8
Coniopteryx tineiformis	2	–	–	–	–	–	–	–	2
Coniopteryx sp.	9	2	4	–	–	–	–	–	15
Parasemidalis fuscipennis	1	–	–	–	–	–	–	–	–
Total no.of specimens	82	80	96	14	6	1	2	25	306
no.of species	17	11	15	5	4	1	2	3	24

3.5 Ecological examinations concerning xylobiontic Coleoptera in the canopy of a Quercus-Fraxinus forest

Carsten Schmidt, Detlef Bernhard & Erik Arndt[1]

Xylobiontic Coleoptera were sampled using window traps and branch eclectors in the canopy of a *Quercus–Fraxinus–Tilia* forest in the "Burgaue" nature conservation area northwest of Leipzig. This study was part of the interdisciplinary LAK crane project. We examined the three autochthonous main tree species (*Quercus robur, Fraxinus excelsior, Tilia cordata*) as well as introduced ones (*Acer pseudoplatanus, Robinia pseudoacacia, Fraxinus pennsylvanica*, and *Quercus rubra*) over six months from April 24–October 24, 2002. The horizontal distribution patterns of xylobiontic Coleoptera are presented based on a total catch of 4 130 individuals and 175 species. Numbers of species and individuals are significantly different between the main trees. The fauna of xylobiontic beetles was poorer on neophytic trees compared to their autochthonous relatives of the same genera (*Quercus, Fraxinus*). Comparably high numbers of species and individuals were found on *Acer pseudoplatanus.* Significant differences in numbers of species and individuals were only found in the ecological guild of mycetophagous beetles on different tree species. Regarding microhabitat guilds, differences between tree species occurred concerning the individual but not the species numbers in the guilds of inhabitants of rotten wood, inhabitants of recently dead wood and fungi. The quantitative largest guild (coloniser of decayed wood) did not show differences between tree species. Only four xylobiontic species were subdominant to dominant, comprising two *Dasytes* species. Even though both *Dasytes* species are regarded as generalists, *Dasytes aeratus* preferred *Quercus robur*, while *Dasytes plumbeus* favoured *Tilia cordata.* We propose a partial niche separation of these two *Dasytes* species. Using a species indicator analysis, 22 species of Coleoptera were identified as significantly preferring a certain tree species or genus: *Quercus robur* (preferred by 1 xylobiontic species), *Q. rubra* (1), *Quercus* spp. (1), *Tilia cordata* (3), *Fraxinus excelsior* (3), *Fraxinus* spp. (1), and *Acer pseudoplatanus* (12). The surprisingly high number of xylobiontic species occurring predominantly on *Acer pseudoplatanus* is due to generalistic species, which significantly prefer *Acer* in the area under investigation.

INTRODUCTION

All species of the order Coleoptera, which by definition are associated with the wood habitat, count as wood-inhabiting, or xylobiontic, beetles (Palm 1959, Bense unpubl.). Xylobiontic Coleoptera are therefore an "ecological group", which, in central Europe, includes representatives from 72 families (Köhler 2000). This extremely species-rich and diverse group can be divided into guilds of defined microhabitat inhabitants (Bense 1998) or feeding preferences (Köhler 2000). A differentiated reflection on guilds of these types allows statements to be made about the naturalness of a location regarding the nature conservational assessment of forests. The investigation of wood-inhabiting beetles was one of the main projects within the Leipzig Canopy Crane Project because the results from earlier investigations (Bense 1998, Jansen & Kirmse 2002) revealed that the Burgaue nature reserve can be considered as a refuge for xylobiontic relict primeval forest species.

The aim of this project was to analyse the horizontal distribution of various species and species groups in the canopy space of this oak-ash-winter lime tree forest. Comparative examinations between several animal groups were undertaken in order that general statements could be projected concerning the canopy fauna of a "natural" forest. The study presented here is an initial ecological assessment of xylobiontic beetles. The following questions were the focus of our investigations: **(1)** are there differences in the fauna of the xylobiontic Coleoptera of various deciduous trees and **(2)** is it possible to detect beetle species preferences for certain species of trees?

MATERIALS AND METHODS

The analysis of xylobiontic Coleoptera was effected using the sampling design described in this volume.

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[1] corresponding author

The capture efficiency of the window traps and branch eclectors used is kept restricted to a narrow range. This makes it possible to record the spatial distribution of xylobiontic Coleoptera in the immediate surroundings which are only mobile to a limited extent, due to their swarming behaviour (Simon & Linsenmair 2001; Bussler *et al.* 2004). The two trap types used reflect various activity patterns (flight or crawling activity). As the investigation shows, considerably fewer animals were caught in the branch eclectors than in the window traps. Since, predominantly, species with just one or two individuals were caught in the branch eclectors, only data from the window traps are considered in the further assessment.

The examination period was during six months between 24/04/ and 24/10/2002. From the total catch of Coleoptera, 48 are included in the assessment, while a few families – for example, Carabidae (ground beetles) and Chrysomelidae (leaf beetles) – were ignored, as they are not xylobiontic beetles in the strict sense. Determination took place on the basis of Freude, Harde & Lohse, volumes 3–11 (1964–83), as well as the supplementary volumes by Lohse & Lucht (1989–93) and Lucht & Klausnitzer (1998). Further, Grüne (1979) was used to determine the Scolytidae. Determination was followed down to the species for all animals; where necessary, the animals (e.g. *aedeagus*) were dissected for this purpose as appropriate. Difficult species or families, were determined or checked by experts (see Acknowledgements). The Coleoptera assessed, together with samples from 2003, which remain to be processed, are kept correspondingly prepared or conserved at the Institute of Biology II at the University of Leipzig.

In order to enable a differentiated assessment, the species were divided according to their determination into ecological guilds in respect of their microhabitats and feeding preferences. The following guilds of microhabitat inhabitants (according to Bense unpubl.) were assessed: **(1)** colonisers of recently dead and diseased wood (hkf); **(2)** colonisers of highly decomposed wood (ht); **(3)** wood fungus colonisers (hp); **(4)** rotten wood colonisers (m). Likewise with regard to feeding preferences (according to Köhler 2000) four guilds were distinguished: **(1)** mycetophagous; **(2)** necro- and saprophagous; **(3)** xylophagous; **(4)** zoophagous.

There were problems with the assessment due to the varyingly large sample number. For example, oak Q2 (1.5 m trunk diameter) fell during a storm on 05/06/2002 and could no longer be used for the canopy investigation. Two window traps and four branch eclectors were lost with Q2. Furthermore, only three representatives of *Acer pseudoplatanus* and one or two representatives each of the various neophytic species. Nevertheless, six representations each of the main tree species were sampled. The reason for the differing sample numbers was a compromise between the request to include neophytes in the investigations and the capacities available for this purpose.

An ANOVA was applied in order to test if differences in numbers of species and individuals were significant.

In order to illustrate the commonalities or differences in the species communities of the investigated tree species, the Euclidean Index was calculated and on the basis of this index a cluster diagram (UPGMA process) was compiled. Using this procedure, a multi-dimensional data set can be depicted as two-dimensional sub-groups resembling one another (clusters) (Lozán & Kausch 1998). The Indicator Species Analysis was used in order to test species preference with regard to a particular locality (here: tree species) (Dufrêne & Legendre 1997).

RESULTS

A total of 4 130 xylobiontic beetles, belonging to 175 species, were caught during the recording period 2002. Of these, 4 057 individuals (175 species) were found in the window traps and just 73 individuals (34 species) in the branch eclectors. Only the catches from the window traps are included in the following assessment.

Differences between individual tree species

Seven different tree species were investigated in 2002. Average numbers of species and individuals of xylobiontic beetles on the tree species are shown in Fig. 1. Species numbers of the main tree species (*Quercus robur*, *Tilia cordata*, and *Fraxinus excelsior*) differ significantly from one another (p = 0.026). If these are compared to the other two tree groups (*Acer pseudoplatanus* and neophytes with *Robina pseudoaccacia*, *Fraxinus pennsylvanica*, and *Quercus rubra*), there is only a significant difference in the neophytes. (p = 0.011). In the case of number of individuals, significant differences are limited to the three main tree species (p = 0.016).

In many respects, *Acer pseudoplatanus* assumes a special ecological position among the analysed trees (see below). The species number is significantly different from the main tree species, but considering species ranges and numbers of individuals it is closer to the *Quercus* species than to the other tree species (Fig. 2). If the xylobiontic Coleoptera are examined differentially according to their feeding preference, then only the mycetophagous species support the differences between tree species described above regarding their species numbers (p = 0.008) and numbers of individuals (p = 0.007).

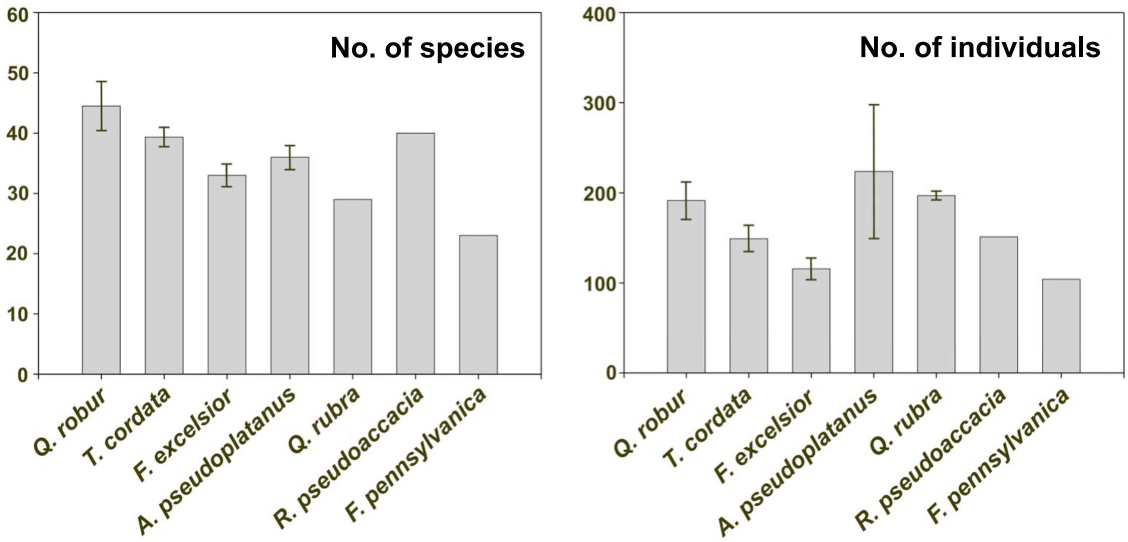

Figure 1 – Average numbers of species and individuals of xylobiontic Coleoptera in window traps of all examined tree species with standard errors.

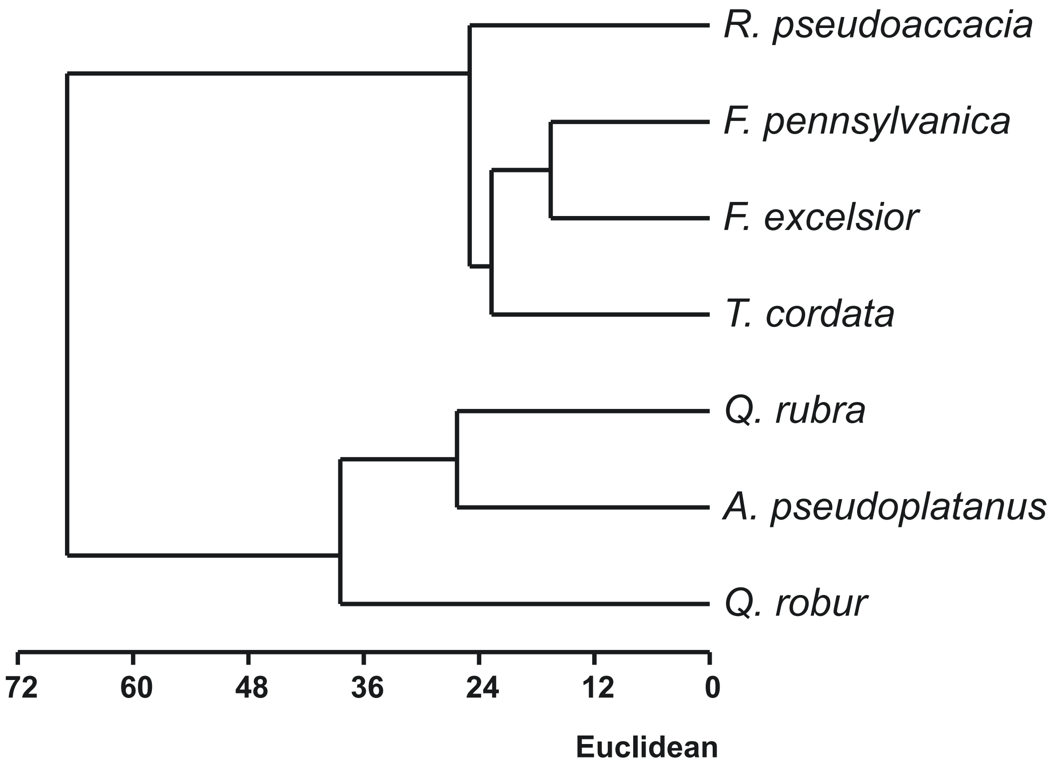

Figure 2 – Cluster analysis of Euclidean index of the tree species based on average data (UPGMA, xylobiontic species only represented by singletons and doubletons are excluded).

Table 1 – Xylobiontic generalists, sampled with window traps in all examined tree species.

Species	Ecology	Microhabitat
Alosterna tabacicolor (DeGeer)	lignicolous	ht
Anaglyptus mysticus Linné	lignicolous	ht
Anaspis rufilabris (Gyllenhal)	lignicolous	ht
Cerylon ferrugineum Stephens	mulm	ht
Cryptarcha undata (Olivier)	succicolous	hkf
Dacne bipustulata (Thunberg)	fungiocolous	hp
Dasytes aeratus Stephens	corticolous	ht
Dasytes plumbeus (Müller)	corticolous	ht
Denticollis linearis (Linné)	mulm	ht
Ennearthron cornutum (Gyllenhal)	fungicolous	ht
Ernoporicus caucasius Lindemann	corticolous	hkf
Ernoporus tiliae Panzer	corticolous	hkf
Glischrochilus quadriguttatus (Fabricius)	corticolous	hkf
Glischrochilus quadripunctatus (Linné)	corticolous	hkf
Hedobia imperalis (Linné)	lignicolous	ht
Hylesinus oleiperda Fabricius	corticolous	hkf
Ischnomera caerulea (Linné)	lignicolous	ht
Leperisinus fraxini (Panzer)	corticolous	hkf
Litargus connexus Geoffroy	corticolous	ht
Mordellistena neuwaldeggiana (Panzer)	lignicolous	ht
Nemosoma elongatum (Linné)	corticolous	hkf
Phloeopora spec	corticolous	ht
Plectophloeus erichsoni (Aubé)	mulm	ht
Rhinosimus planirostris (Fabricius)	corticolous	ht
Rhizophagus bipustulatus Fabricius	corticolous	hkf
Stenostola dubia (Laicharting)	lignicolous	ht

Examined differentially according to individual microhabitats, there are no significant differences at the species level. The number of individuals of single tree species, on the other hand, vary within the guild of wood fungus colonisers (p = 0.002) and rotten wood colonisers (p = 0.022), and within the three main tree species among the colonisers of recently dead and diseased wood (p = 0.003). The largest group (colonisers of already highly decomposed woods; ht according to Bense unpubl.) shows no differences between individual tree species either in numbers of species or individuals.

Generalists

Of the 175 species detected, only four species appeared to be dominant or subdominant, and all others to be recedent to sporadic. Only 10 species were caught on all tree species (referred to in the following as "generalists"; these species are listed in Table 1). In order to investigate whether these generalists are generally evenly distributed or appear on certain tree species more frequently than on others, the two species of the genus *Dasytes* present themselves in particular. On the one hand, *Dasytes* species were found on all tree species, and on the other hand belong to the dominant or subdominant species. Close examination shows that *Dasytes aeratus* Stephens prefers *Quercus robur*, while *Dasytes plumbeus* (Müller) favours *Tilia cordata* (Fig. 3). Both frequent *Acer pseudoplatanus* to an equal extent, but also *Quercus rubra* (the extreme standard error in the case of *Dasytes aeratus* is due to an 'en-masse' occurrence on 25/4/2005 in only one tree), where *Dasytes plumbeus* can be encountered on average in a significantly larger number of individuals.

Fraxinus excelsior is apparently avoided by both. The results lead us to conclude a partial niche differentiation between the two *Dasytes* species.

A preference for certain tree species is revealed for other "generalists" too: *Leperisinus fraxini* (Panzer)[2] (Scolytidae) principally occurs on *Fraxinus* species (Fig. 4), *Anaspis rufilabris* Gyllenhal (Scraptiidae) on *Acer pseudoplatanus*, *Cerylon ferrugineum* Stephens (Cerylonidae) on *Quercus robur* and *Tilia cordata.*

Specialists

In order to detect xylobiontic beetle preferences for certain species of trees a species indicator analysis was carried out. Significant preferences for certain tree species or genera were identified for 22 beetle species (Table 2). Among the specialists for individual tree species, only one species was significant for *Quercus*

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[2] The term "generalist" only applies partially to *Leperisinus fraxini* (see below), but in addition to *Fraxinus* at least 10 other wood species are known to be host trees (Grüne 1979).

robur, but at 44.0%, however, it has a very low preference value. Four species preferred *Tilia cordata*, two *Fraxinus excelsior* and one species, the neophytic *Quercus rubra*. Nine different species showed significant preferences for the non-autochthonous *Acer pseudoplatanus*. A second species indicator analysis at the genus level revealed significant results for five more xylobiontic species (Table 3), among them three more on sycamore. *Ennearthron cornutum* (Gyllenhal) (Cisidae) significantly prefers both of the investigated *Quercus* species and the bark beetle *Leperisinus fraxini*, as in Fig. 4, the *Fraxinus* species. However, at the genus level, all five specialist only have low indicator values at 47–54%.

In addition to the xylobiontic species, which showed significant preferences for certain tree species or tree genera in the species indicator analysis, numerous beetle species, which are categorised in the literature as being tree-specific, were caught; however in our investigations, they attained no significance in the Monte Carlo test due to their very low abundance.

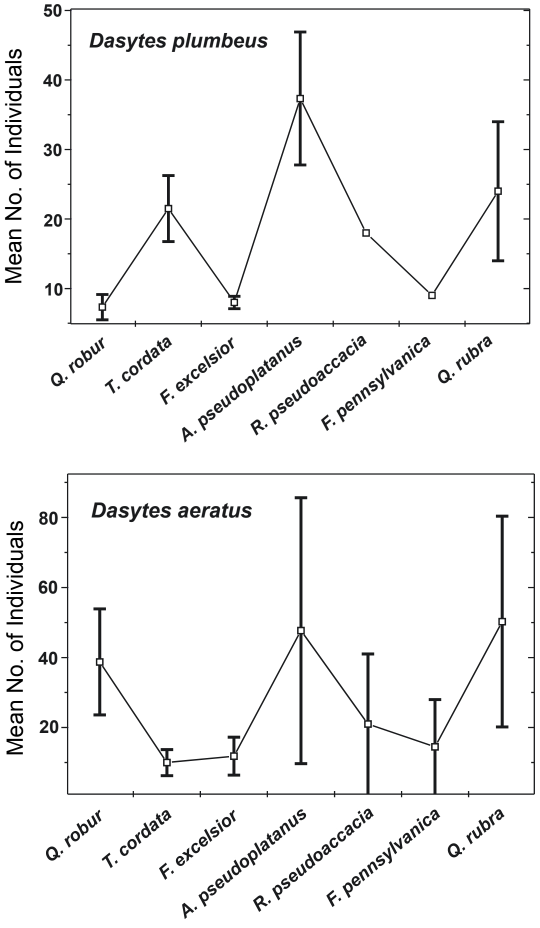

Figure 3 – Average individual numbers of *Dasytes plumbeus* (Müller) and *D. aeratus* Stephens in window traps of all examined tree species with standard errors.

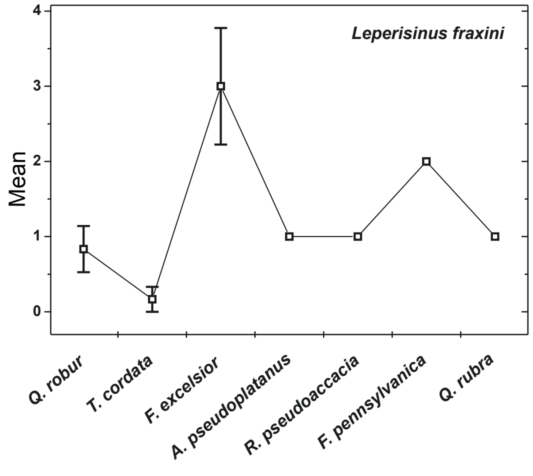

Figure 4 – Average individual numbers of *Leperisinus fraxini* (Panzer) in window traps of all examined tree species with standard error.

Table 4 provides an overview of these species with high tree specificity, but low abundance. Ten of these species are referred to by Köhler (2000) as specialists for *Quercus robur*, five for *Tilia cordata*, one for *Fraxinus excelsior* and two for *Acer pseudoplatanus*.

DISCUSSION

Xylobiontic beetles, as microhabitat specialists, have different claims on their host plant, its location, wood quality and deadwood structure. Because of these specialisations it is possible for individual species to make use of the widest variety of niches within the ecosystem (Köhler 2000). However, the specialisation of individual species simultaneously provides us with the opportunity to examine the ecology of this large insect group occupying the canopy space. Since the area of investigation is a mixture of autochthonous oaks, ash trees and winter lime trees, as well as various planted woods, it was possible to compare the species and individual patterns on native with introduced tree species.

In the literature referring to similar comparisons *Quercus robur* is considered the most species-rich tree (Palm 1959, Bense & Geiss 1998). Therefore, it is not surprising that in the Leipzig floodplain forest, too, most wood-inhabiting beetles inhabiting domestic tree species were found on *Q. robur* (Fig. 1). The other two main tree species, *Tilia cordata* and *Fraxinus excelsior*, show considerably lower species numbers and numbers of individuals. One possible reason for this is the diversity of structure provided by tree species (see e.g. Horchler, this volume). On the one hand, ash trees have fewer microhabitat structures (dead wood, rotten wood, bark structure, fungi etc.) than lime trees or oaks (see also Unterseher Tal, this volume, on the other, they fail by far to reach the age of the old oaks in the stand (more than 250 years; SEELE and PAROLIN *et al.*, this volume).

In addition to microhabitats and deadwood structures, historic and macro-ecological reasons are conceivably responsible for a higher xylobiontic species diversity on *Quercus*. In Europe, in contrast to *Fraxinus* or *Tilia*, *Quercus* is a genus species rich trees with numerous representatives in the Mediterranean region and Pleistocene refuge areas, from where a particularly high number of species may have migrated to central Europe post-glacially and established themselves on *Q. robur*.

Table 2 – Xylobiontic Coleoptera preferring specific tree species based on a species indicator analysis (acc. to DUFRÊNE & LEGENDRE 1997) of window trap samples. Only species with significant values are shown. I-Value: Indicator value, p*: significance.

