Japanese Government. Eventually, in 2001, two new cranes were erected in temperate forests of Germany, in Leipzig and Freising, respectively.

The network now consists of six cranes erected in temperate forests and five in tropical forests (Fig. 18). They will be shortly joined by the Canopy Operation Permanent Access System (COPAS) in French Guiana, a fixed device with a different conception (Chapter 4.3.2). These sites are located in forests from different types, biomes and biogeographical regions, such as northern coniferous forest, mixed temperate forest, decidous broad leaf forest, tropical dry lowland forest, and tropical wet lowland forest. To date, no crane site has been established in Africa.

The International Canopy Crane Network was founded in 1997 (Stork *et al.*, 1997a), during the organisation of a Tropical Forest Canopy Symposium held in Panama in March 1997, and in response to an earlier call to promote the long-term studies of forest canopies (Parker *et al.*, 1993). Sixty-one participants representing 23 nations attended the meeting in Panama, including delegates from UNEP, UNESCO, CIFOR, and IUCN. This meeting complemented a series of International Canopy Conferences held in Sarasota, USA, in 1994 and 1998; and in Cairns, Australia, in 2002, with the next meeting planned for Leipzig, Germany, in 2005.

Each crane site has unique peculiarities and its associates are involved in different research topics. Yet some baseline investigations are common to all sites: identifications of plant and animals present, mapping and measurement of trees, microclimatic studies, etc. The 'Global Canopy Handbook', edited by the Global Canopy Programme (Mitchell *et al.*, 2002), presented the different crane sites of the network, particularly in terms of technical characteristics and costs of installations. In the following sections, the manager(s) of each crane research facility were asked to describe the climate and vegetation of their site and to provide an overview of the past, present and future research at their facility. These findings are further summarized in Chapter 5 and put into the perspective of global canopy research.

4.2. Cranes in temperate forests

4.2.1. Basel, Switzerland

Christian Körner and Gerhard Zotz

Fig. 19. View from the forest floor to the top of the crane, which was set up in a small natural gap of a few m².

Background

The Swiss Canopy Crane (SCC, Fig. 19 and Table 2) was erected with the help of a helicopter in March 1999 at Hofstetten, close to the town of Basel. It is managed by the Institute of Botany, University of Basel, and is sponsored by the Swiss Federal Office of the Environment (BUWAL), the Swiss National Science Foundation (SNF), and the University of Basel. On the fenced research site (*circa* 1ha), there is a field laboratory, power and telephone line. In September 2000 a large-scale canopy enrichment system (web-FACE: Free Air CO_2 Enrichment) was installed, which permitted exposure of 14 adult trees to elevated levels of carbon dioxide (CO_2; a detailed description of this system can be found in Pepin & Körner, 2002).

Table 2. Site and crane characteristics of the Swiss Canopy Crane.

Variables	Characteristics
Location	Hofstetten, 12 km south of the city of Basel in NW Switzerland 47°28' N, 7°30'E
Altitude	550m
Mean annual air temperature	10°C
Mean annual rainfall	990mm
Type of forest	Mixed coniferous temperate forest
Area of forest accessed by the crane	0.28ha (note: the crane is located in a very small natural gap)
Canopy height	32-38m
Crane model	Liebherr 30LC, fixed
Height of tower / Length of jib	45m/30m
Maximum height reached by the gondola	37m
Gondola type	a: Cylindrical, model RM1-300A/32; 65cm in diameter b: Square, model SEC 02/600; 1.2 x 1.2m
Number of persons carried by the gondola	a: 1 person b: 4 persons
In operation since	1999
Main research topics	• Tree responses to CO_2-enrichment in the canopy • Responses of functional leaf types to light and shade in relation to forest canopy structure
Remarks	Fenced research site, equipped with laboratory, power and telephone lines
Management	Institute of Botany, University of Basel
Contacts	Prof. Christian Körner, University of Basel, Ch.Koerner@unibas.ch Dr Gerhard Zotz, University of Basel, gerhard.zotz@unibas.ch
Web site	www.unibas.ch/botschoen/scc/
List of publications	www.unibas.ch/botschoen/scc/
Fees for researchers	Negotiable on a case to case basis

The SCC is administered by the Institute of Botany, University of Basel. Three technicians ensure day-to-day operation of the crane, the web-FACE system and the monitoring of macroclimatic and microclimatic variables. The crane site was primarily selected to allow comparative studies of the impact of elevated CO_2 on mature individuals of typical European forest tree species. In addition to questions related to global change, the high tree species diversity at the site provides a unique opportunity to study various other topics in plant sciences, entomology, or forest pathology (Hoch *et al.*, 2003).

The SCC is located in a typical low-altitude mixed forest of central Europe. The forest is about 100 years old, with tree heights ranging from 32 to 38 m, and a total basal area of 46 m^2 ha^{-1} (Table 3). The stand is characterized by a dominance of beech (*Fagus sylvatica*) and oak (*Quercus petraea/robur*) with representatives of lime (*Tilia platyphyllos*), hornbeam (*Carpinus betulus*), maple (*Acer campestre*), and wild cherry (*Prunus avium*). There are also four coniferous species, European larch (*Larix decidua*), Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), and silver fir (*Abies alba*). Only the latter gymnosperm is currently regenerating while the other three species became established in the late 19th century (they are more light-requiring species). The spatial distribution of tree species within the crane's perimeter is shown in Figure 20. Finally, the site has a strong presence of ivy (*Hedera helix*) reaching the upper canopy. The leaf area index (LAI) of the forest in the crane plot is *circa* 5.

Table 3. Stand characteristics by tree species (measured 1999).

Tree species	Stems per ha	Basal area (m^2 ha^{-1})
Abies alba	57	1.26
Acer campestre	18	1.22
Acer pseudoplatanus	35	0.11
Carpinus betulus	64	2.94
Corylus avellana	11	0.02
Crataegus sp.	3	0.01
Fagus sylvatica	106	11.02
Larix decidua	42	8.71
Picea abies	67	5.82
Pinus silvestris	21	3.26
Prunus avium	7	1.13
Quercus petraea/robur	67	8.46
Tilia platyphyllos	117	2.37
TOTAL	**615**	**46.32**

There is also a rich understorey shrub flora with hazel (*Corylus avellana*), honeysuckle (*Lonicera xylosteum*), spurge laurel (*Daphne laureola*), and the evergreen holly (*Ilex aquifolium*). The herbaceous layer is dominated by *Mercurialis perennis*. Other important species include *Paris quadrifolia*, *Anemone nemorosa*, and *Galium odoratum*. Additional tree species are found in the immediate vicinity of the crane perimeter, for example, ash (*Fraxinus excelsior*), whitebeam (*Sorbus aria*), and a second species of maple (*Acer pseudoplatanus*). Thus, a total of 16 woody species reach the upper forest canopy.

