Part I

Description of the canopy crane investigation site
1 Soil attributes, stand structure, and aspects of forest regeneration

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

ANNETT KRÜGER¹, 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 pleitocene terrace gravel and sands. The soils show clear differences, particularly in grain composition. Soil horizons 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 these 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 leaves, 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 interactions 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

¹corresponding 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 ar-
 eas south of Leipzig from approximately 6 000 BC,
the associated clearing of the forests located there
and incipient agronomic utilization or Holocene cli-
matic 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 sedi-
mentation (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 de-
tritus from the mountain ranges across several kilo-
metres and up to 8 m thick. Gritty and (as a result of de-
creasing water flow) sandy sediments deposited them-
selves 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 there-
fore connected with human settlement. Clear-
ances in the Elster and Pleisse catchment area from
the early Atlantikum 5 000 to 6 000 years ago pro-
vided favourable conditions for the erosion of the now
exposed soil by rainwater in the hydrological catch-
ment. 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 sus-
pended 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

A second principal phase for the accumulation of
fluvial loamy sediments came 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 & Sick-
ert 1998). Up until then, an exceedingly species-rich
hardwood floodplain in addition to the softwood plain was made possible by the prevail-
ing 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 El-
ster in the northern part of Leipzig Lowland. Map from: Top-
ographic card from Saxony, scale 1 : 25 000, number 4 639
(Leipzig oest), 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 water-
courses and their bayous dried out as a result. The
soil attributes changed, formerly strongly groundwa-
ter 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, NOx; German Federal Office Environment and Geology, LfUG 1997) play a large part. While a decrease in SOx 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 Burge 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.

![Soil relief of the LAK crane site](image)

**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 occurring 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 sense 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, relict 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 relict 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 relict 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 relict 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 relict 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 Burgau 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 substanti-
ate, 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. relict 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.

ACKNOWLEDGEMENTS

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REFERENCES


LÄNDERSATZÜMENFASSE SACHSEN (1967) Topographische Karte 1 : 25 000, Blatt 4639 (Leipzig West).


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

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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 pleistocene sand border bioturbation: 19 cm

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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

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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

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

Profile 5
x: 25; y: 84; Right-value: 45 21 613; Hight value: 56 92 388; Height a.s.l.: 101.52 m
soil type: Gley-Vega
soil form: brown Vega-Gley developed from fluvial loam and clay over relict gley developed from fluvial loam and sand
border bioturbation: 22 cm

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Profile 6
x: 25; y: 68; 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

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Profile 7
x: 25; y: 50; 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

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Profile 8
x: 25; y: 30; 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

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<td>rGrGo</td>
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</tr>
<tr>
<td>Gr</td>
<td>179+</td>
<td>7.5YR5/3</td>
<td>Tu2</td>
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### 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

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#### 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

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#### 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

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#### 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

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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 m². This is accordant to a stand density of 500 tree individuals ha⁻¹, a basal area of 34.9 m² 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 bimodal 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 19th 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 Quercus 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 Quercus 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 18th 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 Quercus robur were repressed. The discontinuation of regular inundations as a result of river straitenings enhanced the accumulation of species with a low tolerance against inundations (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).

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<td>Acer platanoides</td>
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<td></td>
<td>Acer pseudoplatanus</td>
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<tr>
<td>Corylaceae</td>
<td>Carpinus betulus</td>
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<td>Fabaceae</td>
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<td>Fagaceae</td>
<td>Quercus robur</td>
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<td>Quercus rubra*</td>
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<tr>
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<td>Crataegus sp.</td>
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<td>Sorbus aucuparia**</td>
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<td>Salicaceae</td>
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<tr>
<td>Corylaceae</td>
<td>Corrylus avellana</td>
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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 organisms.

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).

**REFERENCES**


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

MARKUS RÖHRSCHNEIDER¹, 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 & RUS 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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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 m² of 15 212 m²).

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{plot.png}
\caption{Position of the measuring points on the plot. Tree species are colour coded. The underlying grid is 5 x 5 m.}
\end{figure}
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 heterogeneous 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.

REFERENCES

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

Claudia Schöne & Anke Jentsch¹

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, diasporas 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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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 (Urbanška 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 (Juhasz-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 (Burgau 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 m², which were divided by a fine grained grid measuring 1 m x 1 m.

### Data acquisition: 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 veg-
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.

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 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.
Tree seedling establishment and regeneration dynamics

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 m² floodplain forest area near Leipzig in 2002.
Table 1 – Number, proportion [%] and density [m²] of seedlings and adult trees of various species in a floodplain forest measuring 3 000 m² in size near Leipzig.