Species	**I-Value**	**p***	**Tree species**	**Microhabitat**
Alosterna tabacicolor (DeGeer)	53.3	0.044	*Acer pseudoplatanus*	ht
Anaglyptus mysticus Linné	53.3	0.046	*Acer pseudoplatanus*	ht
Anaspis rufilabris (Gyll.)	44.8	0.027	*Acer pseudoplatanus*	ht
Cryptarcha undata (Olivier)	63.8	0.025	*Acer pseudoplatanus*	ht
Denticolis linearis (Linné)	57.1	0.034	*Acer pseudoplatanus*	hfk
Ernoporicus caucasius Lindemann	83.3	0.004	*Tilia cordata*	hfk
Ernoporus tiliae Panzer	96.9	0.000	*Tilia cordata*	hfk
Glischrochilus quadriguttatus (Fabricius)	63.6	0.020	*Acer pseudoplatanus*	ht
Glischrochilus quadripunctatus (Linné)	66.7	0.015	*Acer pseudoplatanus*	ht
Hylesinus oleiperda Fabricius	82.4	0.000	*Fraxinus excelsior*	hkf
Ischnomera caerulea (Linné)	56.7	0.004	*Fraxinus excelsior*	hp
Mordellistena neuwaldeggiana (Panzer)	60.6	0.031	*Acer pseudoplatanus*	ht
Nemosoma elongatum (Linné)	76.9	0.000	*Tilia cordata*	hkf
Plectophloeus erichsoni (Aubé)	66.7	0.033	*Quercus rubra*	ht
Rhinosimus planirostris (Fabricius)	62.5	0.023	*Acer pseudoplatanus*	ht
Stenostola dubia (Laicharting)	66.7	0.024	*Tilia cordata*	hfk
Symbiotes gibberosus (Lucas)	44	0.024	*Quercus robur*	hfk

Table 3 – Xylobiontic Coleoptera preferring specific tree genera based on a species indicator analysis (acc. to DUFRÊNE & LEGENDRE 1997) of window trap samples. Only species with significant values are shown. I-Value: Indicator value, p*: significance.

Species	**I-Value**	**p***	**Tree**	**Microhabitat**
Alosterna tabacicolor (DeGeer)	56.1	0.013	*Acer*	ht
Anaglyptus mysticus Linné	54.9	0.027	*Acer*	ht
Anaspis rufilabris (Gyllenhal)	51.8	0.011	*Acer*	ht
Cryptarcha undata (Ol.)	77.1	0.003	*Acer*	ht
Dasytes plumbeus (Müller)	47.6	0.01	*Acer*	ht
Denticolis linearis (Linné)	52.6	0.02	*Acer*	hkf
Ennearthron cornutum (Gyllenhal)	50	0.014	*Quercus*	ht
Ernoporicus caucasius Lindemann	83.3	0.002	*Tilia*	hkf
Ernoporus tiliae Panzer	97.3	0	*Tilia*	hkf
Glischrochilus quadriguttatus (Fabricius)	77.5	0.002	*Acer*	ht
Glischrochilus quadripunctatus (Linné)	66.7	0.012	*Acer*	ht
Grammoptera ruficornis (Fabricius)	47.5	0.044	*Acer*	hp
Hylesinus oleiperda Fabricius	89.4	0	*Fraxinus*	hkf
Ischnomera caerulea (Linné)	62.5	0.002	*Fraxinus*	hp
Leperisinus fraxini (Panzer)	50	0.029	*Fraxinus*	hp
Mordellistena neuwaldeggiana (Panzer)	62	0.01	*Acer*	ht
Nemosoma elongatum (Linné)	79.8	0	*Tilia*	hkf
Rhinosimus planirostris (Fabricius)	62.2	0.012	*Acer*	ht
Rhizophagus bipustulatus Fabricius	53.8	0.025	*Acer*	hkf
Stenostola dubia (Laicharting)	66.7	0.004	*Tilia*	hkf

Table 4 – Specialised xylobiontic Coleoptera with 80% or more individuals in window traps occurring on a single tree species, but failing significance in the species indicator analysis (species only represented by singletons and doubletons are excluded). The lacking significance of these species may be connected with too low abundances in our examination.

Tree species	> than 90% of individuals	> than 80% of individuals
Quercus robur	*Allecula morio* (Fabricius) *Dendrophilus punctatus* (Herbst) *Dorcatoma dresdensis* Herbst *Conopalpus brevicollis* Kraatz *Euglenes oculatus* (Paykull)	*Ampedus cardinalis* (Schrödte) *Anaspis melanostoma* Costa *Cryptolestes duplicatus* (Waltl.) *Tetratoma desmaresti* Latreille *Haploglossa marginalis* (Gravenhorst)
Tilia cordata	*Ernoporus tiliae* Panzer *Anobium fulvicorne* Sturm *Exocentrus lusitanus* (Linné) *Stenostola dubia* (Laicharting) *Ernoporicus caucasius* Lindemann	
Faxinus excelsior	*Agrilus olivicolor* Kiesewetter	
Acer pseudoplatanus	*Glischrochilus quadripunctatus* (Linné)	*Mordellistena neuwaldeggiana*

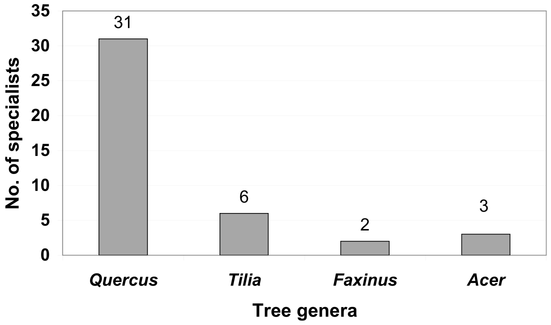

Figure 5 – Xylobiontic Coleoptera specialized on the tree genera *Quercus, Tilia*, and *Fraxinus* acc. to Köhler (2000).

The comparison of species numbers alone does not permit conclusions concerning the species composition of xylobiontic beetles on individual tree species. It is known from the literature that numerous species have specialised in one wood type or tree species (Fig. 5; Köhler 2000). In contradiction to these findings, two species were separated by the species indicator analysis of our data set, which prefer the common ash tree, or four species, respectively, which preferred the winter lime tree; but only one species, which significantly prefers the common oak (Table 2). This surprising result clearly contradicts both values expected due to indications from the literature and the results in Heteroptera from the same traps (Arndt *et al.*, this volume). In addition to the species, which significantly prefer one tree species, a number of xylobiontic species known to be oak specialists were detected by us only as individual specimens or in extremely low abundances on *Q. robur* (Table 4).

The comprehensive trap set, covering seven tree species, brought not only surprising results concerning specialised xylobiontic species, but also concerning generalists, which are found on all trees. The comparison of several tree species distinctively indicates that generalists prefer, or respectively avoid, individual tree species. Most impressive is the example of the dominant species pair *Dasytes plumbeus* and *D. aeratus*. These *Dasytes* species under close examination, largely avoid each other in terms of territory (see Fig. 3) and tend to develop tree preferences, even though both are supposed to be generalists.

Several times, neophytic species have been planted in the structure-rich Leipzig flooplain forest by forestry measures (Seele and Parolin *et al.*, this volume). These trees, introduced to the existing system by man, differ from native species in respect of their xylobiontic fauna. Thus, neophytes hosts fewer species than their native relatives, but they do exhibit a comparably high number of individuals (Fig. 1). One possible reason for this is the absence of specialists (Moren & Southwood 1982). Thus, for example, no specialists were brought to Europe along with the red oak *Quercus rubra* (Gossner 2002). Potential reasons for the lack of specialists are the small dispersion radii and the strict habitat association of xylobiontic species. Therefore, neophytes are primarily colonised by generalists, as demonstrated impressively by the two *Dasytes* species discovered on *Quercus rubra* (Fig. 3). Further, neophytes are colonised by a few specialists from native tree species, which can hence be described as genus-specific. One example is *Leperisinus fraxini* (Fig. 4 and Table 3) on *Fraxinus excelsior* and *F. pennsylvanica*. The cluster representation of the Euclidean Index (Fig. 2; others, such as the Renkonen Index, show the same results) of individual tree species underlines that the neophytic trees and their native relatives host very similar species and that the tree species introduced by man can be regarded as an impoverished variant of autochthonous trees regarding their xylobiontic fauna.

In the crane plot investigation area, a special position is assumed by the rapidly spreading sycamore (*Acer pseudoplatanus*). This tree, not native to central Germany but introduced by the forestry industry, currently already makes up 20% of canopy coverage with its low but wide treetops. The species structure of its xylobiontic fauna cannot be assigned precisely to either of the two groups (native tree species or neophytes) and appears to assume an intermediate position between the two tree groups.

In the present examination, an astonishingly high number of xylobiontic species known as generalists (Köhler 2000) predominantly colonised *Acer pseudoplatanus*. In the species indicator analysis, nine beetle species achieved significance on this tree species; on calculation of specialists at the tree genus level, 12 species were even identified as significant for *Acer*. Indicator values for all species were between 45 and 67%. They are, therefore, comparatively low (see Table 2 and 3) and confirm that the beetle species concerned are probably generalists, which, in the area of investigation, have developed a preference for *Acer*. Yet the sycamore, strictly speaking a neophytic tree species (Kowarik 2003), hosts by far the most tree-specific species among the xylobiontic beetles in our examination, in addition to its in any case high number of species and individuals (Fig. 1). This result is extraordinarily surprising, thus also contradicting (see above) the current opinion regarding particularly high colonisation umbers on common oak. So far, no satisfactory explanation for this result can be presented; the phenomenon should form the subject of further examinations, in a larger geographical context if possible, e.g. the whole of Europe.

Overall, our investigations confirm the high nature conservational significance of the Burgaue nature reserve. We were able to detect a high number of xylobiontic beetle species, of which many are on the Endangered Lists of Saxony (Klausnitzer 1994; 1995) and Germany (Geiser 1998). Further, the results confirm that investigations of xylobiontic species are indispensable for nature conservational surveys in canopy space.

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3.6 Ground beetles (Coleoptera: Carabidae) in the forest canopy: species composition, seasonality, and year-to-year fluctuation

Erik Arndt[1] & Stephan Hielscher

We present a two-year examination of ground beetles (Carabidae) in the canopy of a Central European flood plain forest using window traps and branch-eclectors. The carabid fauna was analysed in 25 trees of *Quercus robur*, *Tilia cordata*, *Fraxinus excelsior*, and some neophytic trees. All traps were fixed at two levels: window traps at heights of 26.6 m and 21.8 m average, branch-eclectors at 26.6 m and 19.8 m average respectively. A total number of 27 species with 242 specimens were recorded in window traps and four species with 19 specimens in branch-eclectors. The most common species in both trap types was *Dromius quadrimaculatus*, a carabid with arboricolous life history. The maximum activity of *Dromius quadrimaculatus* was recorded at the end of July/beginning of August which probably corresponds with appearance of adults of the new generation. The species set of the canopy can be linked to five ecological groups: (1) arboricolous species; (2) species with ground-canopy-interaction; (3) migrating forest species; (4) migrating urban species; (5) aerial plankton. Migrating urban species were recorded five times more often than migrating forest species in the canopy.

INTRODUCTION

Ground beetles (Carabidae) are one of the most important invertebrate indicator groups. They live in all terrestrial habitat types in large numbers. Several species are known to occur in Central European flood plain forests (Zulka 1994a, b; Spang 1996; Wohlgemuth-von Reiche & Grube 1999; Rink & Hettrich 2001). Ground beetles indicate ecological changes in these forests, e.g. in water regime, much earlier than plant species do (Arndt, unpubl., but see Arndt & Pellmann 1996: p. 51). Hygrophilous forest species disappear and ruderal species occur when ecological conditions in flood plain forests change.

However, as in many other taxa the carabid fauna of temperate flood plain forests has only been examined at the ground. It is unknown how many arboricolous species live there, if species from the soil surface are also climbing in the trees, if there are any interactions between carabids and other carnivorous invertebrates, or if migrating carabids occur in the canopy. The possibilities of the crane could bring a lot of new details and solve many open questions of this species rich indicator group.

MATERIALS AND METHODS

The data presented here are derived from a two year examination (2002–2003). The carabid fauna of the tree crowns was examined using window traps and branch eclectors. For details see Arndt & Unterseher, this volume.

The sample design made possible a statistical analysis of the main trees but also showed trends of species composition in neophytic trees which are a result of forest use. Relations between carabid species and trees or structural parameters were calculated using Pearson- or a Kendall's-Tau-b-correlation respectively.

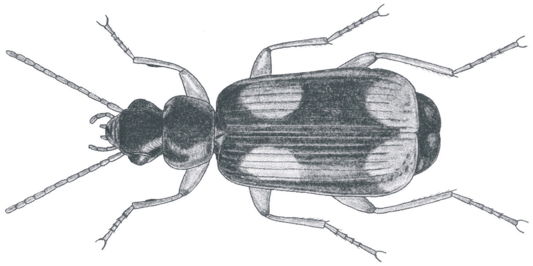

Figure 1 – *Dromius quadrimaculatus* (Linné), the most common species in the forest canopy (redrawn from Lindroth 1986).

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[1] corresponding author

Table 1 – Ground beetles (Carabidae) recorded in window traps (WT) and branch-eclectors (BE) in the study period 2002/03 of the LAK project. The species are listed according to their frequency.

Species	WT 2002	WT 2003	BE 2002	BE 2003
Dromius quadrimaculatus (Linné)	85	85	6	6
Trechus quadristriatus (Schrank)	18	6	1	0
Limodromus assimilis (Paykull)	6	1	5	0
Dromius agilis (Fabricius)	1	3	0	1
Amara aenea (De Geer)	5	0	0	0
Paratachys bistriatus (Duftschmid)	2	0	0	0
Anchomenus dorsalis (Pontoppidan)	2	0	0	0
Ophonus rufibarbis (Fabricius)	2	3	0	0
Loricera pilicornis (Fabricius)	2	0	0	0
Calodromius spilotus (Illiger)	2	0	0	0
Amara similata (Gyllenhal)	2	0	0	0
Harpalus tardus (Panzer)	1	1	0	0
Syntomus foveatus (Geoffroy)	1	0	0	0
Acupalpus parvulus (Sturm)	1	0	0	0
Acupalpus flavicollis (Sturm)	1	0	0	0
Amara aulica (Panzer)	1	0	0	0
Amara consularis Stephens	1	0	0	0
Badister bullatus (Schrank)	1	0	0	0
Bembidion properans (Stephens)	1	0	0	0
Bradycellus verbascii (Duftschmid)	1	0	0	0
Calathus mollis (Marsham)	1	0	0	0
Demetrias monostigma (Samouelle)	1	0	0	0
Microlestes minutulus (Goeze)	1	0	0	0
Amara communis (Panzer)	0	1	0	0
Anisodactylus binotatus (Fabricius)	0	1	0	0
Nothiophilus biguttatus (Fabricius)	0	1	0	0
Pterostichus oblongopunctatus (Fabricius)	0	1	0	0
total	139	103	12	7

RESULTS

Species composition

A total number of 27 species with 242 specimens were recorded in window traps and four species with 19 specimens in branch-eclectors (Table 1). By far the most common species in both trap types was *Dromius quadrimaculatus* (Linné) (Fig. 1) representing 69.7% of the total catch. This species was not recorded at the ground indicating an arboricolous way of live. Two further arboricolous species (*Dromius agilis* (Fabricius) and *Calodromius spilotus* (Illiger)) occurred only in scattered specimens in the traps and seem to be much rarer than *D. quadrimaculatus*. The great majority of the species were recorded in 1 or 2 specimens only. Therefore, only data of *D. quadrimaculatus* are available for statistical analyses.

Life history of *Dromius quadrimaculatus*

The only abundant carabid species in the canopy is *Dromius quadrimaculatus* (182 recorded specimens). It is one of the arboricolous species with an incompletely known life history. Larvae and adults are only found in the canopy, and derived from morphological characters and life history of closely related taxa, it is a carnivorous species.

The used sample design allowed us to test correlations between *D. quadrimaculatus* and the examined tree species as well as structural parameters (height of trap, dead wood portion, leaf coverage). The activity of this beetle in various tree species differed significantly (ANOVA of window traps, both years SS = 32.68, MS = 10.89, F = 32.878, p = 0.0466*, regarding only 2003 the differences are highly significant). *Fraxinus excelsior* was slightly preferred by *D. quadrimaculatus.* No one of the structural parameters correlated with the activity of *D. quadrimaculatus* significantly.

The seasonal activity of this ground beetle was very similar in 2002 and 2003 (Fig. 2). In both years, the activity of *D. quadrimaculatus* was highest at the end of July/beginning of August. About 40% of specimens were caught at this time (Fig. 2). Only one larva was recorded (first instar, first trap period April-middle of May). The early period of this larval record indicates however a completion of larval development in summer and the maximum activity of adults therefore most probably corresponds with the appearance of the new adult generation. The comparable large size of this first instar larva furthermore indicates a shortened larval development of *D. quadrimaculatus*. Nearly all carabids have three larval instars. Only exceptionally do species have two larval instars combined with a very large first instar larva.

It should be noted that these data are in contrast to data and presumptions published earlier on *D. quadrimaculatus* (Burmeister 1939, Turin 2000).

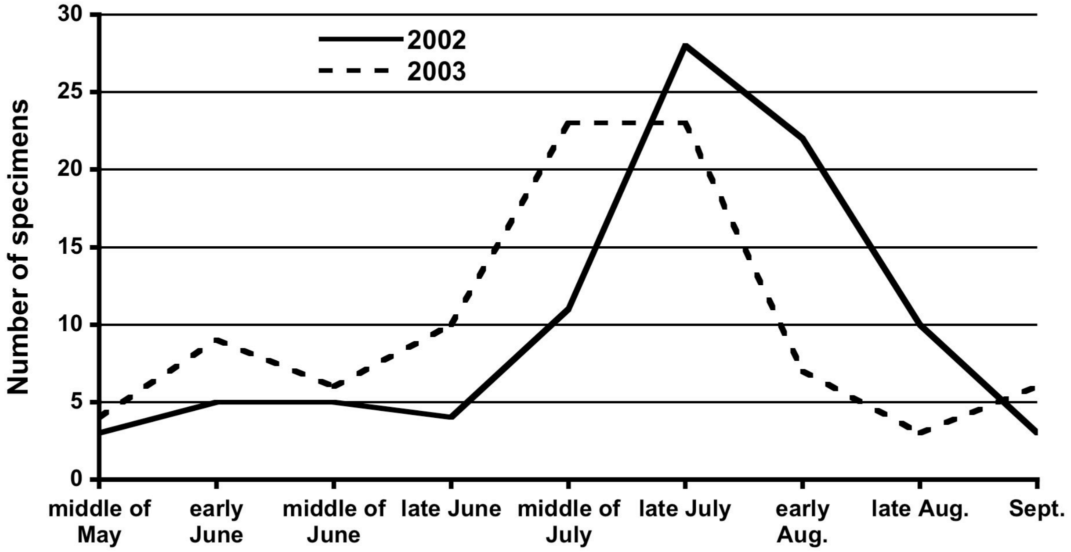

Figure 2 – Seasonal activity of *Dromius quadrimaculatus* in the forest canopy.

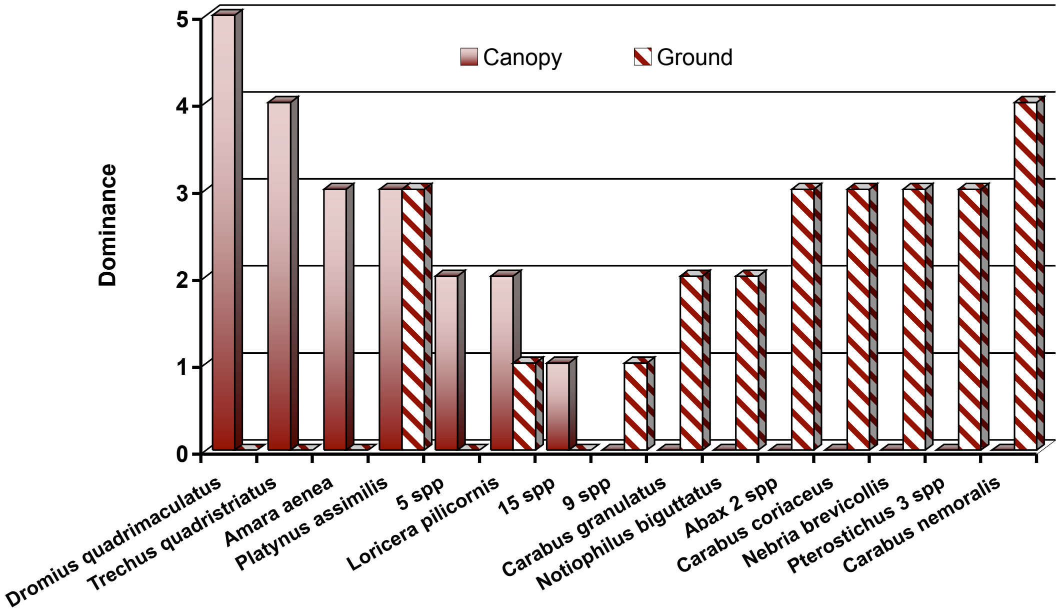

Figure 3 – Dominance and distribution of ground beetles in window traps + branch-eclectors (Canopy) and pitfall traps (Ground) (after Arndt 2005). The figure shows only data of 2002. Species are listed in dominance classes according to Engelmann (1978). 1: $< 1.0\%$. 2: 1.0–3.19%. 3: 3.2–9.99%. 4: 10.0–31.99%. 5: $\geq 32.0\%$. The dominance classes are calculated separately for ground and canopy.

DISCUSSION

Ecological classification of the ground beetles recorded in the canopy

The total number of 27 carabid species in the canopy was much higher than that on the ground (Fig. 3), even if we take into consideration the shorter sample period of the pitfall traps at the ground (Arndt 2005). On the other side the low number of species and specimens in branch-eclectors shows that many species may fly through the forest but only few species are active in the canopy. A detailed analysis of the species list brings to light many ruderal ground beetles untypical of a flood plain forest and shows the close connection to urban habitats which are within 500 m from the plot.

Based on faunistic (Arndt & Pellmann 1997, Arndt & Richter 1996, Winkler, unpubl. master thesis) and ecological data (Turin 2000) we classify five different ecological groups of the carabid species recorded in window traps and branch-eclectors:

Arboricolous species

Adults and larvae of this ground beetle group live in the canopy of trees or under bark. The majority of carabid species of tropical rain forests belong to this ecological type. In Central Europe the group is only represented by *Tachyta nana* (Gyllenhal), species of *Dromius* (s.l.), and if we interpret arboricolous life history in wider sense, by some species of *Lebia* (Latreille). *D. quadrimaculatus*, *D. agilis*, and *C. spilotus* belong to this groups at the examined crane site.

Species with ground-canopy-interaction

A small group of forest species is known to live at the ground, but climbs frequently on trees. Well-known examples are *Calosoma sycophanta* (Linné) and *Calosoma inquisitor* (Linné) hunting caterpillars in the tree crown (Turin 2000). Some *Carabus* species and forest inhabiting *Calathus* species also climb (Evans 1975, Hockmann *et al.* 1989, Machado pers. comm.).

In natural flood plain forests the ability to climb has not only ecological importance for food of larvae and adults which are not able to fly. It is also important as escape behaviour during spring or summer floodings. This is a well known aspect in tropical forests (Adis 1992, Adis & Junk 2002), but not adequately examined in Europe. Long-term examinations in a German flood plain using stem-eclectors showed that numerous carabid species and even larvae are able to escape to the canopy during high water (Perner, Arndt, unpubl. data).

The area of the LAK crane had not been flooded for decades; the recorded ground-canopy-movements in our study were correspondingly low. *Limodromus assimilis* (Paykull) is the only species in our samples which should be related to this group. It was recorded in pitfall traps, stem- and branch-eclectors as well as in window traps. *L. assimilis* hibernates under bark of dead wood, but our results show that the species is also active in the canopy to feed or mate.

Migrating forest species

Several carabid species living at the forest ground are macropterous and able to fly to other forest sites but were not observed climbing as *L. assimilis*. *Pterostichus oblongopunctatus* (Fabricius) is one example. The eurytopic *Loricera pilicornis* (Fabricius) in the widest sense also belongs to this group. It should be noted that only 1.1% of the total catch falls in this group. The conclusion is that most forest species are unable to fly or do not regularly fly.