The regional climate is typical for the humid temperate zone, characterized by rather mild winters and moderately warm summers (Fig. 21). The growing season of the deciduous trees lasts *circa* 170-180 days from the end of late April to mid-October. Average minimum January and maximum July air temperatures near the crane site are -1.4 and 23.9°C, respectively. Annual precipitation in the region averages 990mm, two-thirds of which falls during the growing season. Soils are of the rendzina type on calcareous bedrock (a silty loam with an accessible profile depth of *circa* 30cm and a pH of *circa* 6 in the top 10cm of the profile).

Main research topics and first findings

The central objective of the SCC is the investigation of the responses of mature trees to elevated CO_2, and consequently, the web-FACE system constitutes the 'heart' of the facility. Briefly, pure CO_2 is released through thin tubes, which are woven into the canopy.

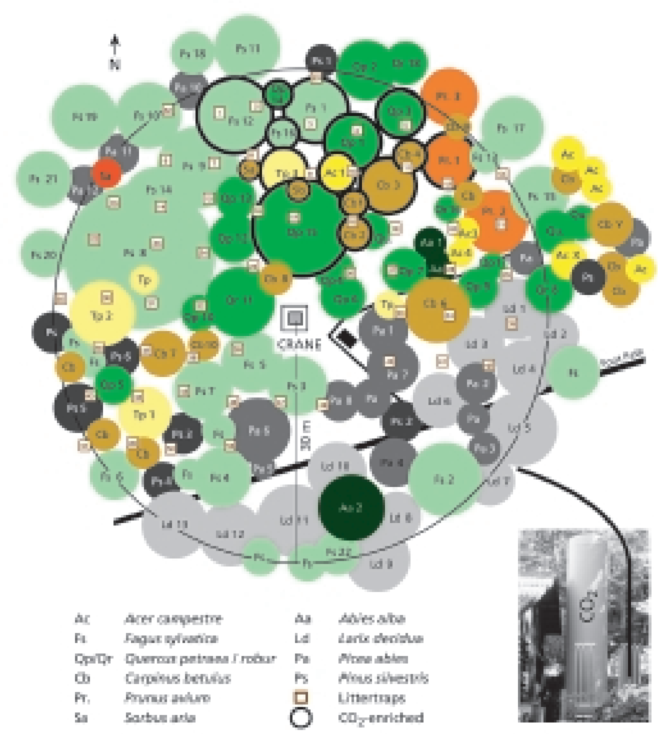


Fig. 20. Tree positions at the SCC site.

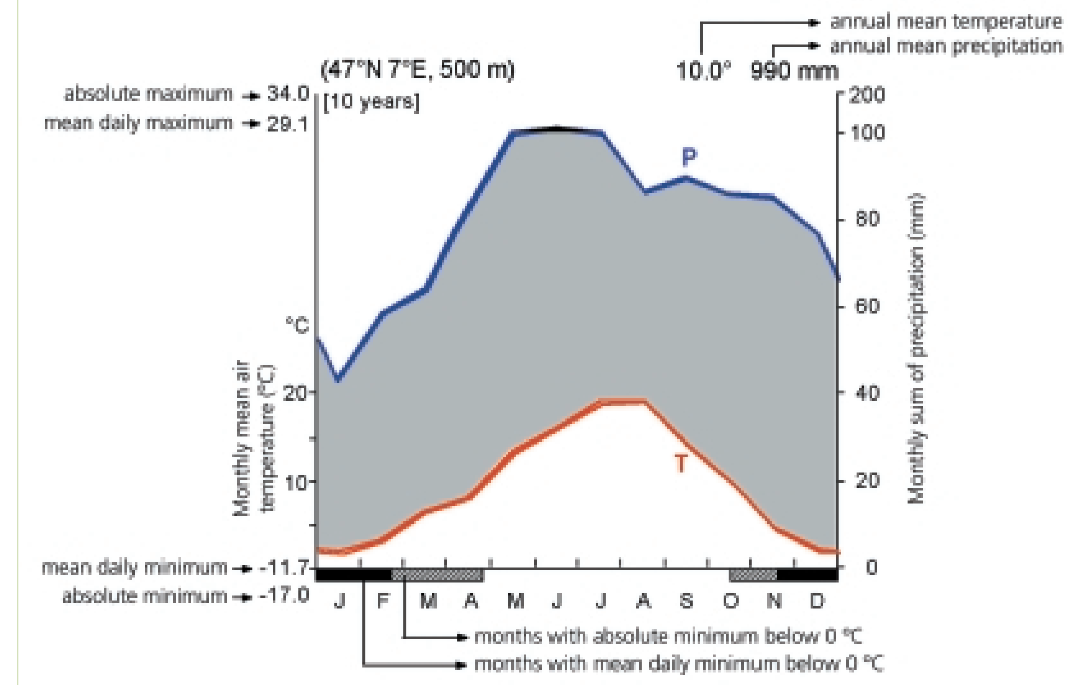


Fig. 21. Climate diagram for the SCC site Metzerlen, near Basel/Hofstetten. Averages are based on 1989-1999 meteorological records.

Fig. 22. Sonja Keel, a master student measuring leaf stomatal conductance on canopy leaves. Standing: Olivier Bignucolo.

The set point CO_2 concentration is controlled by a pulse-width modulation routine. About 2 tonnes of CO_2 per day are needed for 14 tall forest trees (Fig. 20, thick circles). By now we have completed two full growing seasons, in which these trees have been exposed to an average of 510ppm CO_2, which mimics ambient CO_2 concentrations of the near future. During this exposure to high CO_2 we assessed the response of six different tree species by studying leaf gas exchange parameters (Fig. 22), leaf chemical composition, stem sap flux, stable isotopes, tree phenology, increments in diameter at breast height and branch growth patterns.

The first results indicate a number of significant responses to elevated CO_2 in spite of considerable intraspecific and interspecific variation. For example, in broad-leaved trees leaf stomatal conductance was reduced by *circa* 15% on average (Fig. 23); range: -3% in *Fagus sylvatica* to -22% in *Carpinus betulus*) compared to controls at normal CO_2 levels, although differences were only significant in two species. None of the conifers showed a significant difference. Consistent with these results, sap flux data for the same year suggest a reduction of transpiration by almost 10%. Conversely, tree growth showed no clear trend up to the present but much variation between species and years.