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Number of seedlings</th>
<th>Proportion of seedlings [%]</th>
<th>Density of seedlings [m²]</th>
<th>Number of trees</th>
<th>Proportion of trees [%]</th>
<th>Density of trees [m²]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Quercus robur</td>
<td>377</td>
<td>2.15</td>
<td>0.13</td>
<td>2</td>
<td>1.20</td>
<td>0.01</td>
</tr>
<tr>
<td>Acer platanoides</td>
<td>7737</td>
<td>44.15</td>
<td>2.59</td>
<td>46</td>
<td>27.71</td>
<td>0.02</td>
</tr>
<tr>
<td>Acer pseudoplatanus</td>
<td>8821</td>
<td>50.21</td>
<td>2.94</td>
<td>27</td>
<td>16.27</td>
<td>0.01</td>
</tr>
<tr>
<td>Fraxinus excelsior</td>
<td>548</td>
<td>3.12</td>
<td>0.18</td>
<td>21</td>
<td>12.65</td>
<td>0.01</td>
</tr>
<tr>
<td>Ulmus sp.</td>
<td>5</td>
<td>0.03</td>
<td>0.01</td>
<td>7</td>
<td>4.22</td>
<td>0.01</td>
</tr>
<tr>
<td>Tilia sp.</td>
<td>51</td>
<td>0.29</td>
<td>0.02</td>
<td>50</td>
<td>30.12</td>
<td>0.02</td>
</tr>
<tr>
<td>Carpinus betulus</td>
<td>9</td>
<td>0.05</td>
<td>0.01</td>
<td>13</td>
<td>7.83</td>
<td>0.01</td>
</tr>
<tr>
<td>Sum</td>
<td>17 568</td>
<td>100.00</td>
<td>5.9</td>
<td>166</td>
<td>100.00</td>
<td>0.1</td>
</tr>
</tbody>
</table>

Table 2 – Diaspore type, seed weight, dispersal mechanism and shade tolerance of seedlings from 7 floodplain forest tree species. Seed weights are taken from LUFTEINSTEINER 1982, seed quantities per “standard adult tree” from the following authors: a: TAL 2003, b: KÜSSNER 2002 in ROLLOF et al. 2002. n.i.: “not indicated”.

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Diaspore type</th>
<th>Weight [mg]</th>
<th>Dispersal type</th>
<th>Seed quantity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Quercus robur</td>
<td>single-seeded nuts</td>
<td>n.i.</td>
<td>Falling / animal</td>
<td>1 000³</td>
</tr>
<tr>
<td>Acer platanoides</td>
<td>winged fissile fruit</td>
<td>134.5</td>
<td>Wind</td>
<td>10 000³</td>
</tr>
<tr>
<td>Acer pseudoplatanus</td>
<td>winged fissile fruit</td>
<td>128.6</td>
<td>Wind</td>
<td>10 000³</td>
</tr>
<tr>
<td>Fraxinus excelsior</td>
<td>winged nuts</td>
<td>74.8</td>
<td>Wind / animal</td>
<td>76 000³</td>
</tr>
<tr>
<td>Ulmus sp.</td>
<td>winged nuts</td>
<td>n.i.</td>
<td>Wind</td>
<td>114 000³</td>
</tr>
<tr>
<td>Tilia sp.</td>
<td>winged nuts</td>
<td>181.0</td>
<td>Wind / root growth</td>
<td>11 000³</td>
</tr>
<tr>
<td>Carpinus betulus</td>
<td>nuts with bearing leaf</td>
<td>56.8</td>
<td>Wind / animal</td>
<td>n.i.</td>
</tr>
</tbody>
</table>

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 m² section of floodplain forest (cf. Table 1). This corresponds to an average seedling density of 5.9 per m² 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 m² 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**

<table>
<thead>
<tr>
<th>Species</th>
<th>Proportion inside canopy space (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acer pseudoplatanus</td>
<td>29.4</td>
</tr>
<tr>
<td>Acer platanoides</td>
<td>25.9</td>
</tr>
<tr>
<td>Fraxinus excelsior</td>
<td>3.5</td>
</tr>
<tr>
<td>Quercus robur</td>
<td>0.9</td>
</tr>
<tr>
<td>Tilia ssp.</td>
<td>0.02</td>
</tr>
<tr>
<td>Carpinus betulus</td>
<td>0.02</td>
</tr>
<tr>
<td>Ulmus ssp.</td>
<td>0.02</td>
</tr>
</tbody>
</table>

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.](image)

![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.](image)
Tree seedling establishment and regeneration dynamics

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 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 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 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).

![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.](image)

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).

**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.

![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.](image)

**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.
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 understorey 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 organoic 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 aethic 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 acidiy of trunk off-flows, particularly in Quercus and Frazinus, 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 understorey 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 Frazinus 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 Frazinus as a spinning flier, execute rotary movements during flight (Schmidt 2002). The effect of this is that Frazinus 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 Frazinus excelsior is smaller than that of Acer and Carpinus. The average dispersal distance of Frazinus 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, (TAI pers. comm.), are taken into account, this results in a germination rate of 8% (*Acer pseudoplatanus*, on the other hand, approx. 1.4%).

**REFERENCES**