Migrating urban species

The study site is near to the forest edge and the urban areas border the site on the south and north-east within 500 metres. Several recorded species live in open habitats or in ruderal sites. They might fly through the forest migrating to new habitats. *Amara* spp, *Harpalus tardus* (Panzer), *Calathus mollis* (Marsham), *Syntomus foveatus* (Geoffroy), or *Microlestes minutulus* (Goeze) are examples. This group with 9.2% exceeds by far the former group which is one of the most surprising results of the study. Only 4 specimens of this group (less than 0.2% of the pitfall total catch) were recorded at the ground. It may explain why carabids respond so fast to environmental changes: a large number of ruderal species is migrating even in closed forests and is able to settle if "suitable" conditions appear there.

Aerial plankton

Species of this group are of very small size (1–3 mm) and cannot be linked to urban habitats. These small species drift through the canopy. *Paratachys bistriatus* (Duftschmid), *Acupalpus* spp, and even *Trechus quadristriatus* (Schrank) represent this group. All of these species live in ripicolous habitats or on agricultural fields in the environment of the flood plain forest.

ACKNOWLEDGEMENTS

We thank W. Morawetz, P. Horchler, D. Bernhard, and M. Schlegel (University of Leipzig) for co-ordination of the crane project and financial support, as well as J. Adis (Plön) for helpful suggestions and discussions during preparation of the project. U. Simon (Freising) provided the branch eclectors, M. Verhaagh (Karlsruhe) the window traps, and J. Adis the stem eclectors. The project would not be possible without assistance of several students who managed the sampling of material. We are especially indebted to C. Schmidt, and C. Jesche. Finally, we thank M.L. Luff (Newcastle) for proof-reading and linguistic corrections.

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3.7 Diversity and spatio-temporal activity pattern of nocturnal macro-Lepidoptera in a mixed deciduous forest near Leipzig

Uta Fröhlich, Ronald Schiller[1] & Peter J. Horchler

We carried out a study on the macro Lepidopteran fauna in the research plot of the Leipzig Canopy Crane Project. This plot is located in a near-natural mixed deciduous broadleaf forest. The principal objective was to check for the existence of a vertical stratification of the moth's flight height in the forest stand. The underlying assumption was that the animals' flight activity along the vertical plane is influenced by habitat structure or climatic differences within the forest stand. Differences in species composition and total abundance should indicate such stratification. For the study we used the crane gondola to reach different positions within the forest space. From early June to end of September 2003 we used an 8-watt black-light lamp to sample moths at 5 different positions of the crane plot at heights of 2, 10, 20, 25 and 30 m. We first analysed the ecology of the moth community, i.e. we checked the known habitat or feeding preferences of the species collected. Then several diversity indices were calculated (e.g. Fisher's Alpha and the Morisita-Horn similarity index) to determine alpha- and beta-diversity. Using a Principal Coordinates Analysis, we assessed differences in species composition over all samples. To assess the influence of the two environmental factors 'seasonality' and 'flight height' on species composition, we performed a partial Canonical Correspondence Analysis. This analysis allowed partitioning and determining the amount of variation in our data set explained by the factors mentioned above.

Within the study period 1 072 individuals of at least 101 species in 10 families were identified. As general trend fewer individuals and species were found in the canopy as compared to the understorey but variation was high. Within three seasonal groups (early summer, high summer, autumn) a vertical stratification could be detected but marked and significant differences in species composition were only found in early summer. Some species showed preferences to the canopy, however, most species preferred the lower stratum. Diversity differed during the study period with higher diversities in early and high summer. The factor 'seasonality' showed the largest influence on species composition, while 'flight height' had a smaller effect. Partitioning the explainable variation in our data set, the factor 'flight height' explained only 16% while 'seasonality' explained 24%. 58% of the overall variation remained unexplained by the factors included in this study. The relatively small proportion of true forest species (ca. 40%) suggests that the species composition was certainly affected by the location of the study site near the edge of the forest.

INTRODUCTION

There has been growing interest in researching the forest canopy fauna since Erwin's investigations (Erwin 1982) on arthropods in tropical forests. Forest canopies have been identified as important habitats, particularly for arthropods, by numerous investigations in tropical rainforests (e.g. Sutton *et al.* 1983; Basset *et al.* 1992; Kato *et al.* 1995; Beccaloni 1997; Intachat & Holloway 2000; Schulze *et al.* 2001). A similar role of the canopy as special and species-rich habitat can also be suspected for temperate forests. Yet, temperate canopies, with some exceptions (e.g. Simon 1995; Thomas 1996, Le Corff & Marquis 1999; Floren & Schmidl 1999, Tanabe 2002), have remained largely unexplored.

Especially in old-growth mixed forests, the variety of spatial structures within the three-dimensional space creates a multitude of habitats and niching opportunities, which are exploited by butterflies to varying degrees. Among those insects active at night, Lepidoptera are one of the orders, which have received most attention so far. Due to the way their pre-imaginal stages and imagines live, they are often closely associated with one habitat, which is why they are suitable for ecological investigations and the evaluation of a particular area (Kolligs 2000).

As part of the Leipzig Canopy Crane Project it was possible to reach various areas of the forest canopy

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[1] corresponding author

by means of the crane gondola, which was used to carry out light catches in the crane plot in summer 2003. In so doing, central questions of the study were **(1)** Is there a vertical zoning of nocturnal macro-Lepidoptera within the forest? **(2)** Are there differences in diversity between understorey and individual height strata within the forest canopy? **(3)** Which factors influence species composition, and is flight height one of them?

MATERIALS AND METHODS

Choice of location and time

Light catches were carried out in the crane plot for a total of 19 nights over the period from 4th of June to 22nd of September 2003 (Table 1).

Four locations were chosen in the study area, which were suitable for bringing the crane gondola through the canopy down to the ground. Three of the capture locations were in the western area of the plots, one location was chosen in the crane trail. The results of a fifth location, also in the crane trail, were only entered into the species list, since there, light catches only took place on the ground by using a 125 W mixed light lamp.

Light capture

Light catches were carried out manually from the crane gondola at 10, 20, 25, and 30 m as well as on the ground at a height of ca. two metres. An 8 W black-light lamp (Fiebig Lehrmittel, Berlin) was used as light source. It was positioned in the middle of the gondola and operated with a 12 V dry battery. A white cloth suspended behind it was used to reinforce the light intensity and as 'landing' surface. Gondola roof and floor, each ca. 1.50 x 0.70 m, shaded the light from above and below. The relatively weak black-light lamp was chosen to ensure that only moths from the immediate surroundings were attracted. However, various studies, for example by Butler & Kondo (1991) and Muirhead-Thomson (1991), have demonstrated by the example of individual species that even when strong light sources are used (125 and 250 W) only moths which previously fell short of a radius of 10–20 m were registered, meaning that attraction from a distance should be ruled out with feeble illumination.

Furthermore, the attraction distance according to Sotthibandhu & Baker (1979) is influenced by the spatial position of the light source. Approaching distances can increase considerably when the position is changed vertically. This behaviour can be attributed to moths' natural orientation towards moonlight. The receptors used for orientation and to perceive light are located in the upper section of the complex eyes (Sotthibandhu & Baker 1979), which is why only light sources above the individual are approached. The more the position of the light resembles that of the moon, the sooner the light is perceived.

Table 1 – Capture data from the 19 light catches in summer and autumn 2003 (Source for sunset: `http://www.stadtklima.de/webklima/script/sonne.exe`). Abbreviations: gp: small gap; qu: oak gap; tot: deadwood gap; tr1: trail; tr2: trail 2. CET: Central European Time.

Date	Location	Sunset (CET)	Starting time of capture (CET)	Remarks
4th June*	tr1	21:16	22:00	125 W mixed light lamp
16th June	tr2	21:25	22:15	–
24th June	tr2	21:31	22:30	–
26th June*	tr1	21:31	22:15	–
6th July	qu	20:28	22:15	–
14th July	gp	21:22	22:00	Full moon
31st July	qu	21:01	22:00	–
3rd Aug.	qu	20:56	21:45	–
4th Aug.	gp	20:54	22:00	–
13th Aug.	gp	20:38	21:30	Full moon
19th Aug.	gp	20:26	21:15	–
25th Aug.*	tr1	20:14	21:00	–
26th Aug.	tot	20:11	21:00	–
3rd Sept.	tot	19:54	21:15	Rain
7th Sept.	qu	19:45	20:30	–
16th Sept.	gp	19:24	20:45	–
21st Sept.	tot	19:13	21:30	–
22nd Sept.	qu	19:11	20:15	–

*: Results only used to compile species list (Appendix Table 1)

Therefore it can be expected that a change in the flight height of single individuals due to the artificial light is likely to be from below to above. The black-light lamp was shaded in order to minimise this effect. Since capture was done manually, it was impossible to illuminate at all heights at the same time, which is why the duration of collection per light catch and height was reduced to 15 minutes in order to move to the next height on completion.

Light catches were performed four times alternately at all recorded heights; however, the short duration of capture per height precludes a complete record of Lepidopteran fauna. The first capture was commenced approximately one hour after sunset at a height of 30 m. The precise locations and capture data can be viewed in Table 1.

Based on KARSHOLT & RAZOWSKI (1996), the nomenclature follows the "Verzeichnis der Schmetterlinge Deutschlands" [directory of Germany's butterflies] by GAEDICKE & HEINICKE (1999).

Data analysis

The recording of species and individuals is very strongly dependent on the method applied (e.g. light source, collection method) as well as on a number of uncontrollable factors (weather, moonlight). Absolute abundance estimates are not possible due to the method's selectivity, but these are a basic requirement for statements concerning the diversity of species in an area. Species communities are often characterised by the dominance of fewer species with many individuals and by a large number of species, which are less abundant (KREBS 1989).

In order to compare various samples in a meaningful way, a series of indices and methods has been developed (e.g. KREBS 1989; MAGURRAN 1988), including Fisher's Alpha diversity index, used in this study, which is applied to estimate the diversity of moth communities in the canopy. This index works on the assumption that species-abundance ratios follow a logarithmic series (log series). It is influenced principally by the number of species, but is largely independent of sample size (MAGURRAN 1988). In order to identify similarities between the moth catches in the individual height strata (beta diversity), the Morisita-Horn index is used. It is especially suited for samples with many infrequent and little abundant species, which is common in many arthropod records. It is independent of sample size to a relatively high extent (MAGURRAN 1988).

In addition to the use of the Morisita-Horn index, data were analysed by means of a Principal Coordinates Analysis (GOWER 1966) using a Bray-Curtis dissimilarity matrix of the log-abundances of captured species. This method of so called indirect gradient analysis enables the complete data set (samples and species) to be arranged in such a way that the main gradients affecting species composition become visible. Presenting the results graphically enables the (suspected) gradients to be interpreted (e.g. MCCUNE & GRACE 2002).

A direct analysis of the data was performed by means of a partial Canonical Correspondence Analysis (pCCA, BORCARD *et al.* 1992), in order determine the extent to which the influential factors seasonality and flight height can explain the overall variation in the data record. The significance of the factors was estimated using a Monte Carlo permutation test (e.g. MANLY 1997) applying 499 permutations. For univariate analyses, the Mann-Whitney U test and the correlation test according to Pearson were applied. Assessment of the hypotheses being tested is based on a significance level of $p \leq 0.05$. Calculation of the Morisita-Horn index was performed using EstimateS 6.0b1 (COLWELL 1997/2000). Fisher's Alpha diversity index was determined using an add-in for Microsoft Excel 2000 kindly provided by H. ter Steege (freeware available from the Internet[2]). The CANOCO program (TER BRAAK & ŠMILAUER 2002) was used for the multivariate analyses, and graphical depictions of the Principal Coordinates Analyses were done using CanoDraw (TER BRAAK & ŠMILAUER 2002). Statistical tests were carried out using SPSS 11.0 for Windows.

RESULTS

Capture results and abundance structure

During the course of the five-month field study, 953 moths were recorded and attributed to 81 species from ten families. Table 2 shows the division of species and individuals into families. According to this table, 89% of the species and 96% of the individuals belong to the families Noctuidae and Geometridae, while, at 73%, the Noctuidae show the highest proportion of individuals. When the non-standardised light catches are included, a total of 1072 individuals from 101 were recorded. The list of all species detected can be found in Appendix Table 1.

Ecology of Lepidoptera

Stimulated by the classification of insect species ecology used as part of the "Entomofauna Saxonica" project (KLAUSNITZER & REINHARDT 1994), we aimed to provide a similar overview of the composition of Lepidoptera found in this study. The method groups together individual species with sim-

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[2] `http://www.bio.uu.nl/~herba/Guyana/Amazon_plot_network/Index.htm`

ilar ecological preferences. The classification into ecotypes results from observed habitat preferences, edaphic conditions and the plants eaten by the caterpillars (KLAUSNITZER & REINHARDT 1994; 1994; SCHOTTSTÄDT *et al.* 1996; GRAUL & SCHILLER 1999). The ecological analysis of individual species, together with a classification key, is provided in Appendix Table 1.

Table 2 – Family membership , number of species and of individuals determined in this study.

Family	Species	Individuals
Noctuidae	39	690
Geometridae	32	224
Lymantridae	2	22
Drepanidae	2	5
Nolidae	1	3
Notodontidae	1	3
Pantheidae	1	3
Arctiidae	1	1
Cossidae	1	1
Limacodidae	1	1
Total	81	953

Although, according to this classification, over 40% of the species detected preferred forests and forest edges as habitat, at the individual level ecotype composition was clearly dominated by ubiquists and species which normally appear in tree-lined open areas. Typical forest residents were recorded in most cases with very few individuals. These include all species from families, which were recorded less frequently (Table 2). Members of the Noctuidae family show the weakest association to the forest habitat, with almost all species being open-land residents and the largest proportion of ubiquists. Due to the dominance of deltoid moths at all capture heights and the small proportion of genuine deciduous forest residents, no specific pattern in the distribution of eco-types among individual tree strata can be recognised.

Seasonality

The alpha-diversity of individual catches differed during the course of the analysis period. Besides, species composition from the first records differed by up to 100% from the final records.

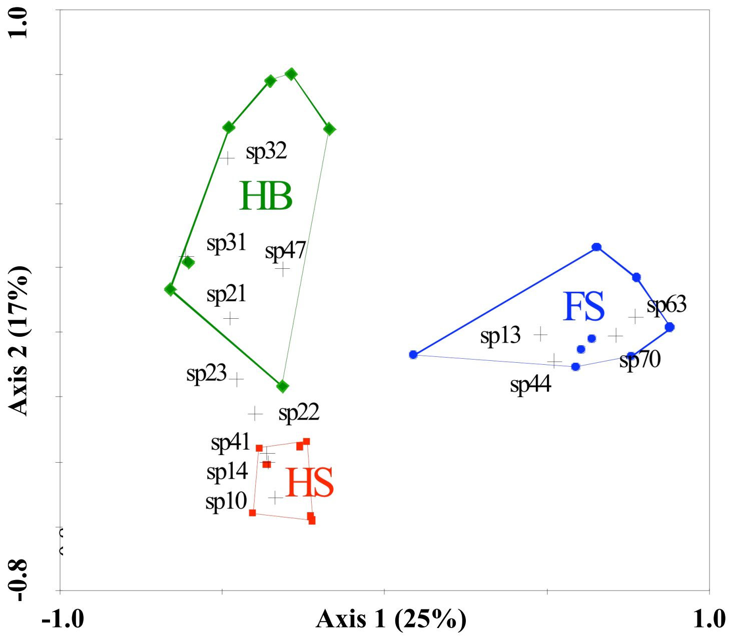

Figure 1 – Biplot of the result of a Principal Coordinates Analysis (Bray-Curtis distance of log abundances). In brackets: percentage of variation explained by the respective ordination axes. Circles, squares and rhombi symbolise individual catches (samples) associated with the respective seasonal group (envelopes). Crosses symbolise those species most closely associated to the seasonal groups. Species scores were calculated as weighted averages. **FS**: early summer: *Agrotis exclamationis* (13), *Cosmia trapezina* (44), *Hydrelia flammeolaria* (63), *Biston betularius* (70). **HS**: high summer: *Agrotis ipsilon* (10), *Xestia c-nigrum* (14), *Hoplondrina ambigua* (41). **HB**: autumn: *Noctua pronuba* (21), *Noctua fimbriata* (22), *Noctua janthina* (23), *Eupsilia transversa* (31), *Agrochola circellaris* (32) and *Hypena proboscidalis* (47).

Seasonal effects, e.g. daily temperature distributions, are likely to affect diversity and make fauna comparisons difficult. For this reason, we attempted to summarise the daily records in seasonal groups with a number of characteristic species. By means of a Principal Coordinates Analysis, the individual redords could be divided into three more or less separated groups due to differences in species composition (Fig. 1). The early summer record (FS) is clearly separated on the x-axis from the high summer (HS) and autumn catches (HB). HS and HB can be separated from each other less clearly, since they have more species in common. Note that only the most indicative species for the seasonal groups are shown.

Further, alpha and beta diversity is always determined by dividing samples into these seasonal groups, in order to minimise seasonal effects. However, this division does not preclude daily weather differences within the seasonal groups, meaning that temperature differences, in particular, influence species composition (Table 4).

Vertical stratification of the Lepidoptera community

Flight height preferences of the most common species

Noctuidae dominate at all flight heights, regarding both species richness and abundance. The high frequency of deltoid moths in the understorey is caused by the two most common species, *Xestia c-nigrum* and *Agrochola circellaris*. The latter species shows a very clear preference for the lower forest stratum (Table 3). Although *Xestia c-nigrum* appears very frequently at all heights, it cannot be assumed from this that a local population was involved on all days since this is a migrant species. Together with these two dominant species, the majority of the species showed a more or less strong association with the lower forest strata. Only few species are represented in the upper canopy with greater abundances. The three Geometrid species *Hydrelia flammeolaria*, *Chloroclystis v-ata*, and *Biston betularius*, in particular, were caught at greater heights. The Noctuidae were less abundant in the upper stratum than in the understorey, while some Geometridae, in contrast, appeared more frequently. The species of the families Notodontidae and Nolidae were found exclusively, although only with a few individuals, in the upper canopy. The abundances of all species per capture height is indicated in Appendix Table 1.

Distribution of species and individuals in the forest canopy

In general there was a clear decrease in the number of captured species and individuals as height increased (Table 4). However, on some very warm days in early and high summer (24^{th} June, 3^{rd} and 4^{th} August), more species were recorded in the upper canopy than in the lower strata. But although on 13^{th} August high temperatures were also recorded at a height of 30 m, no moths were registered on this day above a height of 10 m in the small gap. This light catch took place two weeks after extreme heat and drought, and in addition it had been full moon two days before. The influence of full moon on 14^{th} July seemed to have an effect because only relatively few moths were registered despite a fairly warm average night temperature of 24.2 °C. In general, high species numbers correlated with high numbers of individuals. As height increased, this ratio mostly dwindled, and only on very warm days higher abundances could be recorded in the upper canopy.

Diversity of Lepidoptera in the forest canopy

Alpha diversity

Overall, a general tendency towards a reduction in diversity as height increased was evident throughout the recording period (Fig. 2, Table 4). The highest values of Fisher's alpha were detected on 16^{th} June (53.6) in the crane trail close to the ground. The recording of 25^{th} June at a capture height of 20 m proved also diverse (33.8). At the same time, diversity on the ground was considerably lower (15.17). However, the differences should not be regarded as significant. The two recordings of the 3^{rd} and the 4^{th} August showed higher diversity values in the upper canopy, but these also did not differ significantly from those in the understorey since, particularly on the 3^{rd} August, the samples turned out to be very low.

Fauna similarity (beta-diversity)

Understorey and upper canopy show clear differences in species composition for all three seasonal activity phases (Fig. 2). Adjacent capture sites correlated most closely. As height difference increases, similarity of species compositions drops significantly in early summer ($p < 0.001$). In high summer there were also clear differences between understorey and 30 m capture height, but the species and individuals between 10 m and 30 m were distributed rather homogeneously. Hence, no significant correlation between species composition and flight height was found ($p = 0.082$). Ratios in autumn were similar to the pattern in high summer; here, too, the biggest differences were found between the understorey and the upper strata and overall were significant ($p = 0.015$). However, due to the lower numbers recorded, this trend cannot be compared with the other records straight away. Due to the cooler weather in autumn, we suspect, the majority of species and individuals can be found in the understorey.

Table 3 – Numbers of individuals of the most frequently recorded species at the five capture heights, indicating family membership. Species that show some preference for the upper forest strata are indicated in bold.

Capture height [m]		**2**	**10**	**20**	**25**	**30**
Species	**Family**	**Individuals**				
Agrochola circellaris	Noctuidae	141	32	9	1	–
*Xestia c-nigrum**	Noctuidae	92	81	20	39	3
*Noctua pronuba**	Noctuidae	22	7	2	4	–
Timandra griseata	Geometridae	13	6	–	–	–
Xestia xanthographa	Noctuidae	13	–	–	–	–
Hoplondrina ambigua	Noctuidae	12	2	–	2	2
Campaea margaritata	Geometridae	11	1	–	–	–
*Noctua fimbriata**	Noctuidae	11	2	–	–	–
Noctua janthina	Noctuidae	10	7	2	1	–
Hydrelia flammeolaria	Geometridae	–	1	8	4	13
Chloroclystis v-ata**	Geometridae	3	–	2	1	10
Biston betularius	Geometridae	–	–	15	2	6
Apamea scolopacina**	Noctuidae	3	–	1	–	5
Trachea atriplicis**	Noctuidae	–	1	–	–	3
Nycteola revayana	Nolidae	–	–	–	–	3
Pheosia tremula	Notodontidae	–	–	–	2	1

*: Migrant moth, or moth species suspected of being migratory

**: as caterpillars on grass or herbaceous plants and bushes

Table 4 – Number of species (S) and individuals (n) together with Fisher's alpha of the detected species on all capture days at the five capture heights, indicating temperatures (°C) at 20:00 h (CET) at a height of 30 m [T (30 m)] (Source: Bonn, S. 2003), divided into the seasonal groups (FS: Early summer, HS: High summer, HB: Autumn). Capture days with a higher diversity and/or number of species and individuals in the canopy are indicated in bold. α: Fisher's alpha diversity index.

		T (30 m)	**Understorey**			**10 metres**			**20 metres**			**25 metres**			**30 metres**		
	Date	**(°C)**	**S**	**n**	α	**S**	**n**	α	**S**	**n**	α	**S**	**n**	α	**S**	**n**	α
FS	16. Jun.	19.3	10	11	53.3	–	–	–	8	17	5.9	5	12	3.2			
	24. Jun.	**20.3**	**15**	**24**	**17.1**	–	–	–	**11**	**13**	**33.8**	–	–	–	**17**	**46**	**9.7**
	06. Jul.	18.2	16	27	16.5	8	16	6.4	6	12	4.8	3	3	0	2	5	1.2
	14. Jul.	24.2	3	10	1.4	11	41	4.9	6	18	3.2	6	11	5.4	–	–	–
HS	31. Jul.	23.8	3	3	0	3	2	0	3	4	5.5	8	8	0	1	1	0
	03. Aug.	**29.5**	**8**	**17**	**5.9**	**7**	**28**	**3.0**	**13**	**31**	**8.4**	**7**	**18**	**4.2**	**6**	**8**	**10.9**
	04. Aug.	**28.7**	**16**	**70**	**6.5**	**13**	**52**	**5.6**	**4**	**11**	**2.3**	**15**	**42**	**8.3**	–	–	–
	13. Aug.	27	18	62	8.5	5	22	2.0	–	–	–	–	–	–	–	–	–
	19. Aug.	22.6	6	12	4.8	4	6	5.2	1	2	0.8	–	–	–	–	–	–
HB	26. Aug.	20.5	14	59	5.8	4	8	3.2	2	2	0	–	–	–	–	–	–
	03. Sep.	15.8	6	13	4.3	3	6	2.4	–	–	–	–	–	–	–	–	–
	07. Sep.	20.7	11	28	6.7	–	–	–	–	–	–	–	–	–	–	–	–
	16. Sep.	17.2	1	1	0	2	2	0	2	3	2.6	–	–	–	– 1	3	0.5
	21. Sep.	20.7	5	28	1.8	4	4	0	–	–	–	–	–	–	–	–	–
	22. Sep.	22.9	5	84	1.2	2	31	0.5	1	8	0.3	1	1	0	–	–	–

Although the values of the Morisita-Horn index reveal clear differences in the species compositions of individual height strata, these differences don't appear to be the most important factors discriminating species composition. Assuming that seasonal differences are most important, we carried out separate Principal Coordinates Analyses for FS, HS and HB. If height differences are the second most important factor, species and records, which are characteristic for one height, should show groupings along the biplot's x-axis. This assumption proofed to be true for the FS and HS records but not for HB (results not shown).