Cooperating teams from a number of institutions have examined, for example, isoprene emissions, insect abundances, or the responses of herbivores to leaves that had developed under elevated CO_2. For example, preliminary experiments on the feeding behavior of the generalist herbivore, *Lymantria dispar*, yielded quite contrasting responses to altered food quality (Fig. 24). This result highlights once more the importance of a multi-species approach to study biotic reactions to global change. Yet another methodological focus was stable isotope work. Changes in $\delta^{13}C$ signals under elevated CO_2 (due to the fossil CO_2 source) could be traced from the canopy down to the mycorrhizal fungi.

The knowledge of short-term reactions to elevated CO_2 may have little bearing to an understanding of long-term responses (Körner, 1995). Thus, it is essential that the web-FACE system will operate for at least another five years. Only a prolonged duration of our experiment will permit the distinction of transient reactions from ecologically relevant long-term responses of these mature forest trees. High biodiversity being one of the assets of the SCC site it is also a burden in terms of adequate replication. Thus, it is highly desirable to install replications of the pioneering web-FACE system in a number of other locations within the temperate zone, but also in other forest biomes around the world considering the very nature of global change. Forest ecosystems contain more than 80% of biomass carbon stored in the terrestrial biosphere. An understanding of the response of these systems to global change is a major challenge to modern biology.

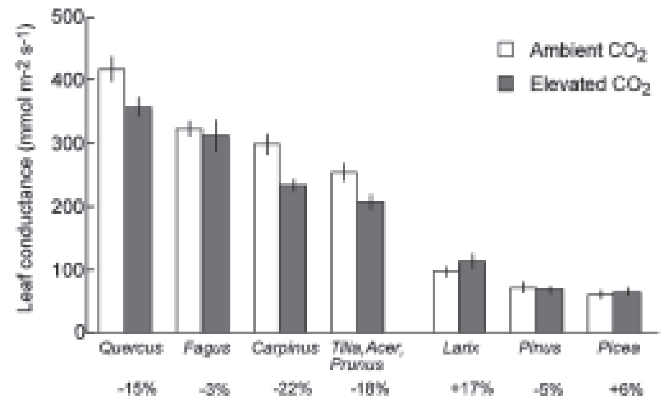


Fig. 23. Differences in leaf conductance to water under ambient and elevated CO_2. Data are means ± SE.

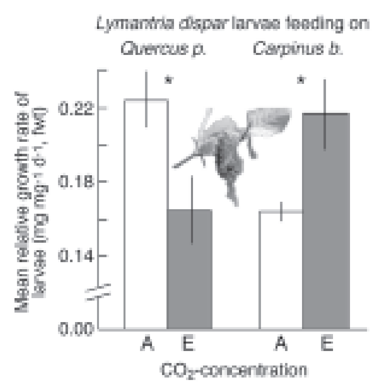


Fig. 24. Differences in growth rate of *Lymantria* larvae feeding on leaves growing under ambient (A) and elevated (E) CO_2. Data are means ± SE.

4.2.2. KROCO, Freising, Germany: Canopy research in a temperate mixed forest of Southern Germany

Karl-Heinz Häberle, Ilja M. Reiter, Angela J. Nunn, Axel Gruppe, Ulrich Simon, Martin Gossner, Herbert Werner, Michael Leuchner, Christian Heerdt, Peter Fabian & Rainer Matyssek

Background

Canopy research is being conducted in a managed forest of beech and spruce (*Fagus sylvatica* and *Picea abies*) in southern Germany, about 40km north of Munich. The study site, Kranzberg forest, includes about 500 spruce and beech trees that form a closed canopy (Pretzsch *et al.*, 1998). Trees are about 60 years old, and the foliage extends from 17m aboveground to the upper canopy edge at 28m (Table 4). Besides the two dominating tree species, individuals of pine (*Pinus sylvestris*), larch (*Larix decidua*), oak (*Quercus robur*), and maple (*Acer pseudoplatanus*) are scattered in the forest plot. Access to the canopy is provided by a research crane and scaffolding (Fig. 25):

- The stationary research crane (KROCO-Kranzberg ozone canopy observation by crane) was installed in April 2001, is operated by permanent power supply and permits sampling and measuring across the entire study site (Table 4).

- The scaffolding consists of four towers, ranging between 27 and 35m in height. Three towers are connected by platforms (12m in length) that allow access at four heights between 17 and 25m above ground to the insolated and shaded crowns of about 30 trees (installed in December 1996). The construction enabled the installation of a unique free-air fumigation system (KROFEX-Kranzberg ozone fumigation experiment) to study the response of mature forest trees to long-term ozone exposure at an enhanced level (Werner & Fabian, 2002; Häberle *et al.*, 1999), an experiment which started in 2000.

Fig. 25. Installations at Kranzberg Forest, D: Canopy crane, towers and platforms with the free-air ozone fumigation system.

Further, equipment for the generation and control of ozone and for the assessment of environmental factors, an ecophysiological field laboratory (analysis of leaf gas exchange, sap flow in xylem, stem, branch, root and soil respiration, growth rates and biomass production), and a central laboratory hut belong to the infrastructure of the experimental site.

The research in the Kranzberg forest is maintained by around 25 national and international groups covering the fields of molecular biology, biochemistry, ecophysiology, plant nutrition, mycorrhizae, phytopathology, zoology, soil science, forestry, air chemistry and modelling, half of them from outside the Munich area. There is interest in extending cooperation with external groups that may contribute in a complementary way to the investigations conducted at the 'Kranzberg Forest'. A core group is meeting every month to coordinate the activities. The main projects running at the site are:

(1) "*Growth and Parasite Defense - Competition for Resources in Economic Plants from Agronomy and Forestry*" (since 1998, funded by 'Deutsche Forschungsgemeinschaft' (DFG), Sonderforschungsbereich 'SFB 607', www.sfb607.de);

(2) "*Risk Assessment of the Enhanced Chronic O_3 Exposure by Means of 'Free-Air' Canopy Fumigation in*

Table 4. Site and crane characteristics of KROCO in Freising.

Variable	Characteristics
Location	Kranzberg Forest, Freising, Bavaria, Germany 48°25'08" N, 11°39'41" E
Altitude	485m
Mean annual air temperature	7.0 - 7.5°C
Mean annual rainfall	730 - 790mm
Type of forest	Managed mixed spruce/beech forest
Area of forest accessed by the crane	0.8ha
Canopy height	28m
Crane model	Potain, fixed, MDT-1s
Height of tower / Length of jib	45m/50m
Maximum height reached by the gondola	35m
Gondola type	Cylindrical, 0.7m in diameter, operated by remote control
Number of persons carried by the gondola	2
In operation since	2001
Main research topics	• Quantification of competitive interactions between adult beech and spruce trees • Study of the regulation of carbon allocation using ozone exposure as an experimental tool of disturbance • Determination of eco-physiological threshold levels of ozone sensitivity of mature forest trees • Temporal and spatial contribution of spruce and beech to the faunal biodiversity in the canopy
Remarks	Fenced research plot of 0.5ha, including the crane and four scaffolding towers (27 to 35m tall) connected by platforms
Management	Technical University of Munich
Contact	Prof Dr Rainer Matyssek, Technische Universität of München, matyssek@wzw.tum.de
Web site	www.sfb607.de
List of publications	www.sfb607.de
Fees for researchers	On demand

a Mixed Beech/Spruce Forest" (since 2000, funded by 'Bayerisches Staatsministerium für Landesentwicklung und Umweltfragen');

(3) "*The Carbon Sink Strength of Beech in a Changing Environment: Experimental Risk Assessment of Mitigation by Chronic Ozone Impact (CASIROZ)*" (since 2002, funded by the European Community within Fifth RTD Framework Programme EVK2-2002-00165 (Ecosystem Vulnerability), www.casiroz.de).

The experimental site belongs to a forest that is 'public property' (i.e., owned by the Federal State of Bavaria) and provided free of charge by the 'Bayerisches Staatsministerium für Landwirtschaft und Forsten'.

In an interdisciplinary approach from the gene to the stand level, the project intends to clarify central mechanisms in plants, regarding the regulatory control of competitiveness and individual plant fitness. In particular, the following research aims are pursued:

- Quantification of competitive interactions between adult beech and spruce trees as based on the resource fluxes involved;
- Clarification of the associated resource allocation, employing experimental 'free-air' ozone (O_3) exposure within the canopy to facilitate the analysis and investigation of regulatory mechanisms and their responsiveness;

- Determination of eco-physiologically meaningful threshold levels in the O_3 sensitivity of adult forest trees and mitigation of their carbon sink strength under enhanced, chronic O_3 exposure.

In parallel to the intensive investigations in the tree crowns the belowground 'canopy' of the roots has recently become a new focus in the research at the site.

The utility of the canopy crane is exemplified by the following three multidisciplinary research activities.

Ecophysiology: light as driving force of competition

Our approach to quantify competitiveness is based on resource flux. Competitiveness is assessed as a hierarchy of efficiency ratios in space sequestration (*resource investment per unit of occupied above and belowground space*), resource acquisition (*resource gain per investment and occupied space*), and 'running costs' (*transpiration, respiration per resource gain and occupied space*). In this way, costs versus benefit relationships are established in the control of resource allocation within and amongst trees as being in relation to exposure to biotic and abiotic impacts (Grams *et al.*, 2002). Here, ozone is used as a perturbant rather than pollutant to unravel the responsiveness and differentiation of such relationships as well as their underlying mechanisms. Another fundamental factor being studied is the naturally occurring light gradient across the canopy and its influence on such costs versus benefit relationships. Additionally, the impact of pathogens, mycorrhizospheric organisms and phytophagous insects is of paramount importance with respect to the rationale of the interdisciplinary research program 'SFB 607' (see above and Matyssek *et al.*, 2002). This implies that impact levels of parasites and their effects on the trees' primary and secondary metabolism be assessed, and that the abundance of insects is surveyed in the stand's canopy.

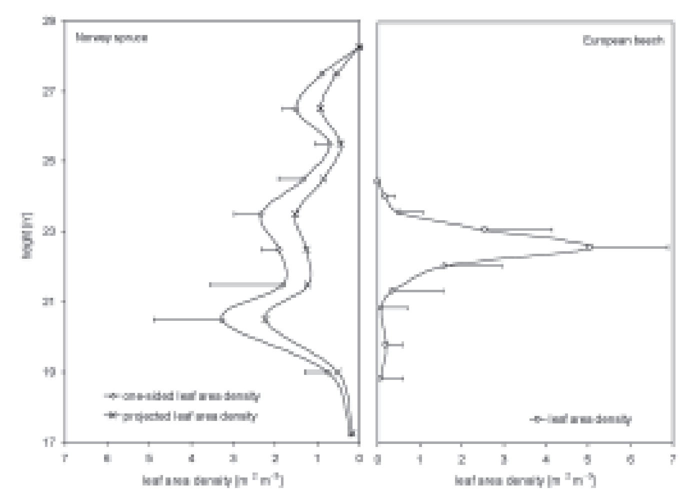


Fig. 26. Leaf area densities (LAD) in the vertical profiles of Norway spruce (*Picea abies* L. [Karst.], n=3) and European beech (*Fagus sylvatica* L., n=7). Measurements were registered electronically with an optical instrument (LAI-2000, Li-cor Ltd., Lincoln, Nebraska, USA). The measurements on spruce were converted into projected needle area by multiplication by $3.59*(\pi/2)^{-1}$ (Fassnacht *et al.*, 1994). The one-sided needle area (Chen & Black, 1992) was calculated with respect to needle morphology, which depended mainly on needle age and position in the crown.

Tree species can differ distinctly in crown structure and in their strategy to exploit canopy volume (Küppers, 1994). This is shown for leaf area densities (LAD) in the vertical profiles of Norway spruce and European beech (Fig. 26). Beech had a pronounced maximum of its LAD at the top of the crown. LAD of spruce was more evenly distributed and increased towards the crown base up to a maximum, which was one third lower in comparison with beech. The irregularities in LAD of spruce reflected the crown structure, where the growth pattern of branches leaves gaps, that allow more light than in beech. At the stand level, beech only had one third of the one sided leaf area index ($5.6m^2\ m^{-2}$) and only half of the projected leaf area index ($10m^2\ m^{-2}$) in comparison with spruce ($15m^2\ m^{-2}$).

Morphological differences between sun and shade branches as well as biotic and abiotic injury to the foliage are dependent on light exposure (Fig. 27). Before autumnal senescence the percentage of damaged and shed leaf area increases in the insolated crown of beech more rapidly in comparison with that shaded. In particular, necrotic areas on leaves in the insolated crown reduce the photoynthetic carbon gain substantially, starting at the end of August. Cicadellidae (leafhoppers) are feeding preferentially on the epidermal layer of shade leaves. Combining datasets from biochemical, ecophysiological and zoological surveys will contribute to a mechanistic understanding of the observations.

Bioclimatology: the challenge of a ‘free-air’ ozone fumigation system

A novel system for continuous and controlled free-air fumigation of mature tree canopies with ozone was set in operation in May 2000 (Figs 28 and 29). Within a volume of $2000m^3$ which comprises the crowns of 10 neighbouring trees, the O_3 levels that prevail at the forest site are experimentally increased to a ‘2 x ambient’ O_3 regime (up to maximum levels of 150ppb O_3; Werner & Fabian, 2002). Five trees each of spruce and beech are exposed to this regime, whilst another group of five of each grow under the ambient O_3 regime (i.e., unchanged O_3 levels) to serve as a ‘control’.