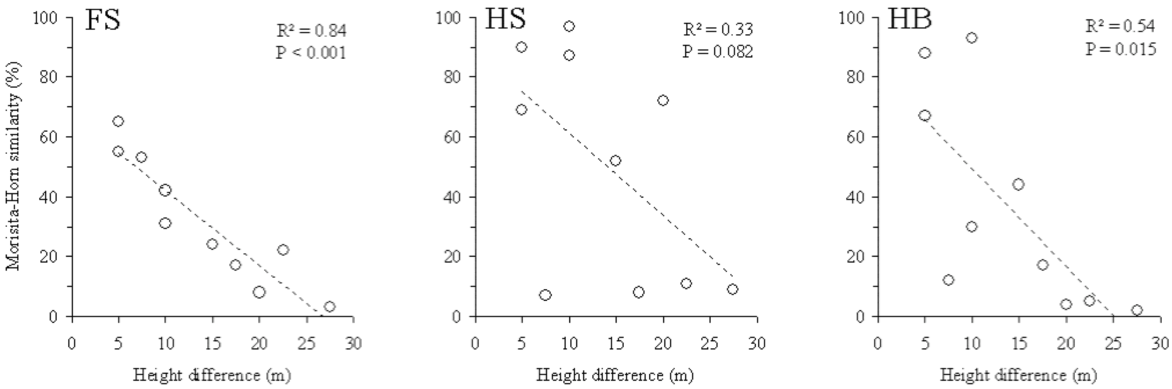

Figure 2 – Average differences in species composition between under storey and upper canopy according to the Morisita-Horn index, for the main phases of activity FS, HS and HB. In FS and HB the reduction in fauna similarities as height increases is significant. Although the results of the Morisita-Horn index show differences in species composition of the individual capture heights, these can be explained to a large extent by the low number of individuals recorded in the upper canopy, as variations in summer and autumn demonstrate.

In the latter case the height vector was closely associated to the biplot's y-axis, suggesting that another unknown factor (on the biplot's x-axis) forms the main gradient in autumn.

Importance of environmental factors

In order to assess the importance of the environmental factors 'seasonality' and 'flight height', a partial Canonical Correspondence Analysis (pCCA) was carried out with all data. The extent to which the seasonal gradient can explain the overall variation was 26% that of the flight height factor, 16%. For both factors, a significant effect ($p < 0.01$) on the moth species composition could be estimated by a Monte Carlo permutation test (499 permutations). The effect of both factors on species composition seems to be largely independent. Only 2% of the variation can be explained by a joint effect of both environmental gradients. 58% of the differences could not be explained by neither of the two factors.

DISCUSSION

Capture method

The effectiveness of light traps is considerably dependent on the lamp type used and the method (Taylor & Brown 1972; Muirhead-Thomson 1991). The use of low-energy black-light lamps has proven to be suitable many times, especially concerning stratification studies of nocturnal insects, and also due to its simple technical outlay (Stewart & Lam Jr. 1968; Kato *et al.* 1995; Thomas 1996; Butler, Kondo & Strazanac 2001; Schulze *et al.* 2001). On the one hand, the low radiation guarantees that only animals close to the light source are attracted (Baker & Sadovy 1978; Sotthibandhu & Baker 1979), on the other hand, evidently fewer individuals were registered than when stronger lamps are used (e.g. 125 and 250 W mixed light lamps) (Steiner & Nikusch 1994).

Using light traps, manual sampling of animals has the advantage compared to automatic traps (Steiner & Nikusch 1994) that all approaching species and individuals can be recorded and especially smaller species are better preserved for determination. However, disadvantages arise with manual sampling by one person especially during stratification studies, because several automatic light traps, working at several heights, would be advantageous for this purpose. By restricting illumination time to 15 minutes per capture height and shading the light upwards and downwards, the intention is to prevent attraction of animals from other height ranges. However, this can neither be completely excluded nor verified using this method. Since the illumination time per height was 4x15 in each case, species were able to be recorded whose main activity does not fall into the first three hours after sunset; but the short capture time per height, even if carried out repeatedly, rules out species which were not found in the close vicinity of the crane gondola.

Using artificial light sources, only those species being attracted to natural light sources (moon, stars) can be recorded (Baker & Sadovy 1978; Sotthibandhu & Baker 1979). Besides this, the reaction of moths to a light source is species, gender and individual-specific. Various moth species react rarely or not at all to the lure of light and cannot be recorded using this method (BAKER & SADOVY 1978). In general, more male moths were registered during light traps (STEWART *et al.* 1969; PLAUT 1971; STEINER & NIKUSCH 1994; KOLLIGS 2000); females are mostly underrepresented. The specific sensitivity with which the respective species react to artificial light sources therefore has a selective effect on the recording method. Due to this, only a partial spectrum of the moth fauna can be recorded (KOLLIGS 2000). Despite these limitations, the light capture method is highly suitable for recording a number of individuals and species in a relatively short time (MUIRHEAD-THOMSON 1991).

Composition of the Lepidoptera community

With 101 species during the five-month field study, only a relatively small section of the moth fauna of the "Burgaue" nature reserve was recorded. ERLACHER (1993) detected 97 Geometrid moths alone for the Burgaue nature reserve between March 1992 and March 1993, while extending the analysis throughout the Burgaue area. Including the second capture area in the "Elster-Pleiße-Auwald" nature reserve in the southern part of the city of Leipzig, ERLACHER (1993) was able to detect 109 Geometrid moth species for the Leipzig forest. In the same period, TRUSCH & VOIGT (1995) recorded 133 species of the Noctuidae family in the two nature reserves. However, details concerning the Burgaue cannot be inferred from this study. The published species list (SCHILLER & GRAUL 1996) with recordings from the years 1986 to 1996 shows 251 moth species for the "Burgaue" nature reserve (among these: Geometridae 103, Noctuidae 57, silkworm moths 25). During these studies, 13 butterfly species were detected which are not listed in the species list of SCHILLER & GRAUL (1996): *Agrotis clavis*, *Agrotis ipsilon*, *Anaplectoides prasina*, *Hoplodrina ambigua*, *Hoplodrina octogenaria*, *Mamestra brassicae*, *Tholera decimalis*, *Xanthia citrago*, *Xestia rhomboidea*, *Xestia xanthographa*, *Chloroclysta siterata*, *Colocasia coryli*, and *Orthonama obstipata*. The Geometrid moth species *Orthonama obstipata* has not been registered in the urban area for several decades, but appears as a migrant moth in other areas of Saxony and Germany, too (SCHOTTSTÄDT *et al.* 1996).

Migrant behaviour

Migrating moth species represent a further problem for evaluating light catches (EITSCHBERGER & REINHARDT 1991), because they only appear temporarily during recordings and/or cannot always be distinguished from a local population. Among the genuine migrant moths, which immigrate every year are *Autographa gamma*, *Agrotis ipsilon*, and *Orthonama obstipata* (EITSCHBERGER & REINHARDT 1991; HAUSMANN 2001). With *Noctua pronuba*, *Noctua fimbriata*, *Agrotis segetum*, *Agrotis exclamationis*, *Xestia c-nigrum*, *Mythimna l-album*, and potentially also *Mamestra brassicae* and *Amphipyra pyramidea* (EITSCHBERGER & REINHARDT 1991), further potentially migratory and sometimes very widely distributed moth species were recorded during our light catches. Besides, other species also undertake dispersion flights and the delimitation from migrant behaviour is unclear.

Ecotype composition of the Lepidoptera community

Species-specific flight capability and activity ties butterflies to one habitat to a varying extent and therefore influences the ecotype pattern of a recording. Geometrid moths are generally known to be poor fliers with negligible dispersion flights (HAUSMANN 2001). They are therefore more strongly tied to the occurrence of feeding plants in the local vegetation than Noctuidae, which fly long distances on the search for food. In transitional areas between various vegetation structures, overlaps and mixtures of moth cenoses are possible, while Noctuidae are recorded more often (ESCHE 1994). Deltoid moths warm themselves up with muscle movements before beginning their flight, which is why they are predestined for microclimatically unfavourable areas such as forest edges and the transition to open land. With 39 species and 73% of individuals, the Noctuidae were the most dominant family in our survey. In ecotype composition, the species of this family show a stronger preference for open areas than all other families. In addition, they presented the largest proportion of ubiquists. By contrast, Geometrid moths are 'cold fliers' and can be found in microclimatically more balanced habitats. The composition of Geometrid fauna is more strongly marked by species that prefer the forest and forest edge to the bordering open land as their habitat. The Geometrids, together with the remainder of the families recorded in this study, are typical for forest and forest edge habitats (ESCHE 1994). The ecotype composition clearly reflects the strong influence of the adjacent open land (ca. 50–70 m away). Examples are typical open land species such as *Agrotis segetum* and *Agrotis exclamationis*. The second most common species, *Agrochola circellaris*, is typical for forest edges (Appendix Table 1).

Importance of the factors 'seasonality' and 'flight height' for the Lepidopteran species composition

Seasonality

Species composition and abundance of Lepidoptera changed during the course of the five-month field study and also varied highly between capture days, which is most likely due to different weather conditions. Early summer proved more diverse than high summer and autumn, even though more individuals were recorded in high summer than in the other two seasons. In the microclimatically less favourable autumn nights moths were only occasionally encountered in the upper canopy.

The different approaching behaviour and differences in diversity between capture nights within one seasonal group can largely be attributed to the weather conditions in the capture nights. On very warm nights, relatively more species and individuals were recorded than in nights with less favourable conditions, such as low temperatures or full moon. Seasonal differences in species composition and abundance are very pronounced in temperate zones and, as can be expected, represent the strongest factor of influence in the present study.

Flight height preference of the moths

Using the light traps, seven species were recorded which appeared more frequently in the upper canopy than in the understorey, or were only recorded there (Appendix Table 1). *Hydrelia flammeolaria*, *Chloroclystis v-ata*, and *Biston betularius*, in particular, appear to have preferred the upper forest stratum as their flight space. These observations are in line with the capture results by Köppel (1997) in a hardwood floodplain forest at the Rhine near Rastatt. During light catches in an oak canopy at a height of 22 m, Köppel recorded 61 species, which were more common in the canopy than in a light trap 20 m below. However, these animals captured in the canopy also included, among others, *Xestia c-nigrum*, *Noctua pronuba*, *Xestia xanthographa*, *Haplondrina ambigua*, *Agrotis segetum*, and *Idaea aversata*, which, in our study, showed a clear preference for the understorey and lower canopy strata. These species are colonising the layers close to the ground as caterpillars and, moreover, are partially migrants. Overall, the majority of species and individuals were also recorded in Köppel's investigations in the lower strata.

Hydrelia flammeolaria is widely distributed and feeds on various deciduous trees, prefeably *Acer* spp. and *Alnus* spp. (Ebert & Steiner 2001). The high abundance of *Acer* spp. in our study site might be responsible for the high abundance of *Hydrelia flammeolaria*. Because of its feeding plant spectrum it is likely to be a common forest canopy dweller. Other authors (e.g. Köppel 1997; Beck & Schulze 2003) also captured *Biston betularius* in greater abundance or exclusively in the canopy of various types of forest. Yet the species was not registered exclusively in the canopy. Although some herbaceous plants and scrubs are also indicated as feeding plants for *B. betularius* (Ebert, Steiner & Trusch 2003), larval ecology suggests a closer association to the forest canopy. The canopy might also be a resting place, since the species is rarely found during the day. Köppel (1997) believes that the habit of remaining in the canopy is associated with using it for 'tree-topping'. Therefore, the results obtained so far suggest that the samples are too small. Besides, observations of caterpillar and moth behaviour are lacking. In order to refine statements concerning the canopy association of individual species, future studies must include the behaviour and larval ecology of populations. *A. circellaris*, common in autumn, demonstrates how difficult allocation to individual strata can be. For example, the young caterpillars develop in the inflorescences of poplars, willows and elms (Steiner 1997). Therefore egg laying appears possible even in higher canopy strata. Later, after the decay of poplar or willow catkins, the caterpillars feed on herbaceous plants. Pupation occurs on the ground, hence, explaining the observed frequency distribution.

On family basis, Noctuidae clearly dominate the species composition in the understorey. In the upper canopy, Geometridae were represented with a relatively high abundance. On very warm days, sometimes more species and individuals were captured in the upper canopy than in the understorey of the same night.

Alpha-diversity at different heights

In the present study, we found rather small differences in alpha-diversity between the various tree strata and the understorey. For almost all comparisons, a trend towards higher diversity of the moth community could be found in the understorey.

Beck & Schulze (2003) recorded in a beech forests in Oberfranken a lower diversity in the canopy than in the understorey. For the Geometridae, these differences were significant at one location. Likewise, Le Corff & Marquis (1999) also found a higher diversity in the lower forest stratum in a North American forest. Thomas (1996) found a higher diversity of Geometridae in the understorey while studying the stratification of moth communities in a temperate deciduous forest in Canada. In this study, however, a higher diversity was found in the forest canopy for the overall recorded moth community. The catches in the understorey and canopy, though, took place independently of one another on various nights.

Beta-diversity at different heights

Pronounced and significant differences in species composition between the different capture heights were found in early summer. In high summer and autumn there were also some differences in stratification but the overall variation was high. The stratification effect is mostly due to differences in abundance and less to differences in species. Captures in the understorey during high summer turned out to be most rich in individuals.

Conclusions and outlook

We conclude that stratification, although detectable in our data set, is not the most dominant factor influencing moth species diversity and composition. Based on the result of the partial CCA, a much stronger effect is caused by the factor seasonality. Nevertheless the observed stratification effect may contribute to provide and maintain additional niches for macro-Lepidoptera and other forest organisms. This is certainly more pronounced for large mixed old growth forests rich in species and structure.

We believe that the observed stratification is due to indirect effects such as microclimatic differences, feeding plants at the ground, and predator avoidance. Especially in spring and autumn, the canopy is likely to be a rather harsh environment with only few specialists adapted to it. This is supported by the observation of more species and individuals in warm midsummer nights than during the other capture periods.

Since many of the recorded moths are non-specialised open land species mostly feeding on herbaceous plants, the presence of such plants at the forest ground certainly favours a high species diversity and abundance. In the tropics, for instance, different flight heights have been accounted for by the availability of food resources (e.g. Kato *et al.* 1995; Beccaloni 1997; Schulze *et al.* 2001). To comment on the question of predator avoidance is rather speculative, because the main predators of adult moths, bats, overall do not prefer special flight heights but obviously do not hunt in the herb layer of the underground. Similarly, birds feeding on caterpillars and occasionally on adult moths during daytime may show a higher hunting activity in the canopy. Overall the reason for the stratification of the moth community might be regarded as a vertical gradient of various stress factors increasing from the forest ground to the upper canopy, while 'thinning' species and individual numbers of macro-Lepidoptera.

Clearly, more stratification studies using a similar methodology are necessary to get a better picture. Such studies should take place within a large area of less or undisturbed old-growth forest and should be repeated for several years to minimise the effect of extreme climatic conditions like those experienced in 2003.

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Appendix Table 1 – List of all species detected in summer and autumn 2003 at the Leipzig crane plot, numbers of individuals at the five capture heights, ecotype, and endangered status of the species; K&R no.: Karsholt & Razowski (1996); *: Light trap 4^{th} June 2003 (125 W mixed light lamp); **: Evidence of caterpillars in the period from 164^{th} May to 314^{st} August; ***: Other evidence; ECO: Ecotypes (E: Euryoecious; O: Open landscapes; OB: Open landscapes with hedges, field/woods, forest edges, avenues; OF: Open landscapes, wet habitats; OM: Open landscapes, moderate habitats; OT: Open landscapes, dry habitats; W: Forest and forest-type woods; WL: Deciduous forest, mixed deciduous forest; Y: Specific substrates [deadwood, detritus, plants, fungi]); ES: Endangered Status (D: Germany, SN: Saxony, 1: Vom Aussterben bedroht [critical], 2: stark gefährdet [endangered], 3: gefährdet [vulnerable], 4: potentiell gefährdet [near threatened], R: extrem selten bzw. im Rückgang begriffen [rare], V: Vorwarnliste [near threatened]; Fischer [1995]; Gelbrecht & Schottstädt [1996]; Fischer & Sobcyk [2002]).

K&R no.	**Family**	**Species**	**Capture height**					**ECO**	**ES**	
			0	**10**	**20**	**25**	**30**		**D**	**SN**
3907	Limacodidae	*Apoda limacodes* (Hufnagel, 1766)					1	WL	–	–
4176	Cossidae	*Zeuzera pyrina* (Linnaeus, 1761)					1	OB	–	–
7481	Drepanidae	*Thyatira batis* (Linnaeus, 1758)	2	1				OB	–	–
7503		*Watsonalla binaria* (Hufnagel, 1767)	2					WL	–	–
7527	Geometridae	*Lomaspilis marginata* (Linnaeus, 1758)	5		1		3	E	–	–
7539		*Semiothisa notata* (Linnaeus, 1758)	1					E	–	–
7542		*Semiothisa liturata* (Clerck, 1759)			3			E	–	–
7547		*Semiothisa clathrata* (Linnaeus, 1758) *						E	–	–
7663		*Colotois pennaria* (Linnaeus, 1761)	1					E	–	–
7686		*Biston betularius* (Linnaeus, 1785)			15	2	6	E	–	–
7754		*Peribatodes rhomboidaria* ([Denis & Schiffermüller], 1775)					1	E	–	–
7777		*Alcis repandata* (Linnaeus, 1758)	1				1	E	–	–
7783		*Hypomecis roboraria* ([Denis & Schiffermüller], 1775) **						E	–	–
7784		*Hypomecis punctinalis* (Scoploi, 1763) *						E	–	–
7796		*Ectropis crepuscularia* ([Denis & Schiffermüller], 1775)	2					E	–	–
7800		*Parectropis similaria* (Hufnagel, 1767) *						WL	–	–
7824		*Cabera pusaria* (Linnaeus, 1758)	4					E	–	–
7828		*Lomographa bimaculata* (Fabricius, 1775) *						E	–	–
7829		*Lomographa temerata* ([Denis & Schiffermüller], 1775)	2				1	E	–	–
7836		*Campaea margaritata* (Linnaeus, 1767)	11	1				E	–	–
7971		*Comibaena bajularia* ([Denis & Schiffermüller], 1775) *						WL	V	4
7980		*Hemithea aestivaria* (Hübner, 1789) **						WL	–	–
8014		*Cyclophora annulata* (Fabricius, 1775)	1	2				WL	V	4
8022		*Cyclophora punctaria* (Linnaeus, 1758)	1			1		E	–	–
8024		*Cyclophora linearia* (Hübner, 1799)	1					WL	–	–
8027		*Timandra griseata* (W. Petersen, 1902)	13	6				E	–	–
8132		*Idaea biselata* (Hufnagel, 1767)	4	18	4	8	1	E	–	–
8184		*Idaea aversata* (Linnaeus, 1758)	2	1	4			E	–	–
8246		*Orthonama obstipata* (Fabricius, 1794)	1		1		1	OB	–	–
8252		*Xanthorhoe spadicearia* ([Denis & Schiffermüller], 1775)	1					E	–	–

Appendix Table 1 continued – List of all species detected in summer and autumn 2003 at the Leipzig crane plot, numbers of individuals at the five capture heights, ecotype, and endangered status of the species.

K&R no.	**Family**	**Species**	**Capture height**					**ECO**	**ES**	
			0	**10**	**20**	**25**	**30**		**D**	**SN**
8253	Geometridae	*Xanthorhoe ferrugata* (Clerck, 1759)	1	2				E	–	–
8254		*Xanthorhoe quadrifasciata* (Clerck, 1759)	1					E	–	–
8255		*Xanthorhoe montanata* ([Denis & Schiffermüller], 1775) *						E	–	–
8275		*Epirrhoe alternata* (O.F.Müller, 1764)	7	3	1		2	E	–	–
8289		*Camptogramma bilineata* (Linnaeus, 1758)	9		1			E	–	–
8314		*Pelurga comitata* (Linnaeus, 1758)	2					E	–	–
8341		*Chloroclysta siterata* (Hufnagel, 1767)	2					WL	–	3
8348		*Chloroclysta truncata* (Hufnagel, 1767)	1					E	–	–
8368		*Electrophaes corylata* (Thunberg 1792) *						E	–	–
8385		*Colostygia pectinaria* (Knoch, 1781) *						E	–	–
8456		*Perizoma alchemillatum* (Linnaeus, 1775)	3	2	4	1		E	–	–
8465		*Perizoma didymatum* (Linnaeus, 1785)	1			1		WL	–	–
8573		*Eupithecia innotata* (Hufnagel, 1767)				1		E	–	–
8601		*Chloroclystis v-ata* (Harworth, 1809)	3		2	1	10	E	–	–
8620		*Aplocera plagiata* (Linnaeus, 1758)	1					OT	–	–
8660		*Hydrelia flammeolaria* (Hufnagel, 1767)		1	8	4	13	E	–	–
8721	Notodontidae	*Drymonia dodonea* ([Denis & Schiffermüller], 1775) *						WL	–	–
8727		*Pheosia tremula* (Clerck, 1759)				2	1	OB	–	–
8789	Noctuidae	*Craniophora ligustri* ([Denis & Schiffermüller], 1775)	5	2	3	3		OB	–	–
8801		*Cryphia algae* (Fabricius, 1775)	1				1	Y	–	3
8846		*Herminia grisealis* ([Denis & Schiffermüller], 1775) *						OB	–	–
8994		*Hypena proboscidalis* (Linnaeus, 1758)	7	1			1	E	–	–
9008		*Rivula serecealis* (Scopoli, 1763)	3			2		OF	–	–
9056		*Autographa gamma* (Linnaeus, 1758)	2					E	–	–
9059		*Autographa pulchrina* (Harworth, 1809) *						OB, OF	–	–
9169		*Trisateles emortualis* ([Denis & Schiffermüller], 1775) *						WL	–	4
9307		*Amphipyra pyramidea* (Linnaeus, 1758)	4	1	1			WL	–	–
9449		*Hoplondrina octogenaria* (Goetze, 1781)			1	1		E	–	–
9454		*Hoplondrina ambigua* ([Denis & Schiffermüller], 1775)	12	2		2	2	OT, OM	–	–
9501		*Trachea atriplicis* (Linnaeus, 1958)		1			3	OB	–	–

Appendix Table 1 continued – List of all species detected in summer and autumn 2003 at the Leipzig crane plot, numbers of individuals at the five capture heights, ecotype, and endangered status of the species.