Ozone is produced by a commercial ozone generator (Ozonia-CSI), the ozone delivery of which can be regulated between 0 and 70 g/hour. To prevent formation of oxides of nitrogen, the ozone generator is operated with oxygen rather than air. With a commercial oxygen generator based on the pressure swing absorption (PSA) technique via a molecular sieve, oxygen is enriched to 90% in air (including passage through a dryer and VOC filter). The use of a 6 to 8 bar compressor and an air flow of about 470l/min proved to be an efficient and low-cost solution. The ozone generator output is fed into a 2000l mixing tank, with a constant flow rate of 1500l/min of ambient air, being added by means of a blower that maintains a tank pressure of 1.2 bar. Differing from the FACE design (Free Air CO_2 Enrichment, see Karnosky *et al.*, 2001, Pinter *et al.*, 2000), which utilises a ring-shaped tube system for fumigation that encircles the experimental area, we use a system of 130 PTFE tubes fitted into the mixing tank by a manifold to conduct the ozone/air mixture directly into the canopies of the study trees. These tubes are fixed in a grid mounted above the canopies, and hang downward, about 80 to 100cm apart from each other. Each tube is equipped with 45 flow-calibrated outlets, 33cm apart from each other, each providing a constant flow rate of about 0,30l/min each.

This methodology ensures an experimentally enhanced and chronic whole-tree exposure to ozone whilst avoiding, in the absence of plant enclosure in chambers or cuvettes, physiological bias through micro-climatic artefacts (which prevail in conventional fumigation studies). The striking advantage is the applicability to adult trees growing in naturally structured forest stands (Karnosky *et al.*, 2001). The technique is suitable for CO_2 fumigation as well.

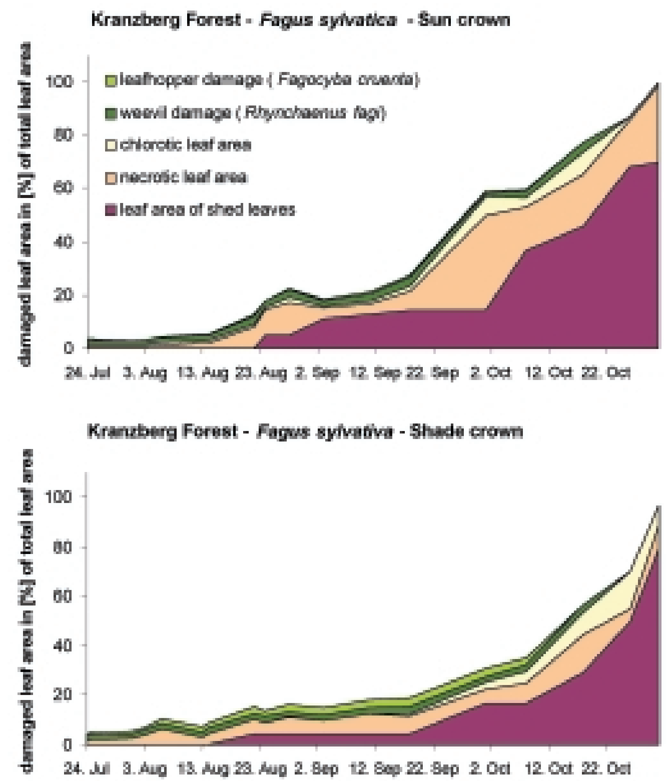


Fig. 27. Percentage of damaged leaf area in the insolated and shaded crown of European beech.

Fig. 28. View on the ‘free air’ ozone fumigation system (KROFEX).

Ozone records (1-hour averages) at 4 heights within the non-fumigated control area are shown in Figure 30 for two weeks in August and September 2000, respectively, along with the reference background ozone level as recorded above the stand canopy at about 50m distant. This background level is not influenced by the fumigation experiment, as indicated by the high correlation with the ozone level recorded at the roof of our institute building, 5km distant from Kranzberg forest. The 1-hour averages at 3 levels

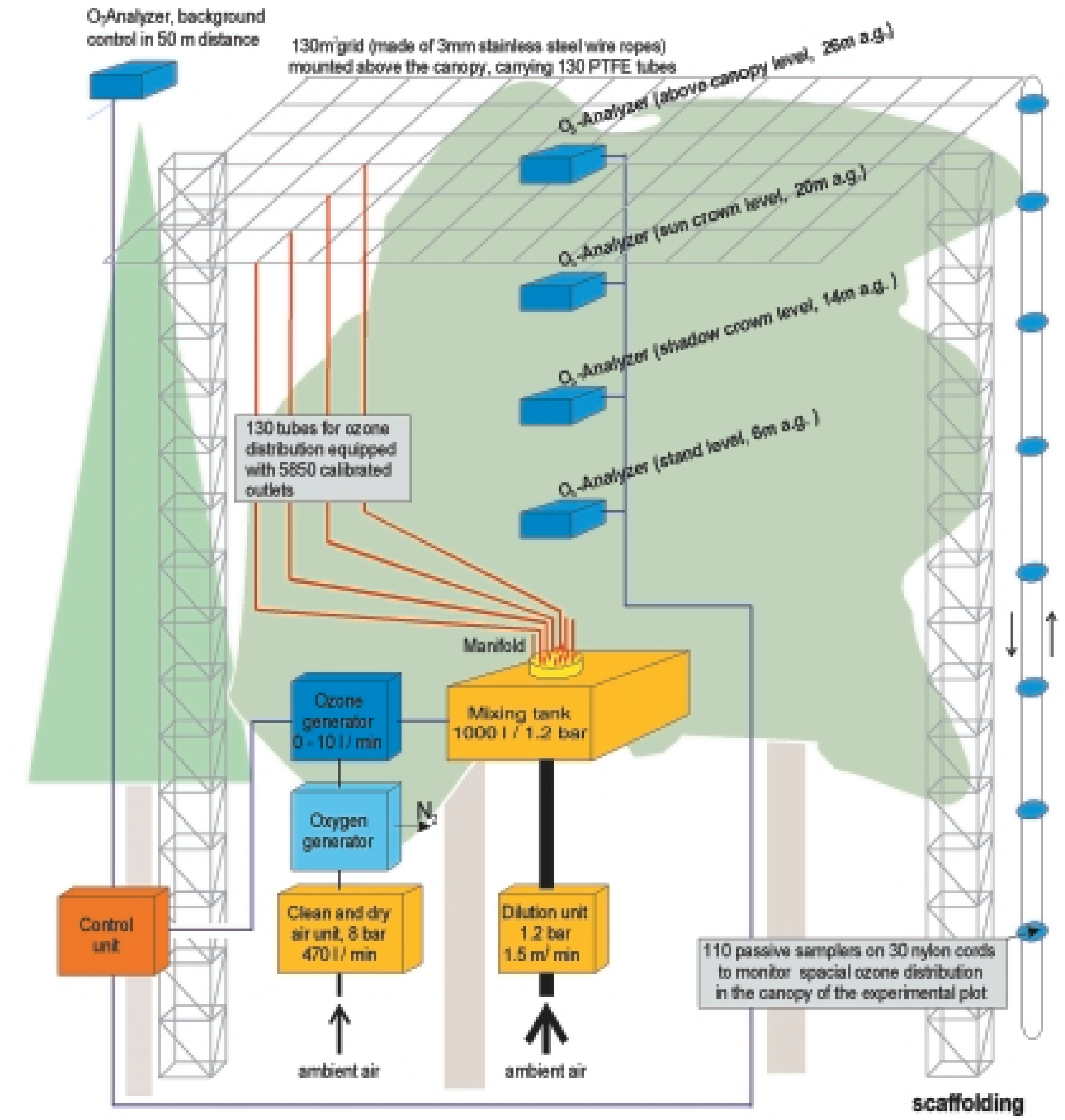


Fig. 29. Schematic diagram showing the principle components of the KROFEX design.

of 14m (shaded crowns), 20m (insolated crowns) and 26m aboveground (directly above the canopy) demonstrate that the entire fumigated crown zone follows approximately ‘2x ambient ozone’. Vertically, the ozone distribution within the canopies is homogeneous within about 20%. No fumigation is performed below the stand canopy. Thus, the control instrument mounted at 6m aboveground does not display elevated ozone levels.

A large number of passive samplers (Werner, 1992; Baumgarten *et al.*, 2000), up to 200 being employed simultaneously, were exposed within the fumigation zone as well as outside, in order to monitor, with high spatial resolution, the ozone distribution in the stand. We used a sampling time of 7 days and, thus, obtained 1-week integrations. As a typical example of the results obtained, the integrated ozone exposure at 20m above ground (insolated crown level) is shown for one week in summer (Fig. 31). Isolines are shown of the extinction of isatine, the product of ozone reaction with the Indigo-dye of the passive

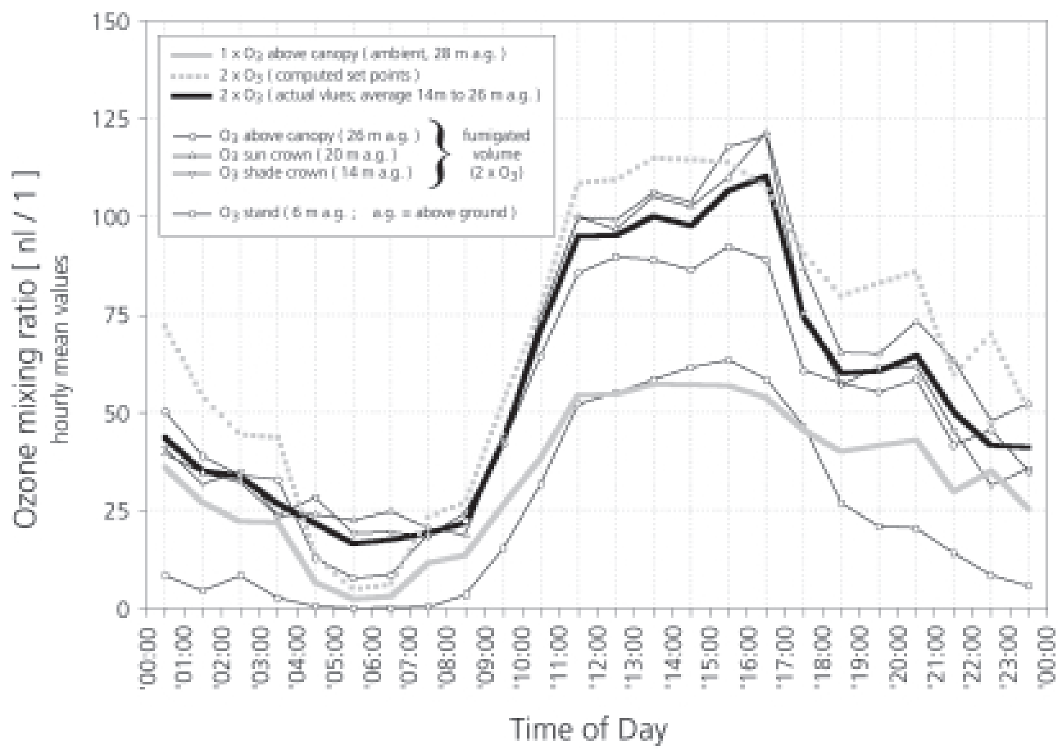


Fig. 30. Diurnal course of ozone concentrations in ambient air (reference, '1 x O_3', above canopy, height: 26m) and in a vertical profile in the fumigated crown volume ('2 x O_3', heights: 14, 20, and 26m) as an example on Sept. 12th, 2000. Elevated levels of ozone occur only in the tree crowns, where the target value (cut at 150 nl l^{-1}, calculated) is reached ('2 x O_3', heights: 14, 20, and 26m), whereas below the fumigated foliage (height: 6m) ozone concentrations are comparable to ambient air.

samplers. This extinction is proportional to the ozone deposition during the exposure time of the samplers and therefore a measure of the integrated external ozone dose of the particular week.

Extinction values of 0.45 to 0.50 prevail within the fumigation zone (Beech = B, spruce = S, Fig. 31). Non-fumigated reference trees (bold letters B and S) are shown, most with extinction values around 0.25. Thus, as is noticeable from Figure 30 as well, ambient ozone in this example was increased by about a factor of 1.8, well within the majority of the other data (not shown), ranging between 1.7 and 2.0.

The concept focuses on the functional performance of tree individuals growing in stands with their multi-factorial biotic and abiotic interactions. The comparison between the two O_3 regimes enables a quantitative risk assessment of a broad spectrum of molecular, biochemical and ecophysiological tree responses under the given site conditions. This allows the examination of tree processes which are at risk or already reflect incipient injury under the unchanged O_3 regime. Each of the study trees is viewed, statistically, as an individual case study, with the intention of deriving consistency patterns from O_3 responses occurring synchronously at the cell, organ and whole-tree level. Mechanistic modelling is used in scaling findings to the stand level. Findings aid the definition of missing, field-relevant measures of O_3 sensitivity in adult forest trees and will make thresholds based on O_3 exposure obsolete while promoting concepts of actual O_3 uptake, i.e. the O_3 flux into leaves through stomata. By this, physiologically and ecologically meaningful O_3 doses are provided with respect to tree acclimatisation to ozone, mitigation in carbon sink strength of trees and stands, and initiation of O_3 injury (Häberle *et al.*, 1999).