K&R no.	Family	Species	Capture height					ECO	ES	
			0	10	20	25	30		D	SN
9548	Noctuidae	*Cosmia affinis* (Linnaeus, 1767)	2	1	1	1		WL	3	2
9550		*Cosmia trapezina* (Linnaeus, 1758)	1	14	6	1	7	OB, W	–	–
9557		*Xanthia aurago* ([Denis & Schiffermüller], 1775)	1	1				WL	–	–
9562		*Xanthia citrago* (Linnaeus, 1758)	2					OB, W	–	–
9566		*Agrochola circellaris* (Hufnagel, 1766)	141	32	9	1		OB, W	–	–
9596		*Eupsilia transversa* (Hufnagel, 1766)	6	3				OB, W	–	–
9748		*Apamea monoglypha* (Hufnagel, 1766)	1		1		1	E	–	–
9774		*Apamea scolopacina* (Esper, 1788)	3		1		5	OB, W	–	–
9895		*Discestra trifolii* (Hufnagel, 1766)	1					OM	–	–
9917		*Lacanobia oleracea* (Linnaeus, 1758)			1			OM	–	–
9987		*Mamestra brassicae* (Linnaeus, 1758)	1					OM	–	–
10001		*Mythimna ferrago* (Fabricius, 1787)	1			1	1	OB	–	–
10007		*Mythimna pallens* (Linnaeus, 1758)			1	2		E	–	–
10022		*Mythimna l-album* (Linnaeus, 1767)	2					OM	–	–
10044		*Orthosia cerasi* (Fabricius, 1775) **						OB, W	–	–
10065		*Tholera decimalis* (Poda, 1761) ***						O	–	–
10082		*Axylia putris* (Linnaeus, 1761)	1	2	1		3	E	–	–
10086		*Ochropleura plecta* (Linnaeus, 1761)	2	4	1	1		E	–	–
10089		*Diarsia mendica* (Fabricius 1775) *						OB, W	–	–
10092		*Diarsia brunnea* ([Denis & Schiffermüller], 1775)	1					E	–	–
10096		*Noctua pronuba* (Linnaeus, 1785)	22	7	2	4		E	–	–
10099		*Noctua comes* (Hübner, 1813)	1			1		OB	–	–
10100		*Noctua fimbriata* (Schreber, 1759)	11	2				OB, W	–	–
10102		*Noctua janthina* ([Denis & Schiffermüller], 1775)	10	7	2	1		OB, W	–	–
10199		*Xestia c-nigrum* (Linnaeus, 1758)	92	81	20	39	3	E	–	–
10201		*Xestia triangulum* (Hufnagel, 1766)			1	2		OB	–	–
10206		*Xestia rhomboidea* (Esper, 1790)	2					OB, WL	–	–
10212		*Xestia xanthographa* ([Denis & Schiffermüller], 1775)	13					E	–	–
10232		*Anaplectoides prasina* ([Denis & Schiffermüller],					1	W	–	–
10346		*Agrotis ipsilon* (Hufnagel, 1766)	1	5	2	1		E	–	–
10348		*Agrotis exclamationis* (Linnaeus, 1758)	3	2		1	4	O	–	–
10350		*Agrotis clavis* (Hufnagel, 1766)			1	1		O	–	–

Appendix Table 1 continued – List of all species detected in summer and autumn 2003 at the Leipzig crane plot, numbers of individuals at the five capture heights, ecotype, and endangered status of the species.

K&R no.	**Family**	**Species**	**Capture height**					**ECO**	**ES**	
			0	**10**	**20**	**25**	**30**		**D**	**SN**
10351		*Agrotis segetum* ([Denis & Schiffermüller], 1775)	6	5	5	2	1	O		
10372	Pantheidae	*Colocasia coryli* (Linnaeus, 1758)			3			WL	–	–
10375	Lymantridae	*Lymantria monacha* (Linnaeus, 1758)	1	12	8			W	–	–
10397		*Orgyia antiqua* (Linnaeus, 1758) **						OB, W	–	–
10406		*Euproctis similis* (Fuessly, 1775)	1					OB	–	–
10441	Nolidae	*Nycteola revayana* (Scopoli, 1772)					3	OB, W	–	3
10449		*Bena prasinana* (Linnaeus 1758) *						WL	–	2
10499	Arctiidae	*Eilema sororcula* (Hufnagel, 1766)			1			Y	–	2
10567		*Spilosoma lubricipeda* (Linnaeus, 1758) *						O	–	–

3.8 Arthropod communities of various deciduous trees in the canopy of the Leipzig riparian forest with special reference to phytophagous Coleoptera

Andreas Floren[1] & Peter Sprick

In spring 2003 the arboreal arthropod fauna of 21 trees of the species *Tilia cordata*, *Quercus robur*, *Fraxinus excelsior*, *Acer pseudoplatanus*, *A. platanoides* and *A. campestre* from the Leipzig riparian forest ("Burgaue") was quantitatively sampled by means of insecticidal knockdown fogging. In total, 96 527 arthropods were obtained. Although the arthropod numbers per tree varied between 1 340 and 8 008 individuals, communities were regular composed both on trees of the same species, as well as on different tree species. Homoptera, Diptera, parasitic Hymenoptera, Psocoptera and Heteroptera had highest relative proportions. On average, Coleoptera represented 4.5% of all arthropods of the communities. Of these, 11.5% belonged to the Chrysomelidae and Curculionoidea, which have been studied in detail. Within these two families, weevils provided 80.4% of all species and 89% of specimens. Altogether 37 species of weevils were found but only 9 species of Chrysomelidae. Eleven remarkable or endangered weevil species and three Chrysomelidae were collected. At the order-level, oaks showed the highest deviations in community composition. In particular, the oak fauna was richer in Coleoptera, Neuroptera and Arachnida. Chrysomelidae and Curculionoidea showed highest species diversity on oaks, too. Neither cumulatively nor for individual tree species the sampling effort was large enough to represent the local species pool. The Leipzig riparian forest showed some noticeable results within the guild of phytophagous Coleoptera caused by the occurrence of remarkably few tree specific specialists, and only few generalists (species as well as individuals). Several generalist species found on the *Acer* tree species were mutually exclusive leading to a separation of the associations of phytophagous Coleoptera.

INTRODUCTION

Other than in the Tropics, canopy ecology of the Temperate Zone is a study area that has been neglected even more (Floren & Schmidl in press). Little is known about the diversity, structure, and dynamics of arboreal arthropods, their importance for many ecosystem processes and how these change as a consequence of anthropogenic disturbance. After placing in the Leipzig riparian forest a construction crane for canopy research purposes, Leipzig has become one of the main canopy research places in Germany.

Since these projects depend on the crane and on the swivel radius of the crane jib in particular, no quantitative so-called destructive collecting methods were allowed. However, as insecticidal knockdown fogging in particular can supply important background information on arthropod diversity and arthropod community composition (Floren & Schmidl 2003) it was agreed that such an investigation should be carried out at a safe distance from the crane site. By applying a non-persistent insecticide (natural pyrethrum), free-living arboreal arthropods can be collected almost quantitatively causing little spatio-temporal disturbance (see also Bussler *et al.* 2004). In this way, it is possible to gain a precise picture of the composition of tree specific arthropod communities. These data can be used to answer basic questions in ecology and nature conservation, like the importance of tree crowns as a habitat of rare or endangered species (e.g. Horstmann *et al.* 1999; Floren & Schmidl 2000; Floren & Linsenmair 2000; Horstmann & Floren 2001; Stork *et al.* 2001), the comparison between old and anthropogenically disturbed forests (Thunes *et al.* 2003; Floren & Linsenmair 2005; Floren & Deeleman 2005), or for studying the food supply of insectivorous animal groups.

In this article, we summarize some of the results of our fogging study in spring 2003. We concentrate on community composition on a high taxonomic level and analyse the phytophagous Curculionoidea and Chrysomelidae (Coleoptera) in detail.

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[1] corresponding author

MATERIALS AND METHODS

The study was carried out in the Leipzig riparian forest (51°20' N; 12°22' E), in a lime-tree rich riparian mixed forest made up of English oak (*Q. robur*), ash (*F. excelsior*) and white elm (*U. laevis*) (Fraxino-Ulmetum). The forest is at least 500 years old and has been used since 1870 mainly as coppice with standards. Due to water engineering measures, which have lead to a continuous sinking of the ground water level, the forest's character is gradually changing into that of a mixed deciduous forest with a high proportion of *Acer* spp. and *F. excelsior* L. (see also Rohrschneider and Seele, this volume).

The trees chosen for the foggings stood on an area of about 2 ha and were not immediately adjacent to one another. The study area lay about 400 m south from the crane site. Here, too, the few older, faunistically interesting trees with a high proportion of dead wood (mainly oaks) were not allowed to be fogged. From the 30th of May to the 2nd of June 21 trees were fogged. These included 4 *Tilia cordata*, 2 *Quercus robur*, 3 *Fraxinus excelsior*, 5 *Acer pseudoplatanus*, 6 *A. platanoides*, and 1 *A. campestre*. At the time of the foggings, the blossoming period of all the tree species was already over. Only on *A. pseudoplatanus* a few blossoms were still present (pers. comm. O. Tal).

Fogging method

The fogging method has already been described and we give only brief information (see Adis *et al.* 1998). Natural pyrethrum was used as insecticide, which is highly arthropod specific, dilutes quickly in the air, and completely degrades within a few hours. The insecticide is diluted in a highly refined white oil without any chemical additives and applied in a concentration of less than 1% active agent. In such small concentration, fogging causes little spatio-temporal disturbance (Floren & Schmidl 2003). Fogging was performed early in the morning when there was no wind. After the fogging, a two-hour waiting period ensued during which the arthropods dropped from the crowns onto collecting sheets that had been stretched out under the trees. In each case, the sheets covered 80 to 90% of the crown projection area, so that the great majority of the arthropod communities were collected.

Statistics

Relative proportions of taxa within and between communities were compared by ANOVA tests, followed by a Tamhane post-hoc test for unequal variances. In order to make arthropod numbers collected by fogging comparable between trees, data were standardised to a collecting area of 1 m^2 and to 100% leaf-cover (measured against the sky). Communities of the phytophagous Coleoptera taxa Chrysomelidae and Curculionoidea were analysed by correspondence analysis (detrended).

Figure 1 – Fogging oak trees from the ground. Arthropods drop into the collecting sheets stretched out beneath the study tree.

RESULTS

Altogether, during the 21 foggings 96 527 arthropods were caught and sorted at least to order-level (see Appendix Table 1). Fig. 2 depicts the main taxa in the trees. The composition of the communities was regular and similar between tree species, although the number of arthropods varied between 1 340 and 8 008 individuals per tree. This becomes particularly clear when comparing the partial figure "All trees", which shows the arthropod community of all combined foggings, with the partial figures created for each individual tree species. Between tree species, only few differences were found in the relative frequencies of orders: the Homoptera, Diptera and parasitic Hymenoptera on *Q. robur* differed at least at the 5%-level from those on *A. pseudoplatanus* (ANOVA, $F = 3.053$, $F = 2.780$, $F = 1.253$, respectively; Tamhane post-hoc test for unequal variances: $p < 0.05$), and Psocoptera on *T. cordata* differed from those on *A. pseudoplatanus* ($F = 2.307$; $p < 0.05$). The most frequent groups (Homoptera, Diptera, Hymenoptera, Psocoptera and Heteroptera) also showed the highest fluctuations, while the relative proportions of the remaining groups only fluctuated slightly, both among homospecific trees and between tree species. Thysanoptera showed the highest fluctuations. For Thysanoptera, Collembola and Acarina it is not known how well they can be collected by foggings (FLOREN & LINSENMAIR 1997). These groups did not reach high enough abundances in the samples and were combined in the group "other arthropods". Mites were combined with Araneae as Arachnida. The most uniform communities (those with the lowest variance) were collected from *A. pseudoplatanus*. Communities on the two oaks differed notably from those on all other trees. Here, Diptera and Homoptera were most frequent, followed by parasitic Hymenoptera (14.5%) and Coleoptera, which represented almost 16% of all arthropods on oak. On the other trees beetles represented on average 4.5% of all arthropods. Eighty percent of the hemimetabolous Hemiptera were nymphs. Neuroptera, too, which usually made up less than 1% of the communities, were clearly more frequent on oak. On the other hand, Psocoptera, which on average represented 8.4% of all arthropods, were found in low abundances (2.8%). Neither species of Lepidoptera, Symphyta or Coleoptera, which possess a potential for mass reproduction, were collected in high abundance.

Apart from the order level composition standardized arthropod numbers (standardization on one square meter and 100% leaf-cover) are given in Appendix Table 2. These numbers are directly comparable between trees. They varied between 34 to 272 arthropods collected per square meter. Both values come from *F. excelsior* and illustrate the large tree specific variability.

Coleoptera

Altogether, 2 956 Coleoptera were collected. Of these, the phytophagous Chrysomelidae and Curculionoidea were analysed in further detail, since they were supposed to be the most likely to show tree specific communities. 11.5% of all collected beetles belonged to these groups, of which 89% were Curculionoidea and 11% Chrysomelidae. Weevils predominated also with regard to species numbers, with 80.4% (37 species), while leaf beetles represented 19.6% (9 species; Table 1). In some cases, the proportion of both groups in the communities varied considerably. While no specimen at all was found on one ash tree, they represented 9% and 12%, respectively, on the other two ashes. By far the highest beetle abundances and species numbers were found on the two oaks.

Table 1 – Diversity of Coleoptera on various trees in the Leipzig riparian forest with special reference to Chrysomelidae and Curculionoidea

	Fraxinus excelsior	*Quercus robur*	*Acer platanoides*	*Acer pseudoplatanus*	*Tilia cordata*	*Acer campestre*	**All trees**
Number of foggings per tree species	3	2	6	5	4	1	21
Total number of beetles	353	698	712	514	519	160	2,956
Mean number of beetles	118±73	349±31	119±51	103±42	130±38	–	269±82.2
Relative proportion of phytophagous beetles	9.1%	29.8%	8.7%	12.3%	4.6%	7.5%	13.6%
Abundance of phytophagous beetles	32	208	62	63	24	12	401
Species of phytophagous beetles	16	27	19	15	11	6	46
Abundance of Chrysomelidae	3	16	7	8	9	1	44 (10.9%)
Species of Chrysomelidae	3	6	3	3	4	1	9 (19.6%)
Abundance of Curculionoidea	29	192	55	55	15	11	357 (89.1%)
Species of Curculionoidea	13	21	16	12	7	5	37 (80.4%)

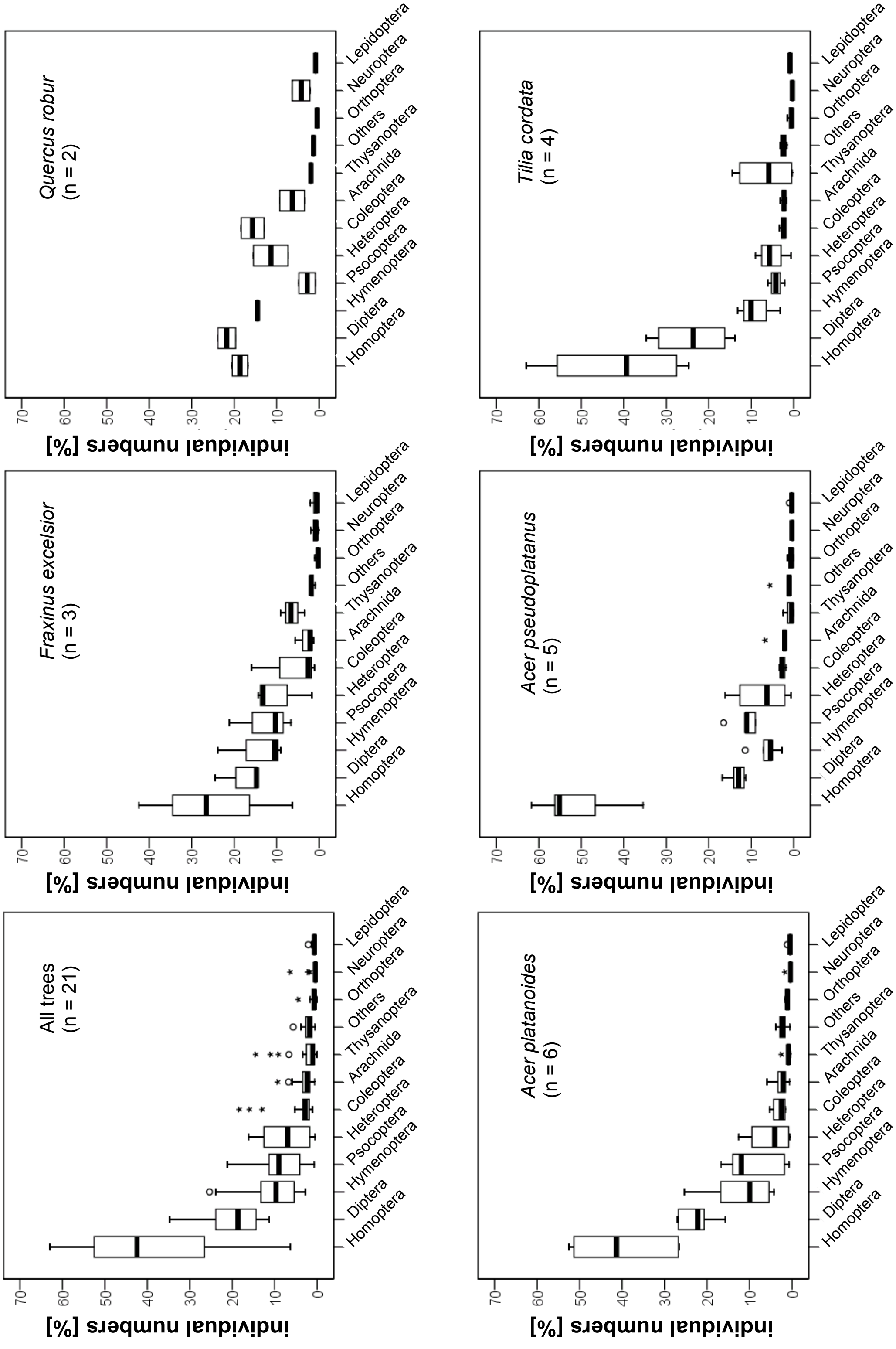

Figure 2 – Relative proportions of arthropod taxa in tree specific communities of various species of deciduous trees. Number of foggings is given in brackets. *A. campestre* was fogged only one time and no figure was computed. Boxes cover 50% of all values (whiskers 75%) and show the median. A circle indicates outlier values between one and three times the box length.

As shown in Fig. 3, a highly significant relation between the number of phytophagous beetle species and the total abundance of beetles exists: the more beetles were present in a fogging sample, the more species would be in this sample (Spearman rank-correlation, $\rho = 0.851$, $p < 0.001$). The outstanding importance of the oak for species diversity of phytophagous beetles can be recognised quite clearly.

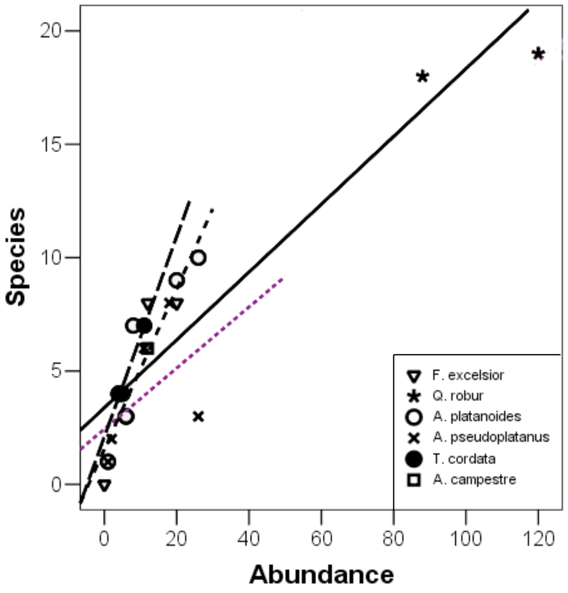

Figure 3 – Relationship between number of species and individuals of phytophagous Coleoptera (Chrysomelidae and Curculionoidea). In addition to the correlation line for all data (long straight line), also the lines for *A. pseudoplatanus*, *A. platanoides* and *T. cordata* are shown (from bottom to top).

A detrended correspondence analysis (DCA) shows a grouping of the phytophagous assemblages between the tree species (Fig. 4). The principal axes 1 and 2 explain 25% of the variance, while the remaining axes explain less than 3%. Assemblages on *A. platanoides* and *A. pseudoplatanus* show a gradual separation along the first axis.

Neither of the *Acer* specialists *Bradybatus kellneri* (Chrysomelidae) and *Deporaus tristis* (Curculionidae), which are known from the area, were collected. Only *A. platanoides* No. 21 could not be separated from *A. pseudoplatanus.* However, only two Curculionidae species (*Phyllobius calcaratus* and *Magdalis flavicornis*) and one Chrysomelidae species (*Aphthona euphorbiae*) were collected from this tree. A similar result was found for *T. cordata* – only tree No. 17 did not group – from which only four species were collected, namely *Phyllobius calcaratus* and the Chrysomelidae *Aphtona euphorbiae*, *Orsodacne cerasi* and *Phyllotreta undulata.* No specialized leaf beetles and weevils are known from *Tilia*. Beetle assemblages on *F. excelsior* showed no similarity, neither among homospecific trees nor between heterospecific trees. However, only 32 beetles, belonging to 16 species, were collected. Among these were the two specialists *Lignyodes enucleator* (6 individuals) and *Stereonychus fraxini* (4 individuals) both Curculionidae. The separation of the phytophagous beetle assemblages was surprising since some of the generalist species showed an unexpected preference for particular tree species. Thus, *Strophosoma capitatum* (17 individuals), *Phyllobius arborator* (3 individuals), *Ph. argentatus* (2 individuals), as well as *Polydrusus flavipes* (2 individuals), and *P. cervinus* (1 individual) were present only on *A. platanoides*, while *Ph. calcaratus* (35 specimens) was caught only on *A. pseudoplatanus. Rhyncolus punctatulus* was the only species present on all three *Acer* tree species although always never with more than two individuals.

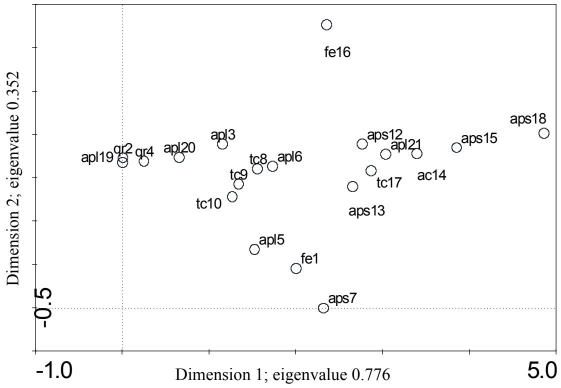

Figure 4 – Ordination diagram of a detrended correspondence analysis (DCA) of phytophagous beetle communities in crowns of various tree species in the Leipzig riparian forest. Sum of all eigenvalues=4.518.

Data on specialisation, faunistics and endangering classification of leaf beetles and weevils

In the following, the species are briefly referred to regarding their host plant association, regional distribution, and endangering (Dieckmann 1972, 1980, 1983, 1988; Mohr 1977; Geiser 1998; Koch 1992; Doguet 1994 and Schneider 2004). As there is no endangering classification available for Saxony, the Red List of the weevils of the neighbouring Saxony-Anhalt is consulted (Schneider 2004), particularly because Leipzig lies close to the border of this ‘Bundesland’. For the leaf beetles (except for the Donaciinae), no regional endangering classification for these regions exists.