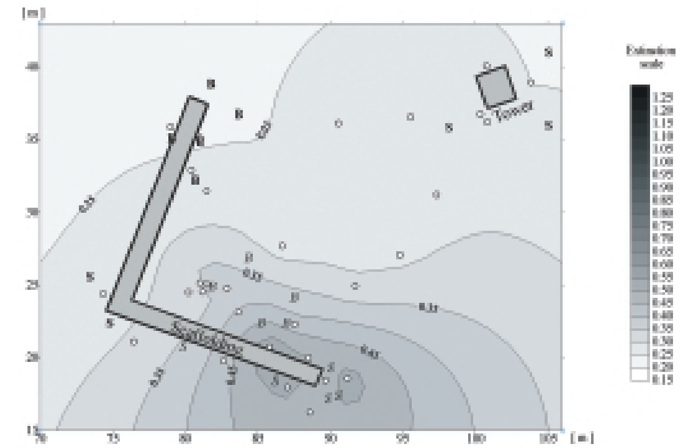


Fig. 31. Distribution of ozone doses cumulated during one week (26.vii.-01.viii. 2000) by passive sampling in the sun crowns 20m above ground level. The fumigated trees ('2 x O_3') are marked by italic, the control trees ('1 x O_3') by bold letters: B = Beech, S = Spruce. Positions of samplers are shown by small circles, isolines of extinction were derived by Kriging's method.

Fig. 32. Branch beating to collect arthropods in winter.

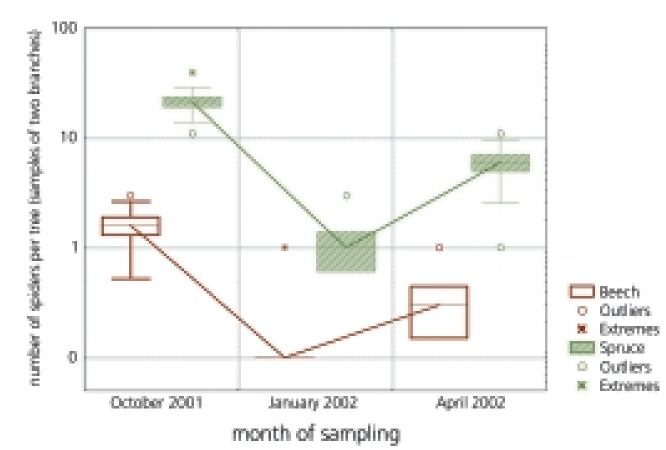


Fig. 33. Means of spider abundance per tree (beating of two branches per tree, see text) in samples from beech (n=10) and spruce (n=10) during winter. Note logarithmic y-axis.

Summarizing recent results from the on-going experiment, beech leaves developed visible symptoms and accelerated autumnal senescence due to the elevated ozone regime whereas spruce appeared to be less susceptible (Nunn *et al.*, 2002). An important finding is that responses from containerised young plants cannot be extrapolated unconditionally to the performance of adult trees under ozone stress.

Animal ecology: the spatial and temporal distribution of biodiversity in tree crowns

The primary aim of our studies is to assess the role of coniferous and deciduous trees as habitats for arthropods in a managed forest, and to examine the role of these tree species for the maintenance of biodiversity in managed forests. Bavarian experience in arthropod ecology of tree crowns derives from the comparison of communities of managed and unmanaged forests at different sites (Simon, 1995, 2001, 2002; Schubert, 1998; Ammer & Schubert, 1999; Gruppe & Schubert, 2001; Gossner & Simon, 2002). The methods have been adapted successfully to the conditions of the Kranzberg forest, facilitated by the canopy crane. Thus, the studies of the arthropod fauna could be extended to the upper and outer canopy of spruce and beech, including seasonal replication. In order to work non-destructively we decided to sample arthropods by branch beating (Fig. 32). We use a funnel with an area of 0.5m², sampling two branches (each more or less covering the funnel opening) of one tree in the upper and outer canopy by standardised beating (ten beats per branch). Sampling was performed in ten spruce trees and ten beech trees in monthly or, during winter, bimonthly intervals.

A bottleneck for the survival of arboreal arthropods in temperate forests is apparently winter time. In exposed tree crowns climatic conditions are even worse than on ground level where the forest cover mitigates extremes in temperature. Our results indicate that all arthropods summed up were much more numerous during winter in spruce as compared to beech (Table 5).

Many groups such as beetles (Coleoptera), Hymenoptera and homopterans, although abundant, even during autumn, were absent on beech in January. The total of arthropods sampled on beech was only one eighth of the number found on spruce. Spiders, an important food source for birds, were an order of magnitude more abundant on branches of spruce in comparison with beech during that period of time (Fig. 33). These first results indicate the importance of more complex structural features in a forest canopy for hibernating arthropods as observed in lower forest strata by Gunnarson (1990, 1996).

The crane allows us to study arthropod communities not only on the scale level of the entire tree crown but also on smaller scales including vertical stratification, direction and differences in branch structure.

Table 5. Total of different arthropod groups in samples of branch beating (n = 20 per tree species) in the upper and outer canopy of beech and spruce at the Kranzberg crane site.

Taxa	Beech			Spruce		
	17.10.01	10.01.02	12.04.02	17.10.01	10.01.02	12.04.02
Coleoptera	20	0	3	27	3	26
Araneae	16	1	3	213	10	60
Blattodea	1	0	0	6	0	0
Dermaptera	7	0	0	1	0	0
Neuroptera	1	0	0	26	0	0
Raphidioptera	0	0	0	0	3	1
Hymenoptera	4	0	4	87	3	7
Heteroptera	7	0	0	11	0	6
Homopterans	43	0	5	61	13	17
Aphidina	1	0	0	5	0	0
Lepidoptera	0	0	0	0	0	1
Holometabolan larvae	1	2	4	8	3	2
Collembola	6	0	1	2	0	10
Acari	0	0	0	0	0	0
Diptera	1	2	0	11	3	6
Thysanoptera	0	0	0	0	2	0
Psocoptera	0	0	0	183	1	1
Total	**108**	**5**	**20**	**641**	**41**	**137**

Perspectives towards future research and cooperation with the canopy community

Research activities will remain concentrated on fundamental questions about the interaction of structure and function in forest trees and the influence of biotic and abiotic stressors. The ozone fumigation experiment will be continued until the end of 2005 at least. Greater effort will be concentrated on the root systems and soil processes since these may be considered as inaccessible as the uppermost canopy.