The following specialists on *Quercus robur* were identified (number of individuals in brackets): *Cryptocephalus querceti* Suffrian, 1848 (8; deciduous wood species; a preference for *Quercus* is assumed; see below), *Altica quercetorum* Foudras, 1860 (2), *Curculio venosus* (Gravenhorst, 1807) (23), *Curculio pellitus* (4), *Curculio glandium* Marsham, 1802 (142), *Curculio pyrrhoceras* Marsham, 1802 (4), *Magdalis exarata* H. Brisout, 1862 (1), *Magdalis flavicornis* (Gyllenhal, 1836) (6), *Coeliodes erythroleucos* (Gmelin, 1790) (13), *Rhynchaenus quercus* (Linnaeus, 1758) (3), *Rhynchaenus signifer* (Creutzer, 1799) (1).

Specialists on *Fraxinus* are: *Lignyodes enucleator* (Panzer, 1798) (6) and *Stereonychus fraxini* (Degeer, 1775) (4) No *Acer* specialists were sampled and no specialised leaf beetle and weevil species are known from *Tilia*.

Further specialists were collected: *Anthonomus ulmi* (Degeer, 1775) (2), *Magdalis armigera* (Fourcroy, 1785) (1) and *Rhynchaenus rufus* (Schrank, 1781) (1), all associated with *Ulmus*; *Betulapion simile* (Kirby, 1811) associated with *Betula* (15); *Magdalis barbicornis* (Latreille, 1804) (1) and *Rhamphus oxyacanthae* (Marsham, 1802) (1) associated with Rosaceae; and *Phratora laticollis* (Suffrian, 1851) (1) associated with Salicaceae.

Polyphagous deciduous forest species: *Orsodacne cerasi* (Linnaeus, 1758) (11), *Cryptocephalus nitidus* (Linnaeus, 1758) (1); *Phyllobius arborator* (Herbst, 1797) (3), *Phyllobius calcaratus* (Fabricius, 1792) (43), *Phyllobius argentatus* (Linnaeus, 1758) (3), *Polydrusus flavipes* (Degeer, 1775) (2), with preference for *Quercus* and *Salix*, *Polydrusus cervinus* (Linnaeus, 1758) (1).

Strophosoma capitatum (Degeer, 1775) (27) is a polyphagous forest inhabitant, while *Barypeithes pellucidus* (Boheman, 1834) (10) is a polyphagous species developing at the roots of woody plants and perennial herbs. Xylobiontic species: *Rhyncolus punctatulus* Boheman, 1838 (5) and *Trachodes hispidus* (Linnaeus, 1758) (1). The following species are typically found in the herb layer: *Phyllotreta undulata* (Kutschera, 1860) (1), *P. ochripes* (Curtis, 1837) (1; both at various Brassicaceae; *P. undulata* eurytop; *P. ochripes* more at semi shade places and in eutrophic swamps), *Aphthona euphorbiae* (Schrank, 1781) (13; polyphagous, mostly at fresh and damp places), *Longitarsus parvulus* (Paykull, 1799) (5; living on *Linum*; however, there must be further host plants, since the species was fogged regularly also in areas lacking *Linum*, unpublished data), *Altica oleracea* (Linnaeus, 1758) (1; polyphagous), *Apteropeda globosa* (Illiger, 1794) (2; silvicolous, living on Lamiaceae and certain Scrophulariaceae, like *Veronica chamaedrys*, *Lathraea*), *Protapion fulvipes* (Fourcroy, 1785) (4; *Trifolium repens*, *T. hybridum*, *Protapion nigritarse* (Kirby, 1808) (4; *T. dubium*, *T. campestre*), *Protapion trifolii* (Linnaeus, 1768) (1; *T. pratense*, *T. medium*), *Oxystoma craccae* (Linnaeus, 1767) (1; *Vicia*), *Eutrichapion viciae* (Paykull, 1800) (2; *Vicia*), *Sitona lineatus* (Linnaeus, 1758) (2; at quite numerous Fabaceae), *Tychius picirostris* (Fabricius, 1787) (2; *Trifolium*), *Tychius meliloti* Stephens, 1831 (4; *Melilotus*), *Ceutorhynchus floralis* (Paykull, 1792) (2; at various Brassicaceae), *Ceutorhynchus sisymbrii* (Dieckmann, 1966) (1; *Sisymbrium loeselii*), *Sirocalodes nigrinus* (Marsham, 1802) (1; *Fumaria*).

Remarkable species

Orsodacne cerasi: the adult beetles of this species were found on blossoms of *Sorbus* or Apiaceae. Little is known about larval development. Due to morphological findings, Cox (1981) supposes that larvae feed on roots. The species occurs mainly in old deciduous forests and in old parks.

Cryptocephalus querceti: according to Mohr (1977), this species was only seldom found in the territory of the new 'Bundesländer' without mentioning the Leipzig district. It is considered endangered (Geiser 1998). Adults are thought to be associated with *Quercus*, *Tilia*, *Betula*, and *Sorbus aucuparia* (Koch 1992) with a preference for *Quercus* (unpubl. data).

Apteropeda globosa: a flea beetle that occurs predominantly in damp, deciduous forests rich in herbs, which colonizes low herbs and shrubs of the families Lamiaceae (*Ajuga reptans*, *Lamium galeobdolon*, *Prunella vulgaris*, *Stachys sylvatica*) and Scrophulariaceae (*Lathraea squamaria*, *Veronica chamaedrys*) (Doguet 1994 and own observations). The larvae mine in the leafs.

Polydrusus flavipes: this is a rare species of low altitude areas that has been frequently mistaken for the similar species *P. impressifrons*, *P. corruscus* or *P. pterygomalis*. It occurs mainly in riparian forests. Being polyphagous, *P. flavipes* shows a preference for *Salix* and *Quercus* (Dieckmann 1980). For the Leipzig district, Dieckmann (1980) mentioned only one locality close to Schkeuditz, which is probably identical with the crane site. In the neighbouring Saxony-Anhalt, the species is regarded as being critically endangered (Schneider 2004).

Rhyncolus punctatulus: a very rare inhabitant of tree hollows of old deciduous forests, as well as of parks with an old tree population. Since Cossoninae are underrepresented in fogging samples because of their way of life, the finding of 5 specimens all from *Acer* spp. is remarkable. According to Dieckmann (1983) no locality is known for the Leipzig district. In Germany and in Saxony-Anhalt it is endangered (Geiser 1998, Schneider 2004).

Lignyodes enucleator: a rare and vulnerable monophagous weevil species in Saxony-Anhalt and Germany, that develops in the fruits of *Fraxinus* species, and occurs only in the southern regions of this 'Bundesland'; no locality known for the Leipzig district (Dieckmann 1988).

Anthonomus ulmi lives mainly in riparian forests on *Ulmus* species. According to Dieckmann (1988), it has been documented both for *U. minor* and *U. laevis.* In Saxony-Anhalt the rather rare species is vulnerable (Schneider 2004).

Curculio pellitus: a rare, thermophilous species that develops in the acorns of *Quercus robur* and *Q. petraea* (Dieckmann 1988); for the Leipzig district the author knew of only two finding sites (Lübschütz and Gössnitz). In Germany, *C. pellitus* is regarded as vulnerable (Geiser 1998).

Magdalis barbicornis: the *Magdalis* species colonize dry twigs and branches of deciduous trees, which are still attached to the tree. *M. barbicornis* is a rare species of Rosaceae, which seems to be mainly distributed in moist deciduous forests. The species has disappeared in the neighbouring Saxony-Anhalt (Schneider 2004).

Magdalis exarata and *M. flavicornis*: these two species live in *Quercus* twigs. *M. flavicornis* also colonizes free standing trees, while *M. exarata* is found mainly in old forests. The fact that *Magdalis* species are well represented in fogging samples (Floren & Schmidl 1999) indicates that many species prefer sunnier crown regions. In Saxony-Anhalt, *M. flavicornis* is a vulnerable species, *M. exarata* being in danger of becoming extinct here and endangered in Germany.

Ceutorhynchus sisymbrii: a continentally distributed species that reaches its north-western distribution in the territory of the new federal states (Dieckmann 1972). It is strictly monophagous in xerothermous ruderal fields living on *Sisymbrium loeselii* and is regarded as endangered in Germany, and vulnerable in Saxony-Anhalt.

Rhynchaenus rufus: a rare species of moist deciduous forests that lives monophagously at *Ulmus*, being endangered in Saxony-Anhalt and vulnerable in Germany.

Rhynchaenus signifer: a small weevil with its main occurrence in moist deciduous forests of lower altitudes. Larvae mine in oak leafs. According to Schneider (2004), it is a vulnerable weevil species in Saxony-Anhalt.

DISCUSSION

Due to the large biodiversity, canopy ecology has for a long time focussed on tropical lowland rain forests (e.g. Basset *et al.* 2003; Linsenmair *et al.* 2001; Stork *et al.* 1997), while it was largely neglected in temperate latitudes. This is slowly starting to change (Floren & Schmidl in press). However, the functional importance of the canopy fauna in forest ecosystems is barely acknowledged (e.g. Weisser & Siemann 2004). The canopy study presented here, has been carried out as a supplementary study to the Leipzig riparian forest crane project (LAK, for the German name of the project: Leipziger-Auwald-Kran Projekt). The advantage of fogging is that it allows to collect free living arthropods almost quantitatively and in a tree specific way without causing too much spatio-temporal disturbance (Floren & Schmidl 2003; Bussler *et al.* 2004). Fogging data supply background information about the size, composition, and structure of arboreal communities, which are essential for a better understanding of many ecosystem processes and ecosystem services.

The fogging data are unique in respect to community structure and composition and can not be obtained by any other method like air eclectors, beating samples, etc. For instance, weevils clearly dominate in the canopy both in respect to species richness and species abundance (cf. Table 2). On average, Chrysomelidae and Curculionoidea represented 11.5% and 46 species of all beetles. Within this group the proportion of endangered or faunistically remarkable species was high and amounted to 14 species or 30%. In contrast, Schmidt (2004) – who collected at the crane site with flight-interception traps and branch-eclectors over a period of six months in 2002 – collected only 25 species of Curculionidae and Apionidae, clearly less than the 37 weevil species from the fogging samples (Schmidt did not evaluate Chrysomelidae). Only two species were exclusively collected with the eclectors (*Hypera contaminata* and *Bradybatus kellneri*). Of all species sampled by fogging, 15 (32.6%) were typical herb layer species, which do not reproduce in the trees. They may instead enter the trees to rest, for their dispersal flight, or for some other reasons. For example, the analysis of August fogging samples from *Q. petraea* near Schweinfurt, showed that several thousand individuals of phytophagous leaf beetle and weevil species from the herb layer and from reaped grain fields had immigrated into the canopy (unpublished data).

An unexpected result of this study was that phytophagous weevils with rhizophagous larvae from the genera *Phyllobius*, *Strophosoma* and *Polydrusus* were always rare. With 43 individuals, *Phyllobius calcaratus* was the most frequent of the phytophagous generalists, *Strophosoma capitatum* (27 individuals) was collected only from five trees and with a maximum of ten specimens, the remaining species were found with no more than three individuals. The number of polyphagous species collected from other forests was similar (Table 2). However, not the low abundances of individual species were remarkable, but rather the low total numbers within this guild. Surprisingly, Schmidt (2004) found no individuals of *Phyllobius*, *Polydrusus* or *Strophosoma* at all. The reasons for this are neither known nor can they be explained by weather-related characteristics (pers. comm. O. Tal).

In contrast to the Leipzig riparian forest, considerably more generalist leaf feeders were found on individual trees in fogging samples from Hainich National Park (Thuringia), the Steigerwald forest (Bavaria) and the Bialowieza primeval forest (Poland), (Table 2).

Generalist leaf feeders always made up the main proportion of Curculionoidea and ranked among the most common species. *Polydrusus pterygomalis*, for example, was the most frequent species in Hainich and found on most trees with hundreds of individuals but was rare on *A. platanoides* (Floren unpublished). In the Steigerwald forest, numbers of generalist leaf feeders with rhizophagous larvae were lower compared to those of Hainich National Park and the Polish primeval forests, but *Strophosoma melanogrammum* appeared in considerable numbers.

The composition of the arthropod communities

As demonstrated by the foggings, the Leipzig riparian forest harbours a rich canopy arthropod fauna. Community size varied strongly between trees. Despite these differences, arthropod communities were regularly structured at the order-level both on homospecific trees as well as between tree species. The predominant groups (Homoptera, Diptera, parasitic Hymenoptera, Psocoptera and Heteroptera) also showed the largest variability in their relative proportions. Regularly composed communities were also found in other studies (Table 2) but had first been described from tropical lowland forest trees (Stork 1991; Floren & Linsenmair 1997). This indicates that community composition on the order level is the result of random processes whereas tree species specific patterns appear at the genus- or species level (Floren unpublished). The correspondence analysis separated the assemblages of phytophagous Coleoptera between tree species surprisingly well. This was a consequence both of the only few specialist species and of low abundances of generalists, of which several species were mutually exclusive. At least for the more frequent species *Strophosoma capitatum* and *Phyllobius calcaratus*, mutual exclusion was most likely not accidentally even if the reason for this separation is not known. As shown by the faunistic data, the genus *Quercus* is particularly important for species diversity (see Floren & Schmidl in press).

The arthropod numbers in the trees

Standardising the number of arthropods to sample size and leaf cover, allows direct comparison of arthropod numbers between trees. These data give an impression of the real numbers of arthropods per volume unit in a tree crown. They are a measure of food availability for insectivorous animals, like birds who feed primarily on soft-skinned, larger arthropods as caterpillars, spiders, or beetles which can also be a quite important food source (Wimmer & Winkel 2000). Furthermore, bats are hunting in the canopy (see Rieger *et al.*, this volume), catching arthropods from leaves and from the bark (Meschede & Heller 2002), as does the tree frog *Hyla arborea*, which has been found in the canopy (Schmidt *et al.* 2003). Standardised arthropod numbers can therefore provide basic information for food-ecological analyses of insectivorous animals in the canopy.

Table 2 – Abundance and species richness of arboreal phytophagous Curculionoidea in various forests. Generalists=polyphagous leaf feeders with rhizophagous larvae. F. exc.: *F. excelsior*, Q. rob.: *Q. robur*, A. pla.: *A. platanoides*, A. psd.: *A. pseudoplatanus*, T. cor.: *T. cordata*, A. cam.: *A. campestre*, F. syl.: *F. sylvatica*, C. bet.: *C. betulus*, U. lae.: *U. laevis.*

	Leipzig riparian forest June 2003	**Hainich June 1997**	**Steigerwald forest August 1995**	**Steigerwald forest May 1996**	**Bialowieza primeval forest June 2001**	**Bialowieza primeval forest June 2001**
Tree species and number of fogged trees	F. exc. (3) Q. rob. (2) A. pla. (6) A. psd. (5) T. cor. (4) A. cam. (1)	F. syl. (6) A. psd. (4) C. bet. (4) A. pla. (1) Q. pet. (1) U. lae. (1)	Q. pet. (10)	Q. pet. (9)	Q. rob. (9) C. bet. (6) A. pla. (1)	Q. rob. (13)
Total number of foggings	21	17	10	9	16	13
Species of Curculionoidea	37	12	25	13	149	28
Sum of all Curculionoidea	357	5,054	369	549	7,468	5,387
Generalist species	6	5	4	2	6	6
Sum generalists	79	4055	203	428	7075	5093

The large variability of arthropod numbers between similar trees might hint towards the importance of chance effects during the colonization of tree crowns. This is also indicated by re-foggings carried out one day after the first fogging in the Steigerwald forest (Bavaria), in the Bialowieza primeval forest (Floren unpublished), and in tropical lowland rain forest (Floren 2003).

In these experiments arthropods were found to vary unpredictably in numbers fluctuating by several hundred percent, indicating that tree communities are highly dynamic systems. Many of the more mobile arthropods are obviously moving freely in the continuum of the canopy staying only for a brief period in a tree crown. Since natural pyrethrum does not leave persistent substances in the trees, the arthropods collected in the re-foggings were certainly specimens, which had immigrated newly. This is also corroborated by investigations of recolonization on *Pinus* trees (Schmidl & Bail unpublished). These results show how heterogeneously food is distributed in the trees, at least when no species is going through a mass reproduction.

To conclude, high species diversity and abundance of arboreal arthropods point to their great importance for many processes in the ecosystems. They influence energy- and nutrient transfer within the ecosystem, reduce plant biomass, and influence population dynamics of arthropods and so on. Their great importance becomes obvious for example when certain species reproduce massively, causing major economic damage. The finding of an unexpectedly high number of faunistically interesting species as well as species new to science in other taxa like parasitic Hymenoptera and Diptera (Horstmann & Floren 2001; Stark in press) is a consequence of the previously limited collecting activity in the canopy. Furthermore, tree specific arthropod communities can be used as a model system in basic and applied research. This should be sufficient reason to consider the canopy in future ecosystem analysis.

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Appendix Table 1 – Absolute numbers and relative proportion of arthropod taxa fogged from individual trees. Abbreviations of trees see Table 2, Lepi.: Lepidoptera

	Fe1		**Fe11**		**Fe16**		**Qr2**		**Qr4**		**Apl3**		**Apl5**		**Apl6**		**Apl18**	
	Abs	**%**																
Coleoptera	201	15.00	68	2.26	84	0.88	327	18.36	371	12.69	207	4.32	137	5.19	120	3.21	99	1.64
Hymenoptera	320	23.88	311	10.36	856	8.98	225	12.63	270	9.23	378	7.90	443	16.79	933	24.93	491	8.14
Formicidae	4	0.30	4	0.13	9	0.09	31	1.74	160	5.47	185	3.86	0	0.00	16	0.43	1	0.02
Diptera	200	14.93	737	24.54	1400	14.69	350	19.65	700	23.94	1279	26.72	713	27.03	830	22.17	1250	20.71
Homoptera	85	6.34	800	26.64	4050	42.49	300	16.84	600	20.52	1800	37.60	700	26.54	1000	26.72	3100	51.37
Heteroptera	180	13.43	53	1.76	1370	14.37	275	15.44	215	7.35	452	9.44	330	12.51	48	1.28	32	0.53
Orthoptera	14	1.04	6	0.20	18	0.19	9	0.51	11	0.38	79	1.65	31	1.18	24	0.64	44	0.73
Araneae	67	5.00	52	1.73 99	1.04	46	2.58	208	7.11	131	2.74	137	5.19	21	0.56	73	1.21	
Acarina	5	0.37	9	0.30	23	0.24	5	0.28	0	0.00	19	0.40	10	0.38	0	0.00	20	0.33
Opiliones	4	0.30	4	0.13	4	0.04	10	0.56	64	2.19	9	0.19	8	0.30	0	0.00	8	0.13
Thysanoptera	90	6.72	274	9.12	330	3.46	34	1.91	60	2.05	39	0.81	21	0.80	94	2.51	40	0.66
Collembola	0	0.00	2	0.07	15	0.16	5	0.28	0	0.00	5	0.10	9	0.34	1	0.03	130	2.15
Neuroptera	27	2.01	5	0.17	70	0.73	113	6.34	64	2.19	17	0.36	45	1.71	18	0.48	17	0.28
Psocoptera	90	6.72	638	21.25	985	10.33	16	0.90	140	4.79	86	1.80	19	0.72	476	12.72	669	11.09
Blattodea	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Lepidoptera Adults	25	1.87	10	0.33	138	1.45	11	0.62	30	1.03	17	0.36	1	0.04	12	0.32	5	0.08
Lepidoptera Larvae	18	1.34	2	0.07	8	0.08	3	0.17	22	0.75	10	0.21	29	1.10	8	0.21	9	0.15
other arthropods	10	0.75	11	0.37	33	0.35	12	0.67	3	0.10	74	1.55	5	0.19	13	0.35	9	0.15
other larvae	0	0.00	17	0.57	39	0.41	9	0.51	6	0.21	0	0.00	0	0.00	129	3.45	38	0.63
all arthropods	1340		3003		9531		1781		2924		4787		2638		3743		6035	

Appendix Table 1 continued – Absolute numbers and relative proportion of arthropod taxa fogged from individual trees. Abbreviations of trees see Table 2, Lepi.: Lepidoptera

	Apl19		**Apl20**		**Aps7**		**Aps12**		**Aps13**		**Aps21**		**Aps15**		**Ac14**		**Tc8**	
	Abs	**%**																
Coleoptera	55	1.50	94	1.60	94	1.67	50	1.72	130	3.34	83	1.77	157	2.47	160	3.08	171	2.14
Hymenoptera	199	5.42	252	4.28	626	11.12	150	5.17	190	4.88	132	2.82	352	5.53	231	4.44	788	9.84
Formicidae	0	0.00	0	0.00	18	0.32	4	0.14	85	2.18	0	0.00	0	0.00	21	0.40	40	0.50
Diptera	576	15.69	1303	22.15	950	16.88	380	13.10	550	14.12	555	11.84	722	11.34	748	14.38	1490	18.61
Homoptera	1932	52.64	2648	45.01	2000	35.53	1800	62.05	2150	55.18	2663	56.83	2995	47.05	2800	53.84	3880	48.45
Heteroptera	29	0.79	407	6.92	715	12.70	18	0.62	83	2.13	299	6.38	1038	16.31	411	7.90	719	8.98
Orthoptera	52	1.42	63	1.07	65	1.15	15	0.52	10	0.26	3	0.06	94	1.48	232	4.46	120	1.50
Araneae	90	2.45	86	1.46	112	1.99	47	1.62	77	1.98	81	1.73	99	1.56	236	4.54	123	1.54
Acarina	0	0.00	0	0.00	260	4.62	15	0.52	0	0.00	0	0.00	18	0.28	15	0.29	35	0.44
Opiliones	1	0.03	4	0.07	8	0.14	1	0.03	19	0.49	1	0.02	1	0.02	33	0.63	28	0.35
Thysanoptera	37	1.01	21	0.36	140	2.49	41	1.41	0	0.00	7	0.15	33	0.52	34	0.65	56	0.70
Collembola	42	1.14	128	2.18	15	0.27	8	0.28	115	2.95	14	0.30	26	0.41	35	0.67	10	0.12
Neuroptera	13	0.35	10	0.17	13	0.23	12	0.41	8	0.21	27	0.58	26	0.41	6	0.12	33	0.41
Psocoptera	614	16.73	820	13.94	510	9.06	330	11.38	350	8.98	782	16.69	709	11.14	104	2.00	326	4.07
Blattodea	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Lepidoptera Adults	0	0.00	16	0.27	25	0.44	5	0.17	13	0.33	0	0.00	2	0.03	8	0.15	43	0.54
Lepidoptera Larvae	7	0.19	4	0.07	20	0.36	8	0.28	6	0.15	5	0.11	7	0.11	59	1.13	27	0.34
other arthropods	1	0.03	27	0.46	37	0.66	6	0.21	18	0.46	14	0.30	21	0.33	62	1.19	119	1.49
other larvae	22	0.60	0	0.00	21	0.37	11.00	0.38	92	2.36	20	0.43	65	1.02	6	0.12	0	0.00
all arthropods	3670		5883		5629		2901		3896		4686		6365		5201		8008	

Appendix Table 1 continued – Absoulte numbers and relative proportion of arthropod taxa fogged from individual trees. Abbreviations of trees see Table 2.

	Tc9		**Tc10**		**Tc17**	
	Abs	**%**				
Coleoptera	80	2.31	141	3.36	127	1.85
Hymenoptera	284	8.21	439	10.47	214	3.12
Formicidae	53	1.53	116	2.77	4	0.06
Diptera	1202	34.74	1210	28.86	950	13.86
Homoptera	1051	30.38	1039	24.78	4312	62.92
Heteroptera	21	0.61	257	6.13	369	5.38
Orthoptera	9	0.26	24	0.57	32	0.47
Araneae	32	0.92	69	1.65	70	1.02
Acarina	20	0.58	50	1.19	75	1.09
Opiliones	6	0.17	13	0.31	4	0.06
Thysanoptera	500	14.45	460	10.97	25	0.36
Collembola	15	0.43	58	1.38	125	1.82
Neuroptera	9	0.26	20	0.48	7	0.10
Psocoptera	76	2.20	185	4.41	415	6.06
Blattodea	0	0.00	0	0.00	0	0.00
Lepi. Adults	4	0.12	25	0.60	12	0.18
Lepi. Larvae	36	1.04	10	0.24	40	0.58
other arthropods	9	0.26	50	1.19	47	0.69
other larvae	53	1.53	27	0.64	25	0.36
all arthropods	3460		4193		6853	

Appendix Table 2 – Arthropods standardised on 1 m^2 and 100% leaf cover for all main taxa. Last line (all arthropods) Values rounded up. Abbreviations of trees see Table 2.

	Fe1	**Fe11**	**Fe16**	**Qr2**	**Qr4**	**Apl3**	**Apl5**	**Apl6**	**Apl18**	**Apl19**	**Apl20**
Coleoptera	5.0	2.8	2.4	9.3	13.3	3.8	3.8	3.3	2.1	2.0	2.2
Hymenoptera	8.1	12.9	24.7	7.3	15.4	10.4	12.3	26.4	10.3	7.1	6.0
Diptera	5.0	30.1	40.0	10.0	25.0	23.7	19.8	23.1	26.0	20.6	31.0
Homoptera	2.1	32.7	115.7	8.6	21.4	33.3	19.4	27.8	64.6	69.0	63.0
Heteroptera	4.5	2.2	39.1	7.9	7.7	8.4	9.2	1.3	0.7	1.0	9.7
Orthoptera	0.4	0.2	0.5	0.3	0.4	1.5	0.9	0.7	0.9	1.9	1.5
Arachnida	1.9	2.7	3.6	1.7	9.7	2.9	4.3	0.6	2.1	3.3	2.1
Thysanoptera	2.3	11.2	9.4	1.0	2.1	0.7	0.6	2.6	0.8	1.3	0.5
Neuroptera	0.7	0.2	2.0	3.2	2.3	0.3	1.3	0.5	0.4	0.5	0.2
Psocoptera	2.3	26.0	28.1	0.5	5.0	1.6	0.5	13.2	13.9	21.9	19.5
Lepidoptera	0.7	0.5	1.2	0.4	0.9	0.5	0.8	0.6	0.4	0.3	0.5
Others	0.6	1.2	5.5	0.7	1.3	1.5	0.4	4.0	3.6	2.3	3.7
All arthropods	34	123	272	51	104	89	73	104	126	131	140

Appendix Table 2 continued – Arthropods standardised on 1 m^2 and 100% leaf cover for all main taxa. Last line (all arthropods) Values rounded up. Abbreviations of trees see Table 2.

Aps7	**Aps12**	**Aps13**	**Aps21**	**Aps15**	**Ac14**	**Tc8**	**Tc9**	**Tc10**	**Tc17**	
Coleoptera	3.5	2.0	4.1	2.0	4.4	3.6	4.8	2.5	3.1	2.6
Hymenoptera	23.9	6.3	8.6	3.3	9.8	5.6	23.0	10.5	12.3	4.5
Diptera	35.2	15.5	17.2	13.7	20.1	16.6	41.4	37.6	26.9	19.8
Homoptera	74.1	73.5	67.2	65.8	83.2	62.2	107.8	32.8	23.1	89.8
Heteroptera	26.5	0.7	2.6	7.4	28.8	9.1	20.0	0.7	5.7	7.7
Orthoptera	2.4	0.6	0.3	0.1	2.6	5.2	3.3	0.3	0.5	0.7
Arachnida	14.1	2.6	3.0	2.0	3.3	6.3	5.2	1.8	2.9	3.1
Thysanoptera	5.2	1.7	0.0	0.2	0.9	0.8	1.6	15.6	10.2	0.5
Neuroptera	0.5	0.5	0.3	0.7	0.7	0.1	0.9	0.3	0.4	0.1
Psocoptera	18.9	13.5	10.9	19.3	19.7	2.3	9.1	2.4	4.1	8.6
Lepidoptera	2.1	0.6	0.8	0.5	0.8	1.5	1.9	1.4	0.8	1.1
Others	2.3	1.0	6.9	0.8	2.6	2.3	3.6	2.3	3.0	4.1
All arthropods	208	118	122	116	177	116	222	108	93	143

3.9 Vertical stratification of bat activity in a deciduous forest

INGO RIEGER[1] & PETER NAGEL

The use of the Leipzig Canopy Crane (LAK) allowed a three-dimensional survey of bat activity (measured as ultrasonic activity) in a deciduous forest in central Germany. During an intense sampling period of two weeks in summer 2002, bat ultrasounds from 20 detectors were recorded simultaneously. The detectors were placed at four habitat types like windthrow gap or canopy depression and distributed vertically from the top canopy layer to the bush layer. Almost half of the detectors were in places where bats passed within the detectors sensitivity cone. The variation in the amount of recorded data was surprisingly high: The inter-night variability of the data from one detector was high as was the variation between detectors during one night. Bat activity was higher in the second half of the night than in the first. It was originally assumed that bats hunting in forests preferred to use areas on top of the forest canopy. This study confirmed not only this initial assumption but indicated also that the bats were active in the lower canopy and trunk layer. The detection of discrete patterns of spatial and temporal use of the three-dimensional forest environment appears possible with the described methods but only long-term studies covering the whole flight season will produce more statistically significant results.

INTRODUCTION

Knowledge on the pattern of spatial and temporal use of habitat forms part of the fundamental characterization of animal species. It also serves as a basis for a range of practical applications (ROSE *et al.* 2006). In conservation biogeography information on the spatio-temporal behaviour of animals contributes significantly to the design of adequate management for the preservation of biodiversity (NAGEL 1999).

Observations of Daubenton's Bats, *Myotis daubentoni*, in the area of Rhine falls (47.6°N, 8.6°E) show that these animals not only hunt over the river, but move to nearby forests and hunt there. In these studies, the activities of some 30 radio-tagged Daubenton's bats were recorded. The activity area of these radio-tagged individuals flying in forests, was identified at a tolerance of less than 50 m. If observer and radio-tagged animal were both in the forest, the observer received the radio signal, but never any ultrasonic orientation sounds on the bat detectors, so one must assume that the radio-tagged Daubenton's bats were flying in or above the canopy level out of range of bat detectors. It is assumed, therefore, that the Daubenton's bats hunting in forests were active on top of the canopy, most probably in canopy depressions (NYHOLM 1965, RIEGER *et al.* 1992, RIEGER & ALDER 1994, RIEGER, unpublished observations).

A deciduous forest provides different ecological niches where different bat species might forage. Morphology and behaviour of bat species are consequently adapted to their preferred ecological niches (e.g. SCHNITZLER & KALKO, 2001). Until now, systematic and long term studies on bat foraging behaviour in forests are not available; the only available data are based on radio-telemetry feedback (e.g. GÜTTINGER 1997; ALTRINGHAM *et al.* 1998; KERTH *et al.* 2001), thermography and anecdotal observations (e.g. NYHOLM 1965; AHLÈN 1981; RACEY & SWIFT 1985; GROUPE MAMMALOGIQUE NORMAND 1988; WALSH & HARRIS 1996; RACEY 1998; CIECHANOWSKI 2002).

Equipment allowing a bat observer to be close to areas and levels in a forest far above the ground where Daubenton's bats may be active would help to test the assumption for this and other species. The canopy observation crane of the Leipzig Canopy Crane Project (MORAWETZ & HORCHLER 2002) provided these conditions. Around the project area, the following bat species were recorded: Daubenton's bat, *Myotis daubentoni*, Greater Mouse-eared Bat, *Myotis myotis*, Barbastelle bat, *Barbastella barbastellus*, Brown Long-eared Bat, *Plecotus auritus*, Grey Long-eared Bat, *Plecotus austriacus*, Parti-coloured bat, *Vespertilio murinus*, Serotine bat, *Eptesicus serotinus*, Pipistrelle Bat, *Pipistrellus pipistrellus*, Soprano Pipistrelle, *Pipistrellus pygmaeus*, Nathusius' Pipistrelle, *Pipistrellus nathusii*, Noctule Bat, *Nyctalus noctula* (SCHOBER 1989; 1997; SCHOBER & MEYER 1995),

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[1] corresponding author

to which Leisler's bat, *Nyctalus leisleri*, Bechstein's bat, *Myotis bechsteini*, and Brandt's or Whiskered bat, *Myotis brandti/mystacinus* have recently been added (Fichtner 2004). It was decided to three-dimensionally register the bat activity in order to obtain information on the way bats forage in a deciduous forest. A comparable three-dimensional bat screening in a Central European forest hunting habitat has not been carried out before. A similar study was done at the Wind River Canopy Crane Facility in the Cascade Mountains (Washington, USA) by Hayes & Gruver (2000). They found a substantial difference in the use of vertical structure by bats, among both *Myotis* and non-*Myotis* species, and changes that occurred even within the same night. Kalcounis *et al.* (1999) collected data on vertical stratification of bat activity in a North American forest using BOREAS flux towers. Their monitoring of echolocation calls through different forest canopy layers indicates a species specific use of canopy layers. Wunder & Carey (1996) concluded that foraging behaviour of bats in forests in the northwestern USA is highly variable between bat species as well as between habitats.

The goal of the present study was to obtain a first overview of the bats' vertical and horizontal habitat use linked with the daily temporal distribution of bat activity in a Central European deciduous forest.

MATERIALS AND METHODS

In the north-western part of the extensive floodplains around the city of Leipzig (51°20'16"N, 12°22'26"E), the Department of Systematic Botany of the University of Leipzig installed in 2001 a crane system in a deciduous, former floodplain forest. In a gondola, scientists can reach over a surface of 1.6 ha nearly every point between ground level and 33 m above ground level (Morawetz & Horchler 2002).

The following trees grow naturally in the study forest: *Acer campestre*, *Acer platanoides*, *Acer pseudoplatanus*, *Carpinus betulus*, *Fraxinus excelsior*, *Quercus robur*, *Tilia cordata*, *Ulmus glabra*, *Ulmus minor*. The following species have been planted: *Aesculus hippocastanum*, *Fraxinus pennsylvanica*, *Populus* x *canadensis*, *Quercus rubra*, *Robinia pseudoacacia*. Dominant tree species are *Acer pseudoplatanus*, *Fraxinus excelsior*, *Tilia cordata*, *Acer platanoides*, *Carpinus betulus*, *Ulmus* cf. *minor*, *Quercus robur* (Seele 2004). The highest trees in the study forest reach heights of 35 to 40 m. Daubenton's bats use running and standing water as foraging places. Such habitats are present within a radius of a few hundred metres from the study site.

In order to obtain information on the temporal and spatial distribution of bats in the forest, four recording units were used. At the heart of each recording unit was a computer (running the software VRS Recording System, NCH Swift Sound) which recorded sound information provided by the bat detectors. Five ultrasonic detectors (type SBD2 of Nevada Bat Technology) were attached to the computer of each recording unit. The SBD2-detector uses a transducer (Ultrasonic transducer 255-400sr16, Mouser Electronics).

The signals of the SBD2 detectors allow evaluations of the time patterns of the ultrasounds such as duration of sound events (= an uninterrupted sound track recorded by the VRS software), pulse durations and length of intervals between pulses (Fig. 1). All bat detectors were calibrated using the sound sensitivity level of the VRS Recording System software.

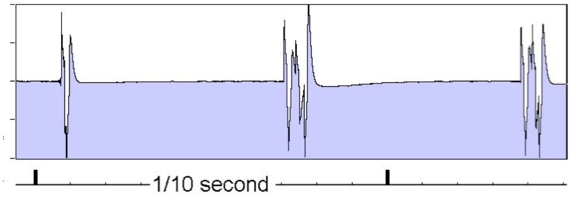

Figure 1 – Amplitude course of 0.15 seconds of a sound event recorded with an SBD2-Bat-Detector. This type of signal allows studies on time patterns of the ultrasounds such as duration of sound events, pulse durations and length of intervals between pulses.

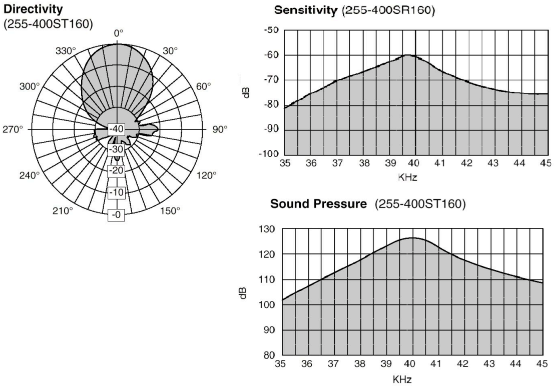

Figure 2 – Directivity, sensitivity and sound pressure of the Ultrasonic transducer 255-400sr16 from Mouser Electronics, used in the SBD2 Bat Detector (data from the data sheet; `www.mouser.com`).

The SBD2-detector records ultrasonic frequencies around 40 kHz (Fig. 2). It thus indicates the presence of *Myotis daubentoni*, *Pipistrellus nathusii*, *P. pipistrellus* (confirmed in pre-tests), most probably also the infrequent individuals of *Myotis myotis* and *Barbastella barbastellus*.

The four recording units were positioned in different habitats in the study forest (1 Forest SE, a canopy depression; 2 Rail track N, a vertical channel of a width of approximately 5 m, 3 Rail track S, forest gap of 10 to 15 m width, 4 Forest NW, a clearing caused by windthrow of an oak tree) (Fig. 3, 4). The five detectors attached to a recording unit were installed on levels 5 m, 10 m, 15 m, 25 m and 35 m (± 20%) above ground (bush layer, trunk layer, sub, middle and top canopy). The recording units operated from July 12 to July 24 in 2002. In two nights (July 16 and 17), the recording units were switched off because of thunderstorms. Daily, the data recorded during the previous night was copied on a backup computer and at the same time it was tested if the detectors were working properly.

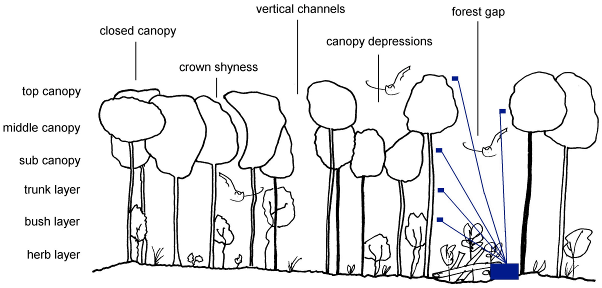

Figure 3 – Schematic view of the different vertical layers within the floodplain forest which might be important for animal stratification. Horizontally different kinds of openings are indicated beginning from the closed canopy to small openings as performed by crown shyness, narrow vertical channels towards the ground, canopy depressions and larger forest gaps (drawing by W. Morawetz). The detectors were positioned on the vertical levels bush (some 5 metres above ground), trunk (10 m), sub canopy (15 m), middle canopy (25 m), top canopy (35 m).

For the data analysis, only ultrasonic recordings were used that agreed with the following conditions: (1) recorded between sunset (around 21:20 h) and sunrise (around 05:15 h); (2) duration longer than 1.13 seconds – this was the shortest sound event recorded by the VRS software: the recording was initiated by a short pulse and stopped after 1.13 seconds with incoming noise with amplitudes lower than the selected threshold; Some 5 000 recorded sound files were obtained under these conditions.

The meteorological data (10 min temperature means [with a degree of accuracy of 0.1 °C]; mean wind velocity in 10 min [0.1 m/s]; precipitation sum in 10 min [0.1 mm]) originate from the meteorological station Leipzig Schkeuditz, located some 10 km west of the study forest (51.26°N, 12.14°E; Mirakel database). Weather conditions at Schkeuditz were similar to those at the study area.

Figure 4 – Arial view of the crane range, crane rail track (length: 120 metres), location of control units 1 to 4: unit 1: Forest SE – a canopy depression; unit 2: Rail track N – an approximately 5 m broad vertical channel; unit 3: Rail track S – the crane rail track is in a 10 to 15 m wide forest gap; unit 4: Forest NW – a recent clearing in the forest, due to a huge oak tree blown down in a heavy storm.

RESULTS

With the hardware and software equipment used in this study, it was not possible to attribute ultrasonic activity to particular bat species. Based on observations during dawn together with information from a heterodyning bat detector (Pettersson D200) it is known that the study forest is used by the Noctule (ultrasonic sound at around 20 kHz), Serotine bat (around 30 kHz) and Soprano Pipistrelle (around 55 kHz). The SBD2- Detectors do not process the ultrasonic sounds of these species. The same applies to the ultrasonic sounds emitted by Parti-coloured bats and the Barbastelle Bat (around 30 kHz) known to exist in the Leipzig area (SCHOBER & MEYER 1995, FICHTNER 2004). Because of their very quiet calls, it is improbable that the two long-eared bat species were recorded. Considering all these factors, it is assumed that Daubenton's bat, Greater Mouse-eared Bat, Pipistrelle Bat and Nathusius' Pipistrelle contributed to the set of ultrasound recordings analysed in the present study. Furthermore, in the north and in the south of the crane area, two flight paths of Daubenton's bat were found. This observation supports the idea that Daubenton's bats might be responsible for a considerable proportion of the entire bat activity in the study forest.

During eleven control nights from July 12 to 24, the four recording units, each with five ultrasonic detectors, recorded ultrasonic sound files with a total duration of more than 24 hours. On average, each of the 20 detectors recorded 6.5 min ultrasonic sound per night. During the night of July 18, ultrasonic activity was 18 times higher than in the night with the lowest ultrasonic activity (July 20). In most nights, seven to nine of the 20 detectors recorded ultrasonic signals, only during nights with very low bat activity (measured as ultrasonic activity; July 20 and 24) were the numbers of active detectors as low as 4 and 6 (Table 1).

Table 1 – Ultrasonic recordings in eleven control nights in July 2002.

July, night of	Total time [min] of the registered ultrasonic events per control night from 20 detectors	Number of active detectors
12	89	8
13	449	9
14	113	9
15	32	9
16-17	thunderstorm	
18	455	8
19	137	9
20	2	4
21	6	8
22	14	7
23	143	7
24	3	6

For the eleven control nights no obvious correlations between weather parameters and bat activity were evident (the data set is to small for a sound statistical analysis). During one night with rather high wind activity (July 18 to 19) bat activity increased, in a second night with high winds (July 21 to 22), bat activity did not increase (Fig. 5).

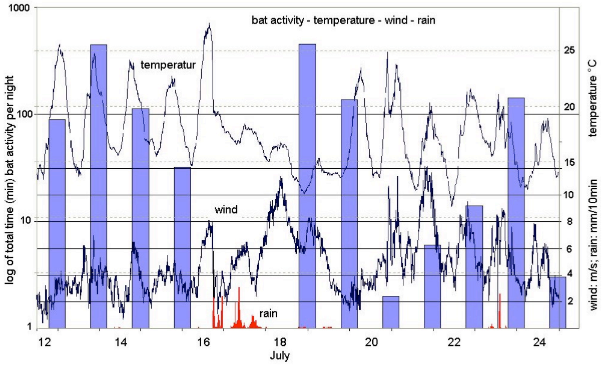

Figure 5 – Bat activity (measured as minutes per night with ultrasonic activity on at least one detector) as compared to meteorological data (wind speed in metres per second; rain in millimetres by 10 min; mean air temperature in [°C]).

The bat activity varied greatly between recording units. The recording unit with the highest bat activity recorded 3.6 times more activity than the recording unit with lowest bat activity (Table 2). Approximately four fifth of the entire bat activity was recorded at the two recording units in the forest (recording units 'Forest SE' and 'Forest NW'). At three of the four recording units, the mean duration of a bat flying within the sensitivity cone of a detector was in the range of a quarter of a minute. At the recording unit 'Rail track S' (a point with forest clearing character), the mean duration of a bat within the sensitivity cone was about three times longer (Table 2).

Table 2 – Comparison of the bat activity at four different control units (data from all five detectors of a control unit).

Control unit	Total recording time [min] of all 5 detectores of the control unit	Number of events	Mean duration [min] per event
Forest SE	824	2464	0.33
Rail track N	250	995	0.25
Rail track S	181	221	0.82
Forest NW	324	1405	0.23
total	1579	5085	0.31 (average)

Approximately three quarters of the bat activity was recorded by detectors in the upper canopy range (25 to 35 m above ground). The fourth quarter of bat activity was more or less evenly distributed between bush, trunk and lower canopy range. The vertical distribution of the bat activity varied between recording units. Neither of the samples from the two recording units in the crane track ('Rail track N' and 'Rail track S') recorded bat activity at bush and trunk level (5 and 10 metres above ground) (Table 3).

Table 3 – Three-dimensional distribution of the bat activity during eleven control nights in July 2002; a: the whole data set originates from only one night (July 18 to 19); b: no data from the nights from July 19 to July 24 due to malfunctioning of the detector; c: no data from July 19.

	Total duration of recording at four control units [min]									
Detector height above ground ± 20% [m]	**Forest SE**		**Rail track N**		**Rail track S**		**Forest NW**		**Total**	
	min	**%**	**min**	**%**	**min**	**%**	**min**	**%**	**min**	**%**
35	476	58	218 (b)	87	0	0	82 (c)	25	776	49
25	58	7	32	13	0	0	209 (c)	65	229	19
15	75	9	0	0	181	100	0 (c)	0	256	16
10	0	0	0	0	0	0	19 (c)	6	19	1
5	215 (a)	29	0	0	0	0	14 (c)	4	229	15
total	824	100	250	100	181	100	324	100	1579	100

Table 4 – Distribution of the bat activity between sunset (21:20 h) and sunrise (05:15 h) during eleven control nights in July 2002.

Relative time of day 1.0 = 24.00 h		**Total duration of recorded ultrasound [min]**	**Number of events**	**Mean duration per event [min]**
from (CEST)	**to (CEST)**			
0.825	0.85	0	0	0
0.85	0.875	81	202	0.4
0.875	0.9	208	619	0.34
0.9	0.925	235	891	0.26
0.925	0.95	203	764	0.27
0.95	0.975	167	548	0.3
0.975	0	127	554	0.23
0	0.025	154	624	0.25
0.025	0.05	202	728	0.28
0.05	0.075	233	798	0.29
0.075	0.1	260	835	0.31
0.1	0.125	219	791	0.28
0.125	0.15	216	767	0.28
0.15	0.175	245	892	0.27
0.175	0.2	215	779	0.28
0.2	0.225	111	339	0.33
0.225	0.25	13	39	0.33
0.25	0.275	0	0	0

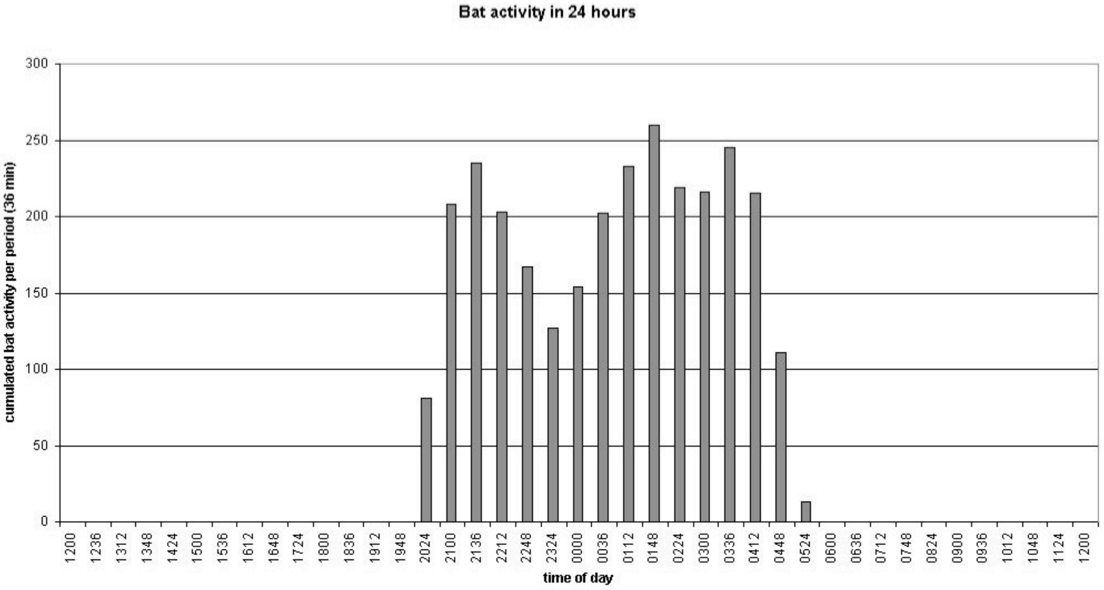

Figure 6 – Bat activity in the course of the night (cumulation of duration of all recorded sound events in the respective 36 min periods); summary of the data from eleven control nights in July 2002.

The bat activity in the forest reached a first maximum shortly before 22:00 h (CEST Central European Summer Time, about 40 min after sunset), and an activity minimum was noted around midnight (about 2 hours after sunset). Subsequently, the activity increased again and achieved around 02:30 h the highest value. Bat activity continued to be high until an abrupt end around sunrise (05:15 h). There was more bat activity in the second half of the night than in the first (Table 4, Fig. 6). The highest bat activities were recorded by the detectors in the top canopy level of recording units 'Forest SE' and 'Rail track N'. On average one ultrasonic event per minute was recorded between sunset and sunrise in the top canopy of recording unit 'Forest SE'.

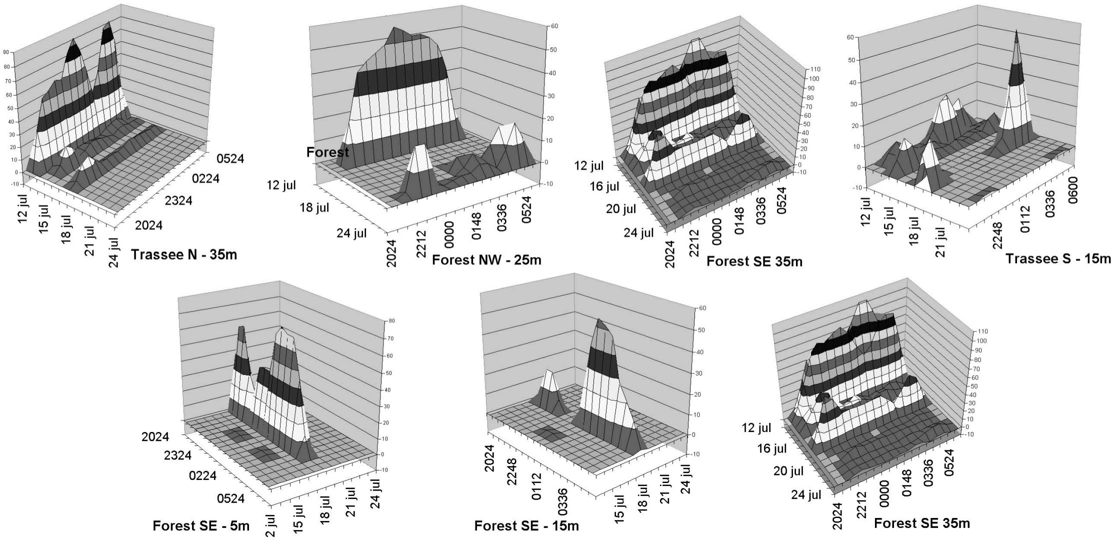

Figure 7 – Bat activity samples at selected detectors between sunset (21:20 h) and sunrise (05:15 h) during 11 control nights in July 2002.

During the two study weeks, no obvious general pattern of bat activity, valid for all recording units, was found. Bat activity changed from night to night within one night, from recording unit to recording unit and within a recording unit from level to level (Fig. 7).

The activity patterns of the 5 and 15 m detectors of recording unit 'Forest SE' show a certain similarity that allows assumptions that bats may use here a three dimensional space between lower canopy and forest ground.

DISCUSSION

Ecological studies of bats foraging in forests easily encounter limits because it is difficult to continuously observe the animals in this type of habitat (Patriquin & Barclay 2003). Most descriptions of behaviour of European forest bats are based on sporadic observations (Nyholm 1965, Benk 1981, Groupe Mammalogique Normand 1988, Ahlèn & Gerell 1989, Dietz 1993, Rydell *et al.* 1994, Zahn & Krüger-Barvels 1996, Güttinger 1997). The methods used by Kalcounis *et al.* (1999) are comparable to our methods.

The present study is based on 20 simultaneously running detectors. During the short, two weeks study, 9 out of the 20 detectors (45%) provided bat ultrasonic data whereas 11 detectors (55%) detected nothing. This indicates that bats flying in a forest have very specific patterns of use of the micro-habitats within a forest. But only a long term study would reveal if the observed patterns are an artefact of variation in daily patterns of activity, because with additional sampling such a pattern would either be dissolved or enhanced.

The forest investigated in Leipzig represents a rather old stand with a normal distribution of stem diameters and trees from seedlings to ca. 300 years old oaks. This diversity in age classes and distribution and the high species richness (16 tree species) causes a rather irregular structure of the forest canopy and surface (see Fig. 3): We encounter parts with extremely closed canopy, parts with crown-shyness of different tree species and therefore open 'ways' of 30–50 cm width (see Morawetz 1998), small to larger depressions within the canopy due to different species or age of trees, vertical channels of 3–5 m in diameter. from the ground to the canopy and larger openings from fallen trees. It was originally assumed that bats hunting in forests preferred to use areas on top of the forest canopy. This study confirmed not only this initial assumption but indicated also that the bats were active in the lower canopy and trunk level (see 'Forest SE'). In the light of the above described structure analysis, and taking into account that clutter measurements are not available, we might interpret that the bats look for the best ways for flying. They find them above and below the canopy, in some places also in the canopy, depending on the local structure and tree species composition. Bat activity may also depend on the type of foliage of the different tree species, which can be partly very dense and partly more open and thus possibly giving space for flying animals.

Taking into account that only data of a short-term study are available, we assume that neither an apparent three dimensional activity pattern nor a random activity pattern of bats flying in forests could be recognized. The temporal activity patterns possibly are related to the presence and density of insects which vary during the night. Due to the fact that a bat passes a detector sensitivity cone within about a quarter of a second (Table 2, 4), one can conclude that bats flying in the forest use much larger spaces than those covered by the sensitivity cones of a detector. This interpretation applies, with one exception, to all detectors where bats passes were recorded. The exception is the 15-m-detector at the recording unit 'Rail track S' (Table 3). 'Rail track S' has similarities with a forest clearing. Here a bat stayed approximately three times longer within the range of the sensitivity cone of the detector than elsewhere. Possibly this forest clearing was used by a bat species different from that flying in the vicinity of the other recording units. Here again, a long term study is urgently needed.

There are few investigations on the flying and hunting behaviour of Central European bats in forests (e.g. Nyholm 1965; Benk 1981; Groupe Mamalogique Normandie 1988; Ahlèn & Gerell 1989; Dietz 1993; Rydell *et al.* 1994; Zahn & Krüger-Barvels 1996; Güttinger 1997; Kerth *et al.* 2001). Based on the available information and our own observations, it was to be expected that several different bat species in the forest, i.e. in a three-dimensional area with many different micro-habitats, would show more variability in their behaviour as compared to for example one single species like Daubenton's bats that hunts over rivers, ponds or lakes or regularly uses the same two or three flight paths (Rieger *et al.* 1992, Rieger & Walzthöny 1993, Rieger 1996, 1997). In fact the variability in the behaviour of the bats flying in the forest was even higher than expected (Fig. 7).

The findings presented in Table 2 can be seen in the light of a high variability between the recording points. The flying conditions at 'Rail track S' are completely different to the flying conditions at other recording points because 'Rail track S' resembles a forest clearance. Flying conditions here are different to those within or above canopy. One can assume that the flying conditions at 'Rail track S' suits bat species that prefer flying in open spaces (e.g. *Eptesicus*, *Nyc-*

talus). Such species often use long range echolocation calls. This could account for the fact that mean duration of the recorded calls at 'Rail track S' is longer than at other recording units (see Table 2) (see also Swystun *et al.* 2001; Hogberg *et al.* 2002; Patriquin & Barclay 2003.).

Because of the great variability, it was impossible to recognize any relations between bat activity, characteristics of the small-scale forest structure, and weather parameters. Further and long term studies will be needed before we begin to understand the requirements of bats for micro-habitats in forests.

We reached the goal of the present study and obtained for the first time an impression of the daily 'when' and the three-dimensional 'where' of bats in a temperate deciduous forest. We demonstrated that automatic and simultaneous three-dimensional bat activity recording in a forest is possible. Subsequent studies can now be planned more precisely as we now know places and habitats in the study forest where bats are active. Long term studies using our method would help to understand how bats use a deciduous forest during the whole hunting season, and to detect more precisely a possible distinct species-specific use of the three-dimensional space.

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

Martin Unterseher[1] & Ophir Tal

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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 (Lodge & Cantrell 1995; Unterseher *et al.* 2005), arthropods (Corbet 1961; Novotny & Basset 2000; Basset *et al.* 2003) and various epiphytes, including lichenized fungi (McCune *et al.* 2000; Freiberg 2001).

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 (Kuuluvainen & Pukkala 1987; 1989; Anhuf & Rollenbeck 2001), quantity of available water (Bellot *et al.* 1999), diurnal and annual gradients in temperature, and the quality and amount 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. Lodge & Cantrell 1995; Hallenberg & Parmasto 1998; McCune *et al.* 2000; Unterseher *et al.* 2005). Light is obviously a critical resource in the canopy, and in case of direct solar radiation, immediately influences the temperature on surfaces of branches (Dirmhirn 1961; Haddow & Corbet 1961; Théry 2001).

Despite more than 20 years of intensive canopy research (e.g. Erwin 1982; Morawetz 1998; Ozanne *et al.* 2003), 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.Lodge & Cantrell 1995; McCune

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[1] corresponding author

et al. 2000; Keller *et al.* 2004; Keller 2004; Unterseher *et al.* 2005). 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. Sherwood 1981; Boddy 1992; Hedger *et al.* 1993; Lodge & Cantrell 1995; Keller 2004). 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. Ingold 1954; Munk 1957; Nuñez 1996). 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 1982, 1983, 1984; Chapela & Boddy 1988a–c; Griffith & Boddy 1988, 1989, 1991a–c).

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.

MATERIALS 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 diameter at breast height including four introduced tree species [Morawetz & Horchler 2004]). The actual canopy is mainly formed by oak (*Quercus robur*) trees (older than 250 years, 7% canopy cover) and younger trees of ash (*Fraxinus excelsior*), sycamore, and lime (*Tilia cordata*) (younger than 130 years, 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 Mitchell *et al.* (2002), Lowman & Rinker (2004), and Basset *et al.* (2004).

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 diameter, 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 McCune (1994) and 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 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). 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" (Clarke 1993; McCune & Grace 2002).

Hierarchical clustering

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

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.

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		

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

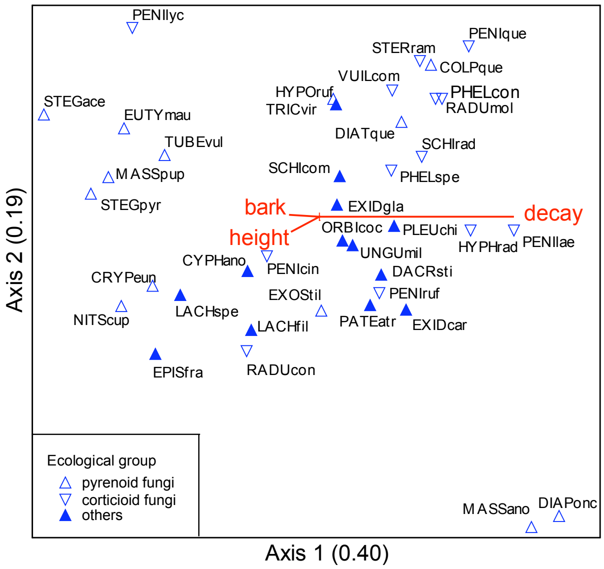

Figure 1 – Ordination of species in sample space with environmental variables overlaid as joint plot. Symbols indicate different groups of fungi (see Material and Methods). The lines radiating from the centroid indicate the relative strength and direction of correlation of variables with the ordination.

The fungal community differed strongly between habitats (Fig. 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). 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 (Fig. 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, $p < 0.001$, $n = 3\,336$ each). Comparable patterns existed for relative humidity (53% and 47% respectively). Saturation (100% relative humidity) was reached on 11 of 79 days at 6 m above ground, and on 7 days at 29 m above ground.

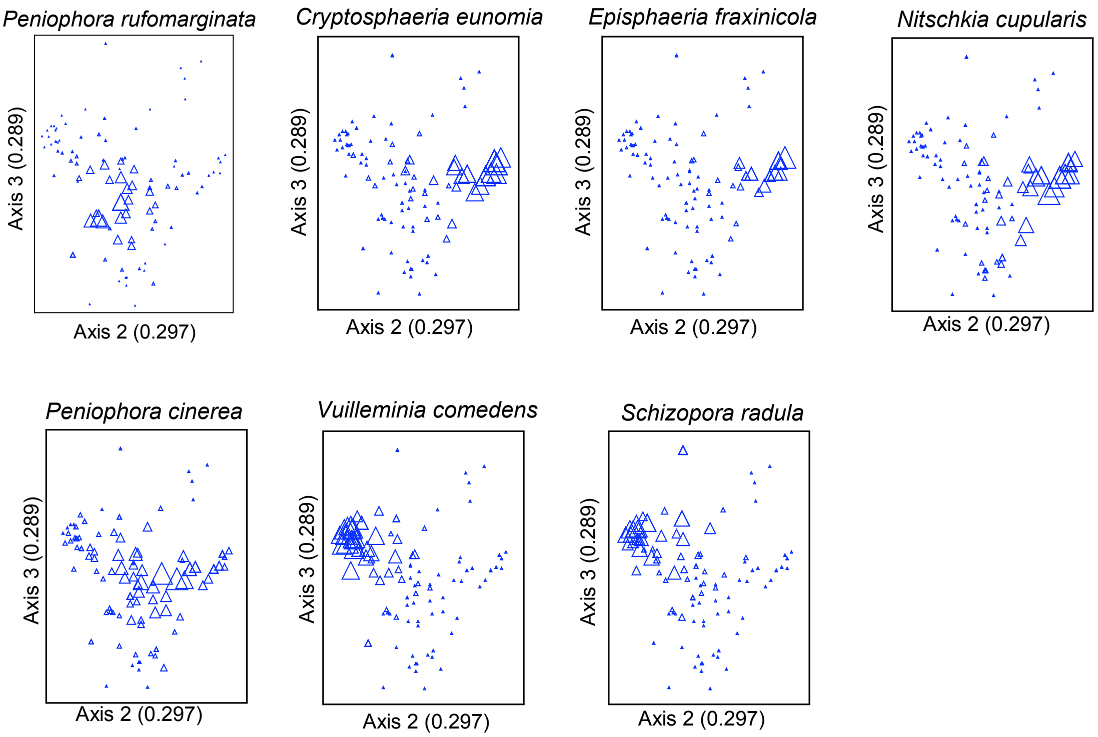

Figure 2 – Abundances of seven different fungal species. In each ordination the abundance is overlaid on an ordination of sample units. The size of the symbols in the graphs is proportional to the abundance of the fungi.

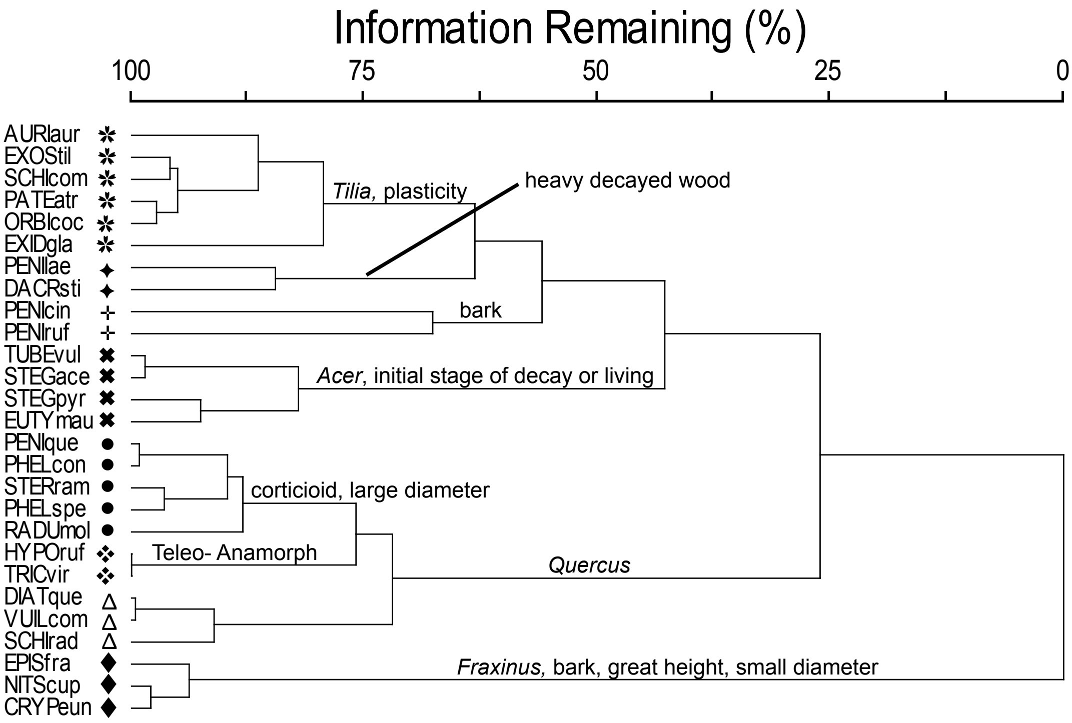

Figure 3 – Hierarchical dendrogram from cluster analysis. Species groups are indicated with different symbols.

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.

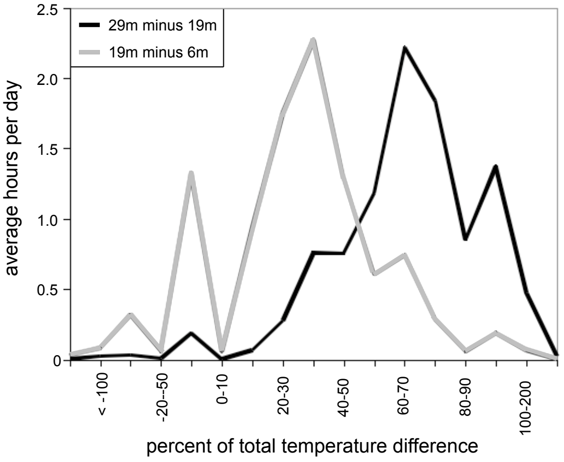

Figure 4 – Differences in temperature between 6 m and 29 m above ground divided into two seperated comparisons: The upper with the middle (black line) and the middle with the lower canopy (grey line). Negative values on the x axis indicate that temperatures measured at 6 m were higher than at 19 m and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

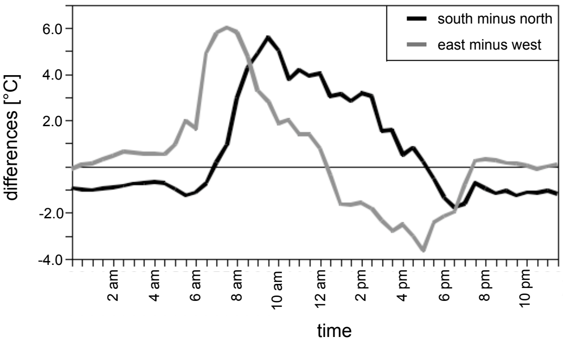

Figure 5 – Four sensors around a branch of *Tilia cordata* measured temperature in 29 m height at the four cardinal points. Differences between north and south (black line) and east and west (grey line) are shown as 30 min averages from 2 April 2004 till 19 May 2004. The black sensors with a diameter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

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).

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 (Boddy 1983; Griffith & Boddy 1991a–c; Helfer & Schmid 1990; Pearce 2000; Unterseher *et al.* 2005), and is highly variable in time and space (Lodge & Cantrell 1995; Frankland 1998). 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.

Fig. 6 shows the canopy surface of the Leipzig crane plot (Markus Rohrschneider, this volume). 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.

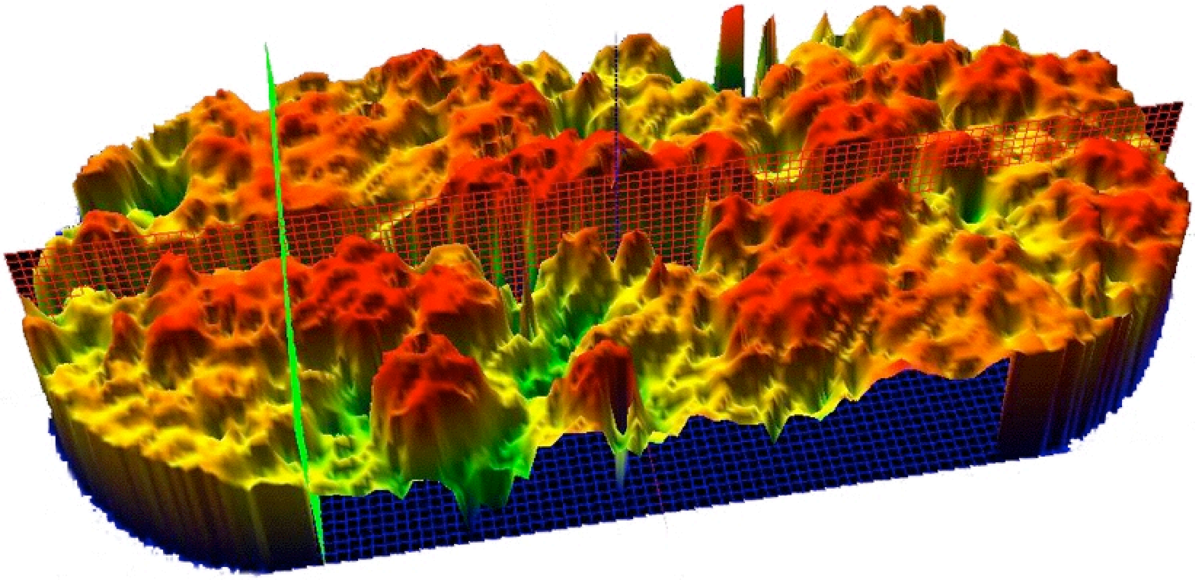

Figure 6 – Computer generated, 3-D canopy surface model of the Leipzig canopy crane study site based on 4500 single perpendicular measures. The railroad track on which the construction crane can be moved is visible as large gap from the left to the right. The study site measures 200 m from north to south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

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 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 (Moser 1983; Ellis & Ellis 1988; Dam & Dam-Elings 1991). *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 (ROGERS 1979; PETRINI *et al.* 1995; WORRALL *et al.* 1997). *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 weeks 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 (Fig. 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.

Considering that wood-decay fungi in the canopy are a mostly inconspicuous but important component of the biota of forest ecosystems (Stone *et al.* 1996; Hallenberg & Parmasto 1998; Unterseher *et al.* 2005) 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.

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