Stand thinning by removing trees from the research plot within the next three years will allow the study of dynamic competition for light in the canopy and at the forest ground. Experiments using stable isotope techniques intend to give a sound understanding of the processes of carbon and nitrogen allocation in the trees.

Exchanging experience with international partner groups active in canopy research will facilitate standardisation of methods in canopy research (e.g., classification of herbivore damage, quantification of competitiveness, statistical approaches and modelling). Colleagues planning investigations complementary to those conducted at present are welcome to join the research activities at the Kranzberg forest.

Acknowledgements

The authors acknowledge the valuable help and assistance by B. Baumeister, T. Feuerbach, N. Hofmann, G. Jakobi, A. Jungermann, A. König, A. Knötig, P. Kuba, J. Lebherz, B. Rappenglück, H. Reitmayer and I. Süss. We are grateful to Prof. Dr. M. Kazda, University of Ulm, for providing us with his LAI-2000 instrument.

4.2.3. Leipzig Canopy Crane Project (LAK), Germany

Wilfried Morawetz & Peter J. Horchler

Background

In 1995, W. Morawetz initiated the development of a project in Southern Venezuela (Surumoni Project, Chapter 4.3.4), which involved the first tower crane moving on a rail track (120m long) inside a forest. Three years later, he planned to install a similar crane system in a central European temperate deciduous forest. The incentive was to compare functional processes in an Amazonian forest with those in a temperate European forest. In close co-operation with the Centre for Environmental Research Leipzig-Halle (UFZ) and with strong support from the mayor of Leipzig, a crane system almost identical to that used at Surumoni was installed in March 2001 within a nature protection area (NSG Burgaue), in the north-western part of the extensive floodplains within the city of Leipzig (Project LAK, 'Leipziger Auwaldkran'; Morawetz & Horchler, 2002).

The criteria to choose the location of the crane included:

- the existence of good baseline information on biotic and environmental data;
- a forest stand with high tree diversity and near-natural species composition and structure;
- minimal logistic constraints on reaching the location e.g. the possibility to use public transport; and
- a well structured floodplain forest comparable to a tropical rain forest.

The site finally selected also included the following: (1) a pre-existing dyke on which the rail track was built with minor disturbance to the forest; (2) the presence of a nearby building which could be used as a field laboratory; and (3) the likelihood that the forest will be flooded in future years.

Fig. 34. Aerial view of the Leipzig crane plot area (June 2002).

Table 6. Site and crane characteristics of LAK in Leipzig.

Variable	Characteristics
Location	Floodplain in the city area of Leipzig, Germany 51°20′16″N, 12°22′26″E
Altitude	102m
Mean annual air temperature	8.8°C
Mean annual rainfall	512mm
Type of forest	Floodplain forest of the upper alluvial zone (Querco-Ulmetum)
Area of forest accessed by the crane	1.6ha
Canopy height	Max. 36m
Crane model	Liebherr 71EC, mobile on a 120m track
Height of tower / Length of jib	40m/45m
Maximum height reached by the gondola	ca. 33m
Gondola types	Rectangular, *circa* 1m by 1.5m, 2.2m high, weight 190kg (max 440kg) Cylindrical, diameter 0.9m, 2.7m high, weight 160kg (max 500 kg)
Number of persons carried by the gondola	3, 2
In operation since	2001
Main research topics	Interdisciplinary research on the functioning of the forest ecosystem, including studies related to biodiversity, biological processes, climate and soil. For biodiversity, these include: • Inventory of canopy organisms • Spatiotemporal patterns of canopy organisms and environmental correlates • Role of selected species and species groups on forest functioning • Human impact and its influence on forest functioning
Remarks	The set up is near identical to that of the Surumoni crane (Chapter 4.3.4)
Management	University of Leipzig, Institute of Botany, Systematic Botany
Contacts	Prof. Wilfried Morawetz, University of Leipzig, morawetz@uni-leipzig.de Peter Horchler, University of Leipzig, horchler@uni-leipzig.de
Web site	www.uni-leipzig.de/~instbota/LAK.htm
List of publications	Soon on the web site
Fees for researchers	25 ¤ per hour; fee for long term investigations can be negotiated

Project management

The project is managed by both authors of this chapter and is hosted at the Institute of Botany of the University of Leipzig. The project is a non-profit and strictly scientific enterprise. The Federal Ministry of Education and Research provided an initial three-year grant (¤350,000) to install, maintain and administer the crane. Whilst the crane administration itself does not fund any project, proposals for further funding are pending. To cover part of the operating costs, a fee of ¤25 per hour is charged to all researchers using the crane. However, costs applying to significant projects, such as long term investigations, are negotiable. Visiting researchers should apply by e-mail to one of the authors describing their research project and desired time to use the crane. This should be done at least 3 (to 6) months in advance in order to reserve crane time.

The Leipzig Crane is a Liebherr 71EC construction crane, movable on a 120m long rail track (Fig. 34 and Table 6), very similar to the Surumoni Canopy Crane. Researchers have access to a forest area of about 1.6ha and reaching 33m high, by means of two types of gondolas. The purchase of the second-hand crane, which needed some maintenance work, was partly sponsored by the Liebherr company, to whom the authors are very grateful.

Table 7. Tree species composition (trees with dbh≥5 cm) in the 1.6ha Leipzig Canopy Crane plot and their rank of importance. The Importance Value Index (IVI: Curtis & McIntosh, 1951) is the sum of the relative number of species (Abundance), relative number of occurrences in all 10 by 10m grid cells of the crane plot (Frequency) and relative basal area (BA). The relative Abundance, Frequency and BA have been omitted. Note that the total of the IVI is 300%.

Species	Abundance	BA (m²)	Frequency	IVI (%)
Acer pseudoplatanus	226	13.72	119	69.3
Fraxinus excelsior	111	24.09	78	65.2
Tilia cordata	229	10.56	112	63.3
Acer platanoides	154	2.52	73	34.9
Ulmus cf. minor	93	0.99	41	19.6
Carpinus betulus	67	2.61	42	19.6
Quercus robur	15	6.56	11	14.1
Quercus rubra	4	1.01	4	2.8
Ulmus cf. glabra	7	0.04	7	2.2
Fraxinus pennsylvanica	5	0.29	4	1.8
Acer campestre	4	0.35	4	1.8
Cerasus avium	4	0.33	4	1.7
Robinia pseudoacacia	3	0.5	3	1.3
Aesculus hippocastanum	4	0.3	3	1.1
Populus x canadensis	2	0.21	2	0.9
Crataegus sp.	1	0.01	1	0.3
Totals:	929	63.57	508	300

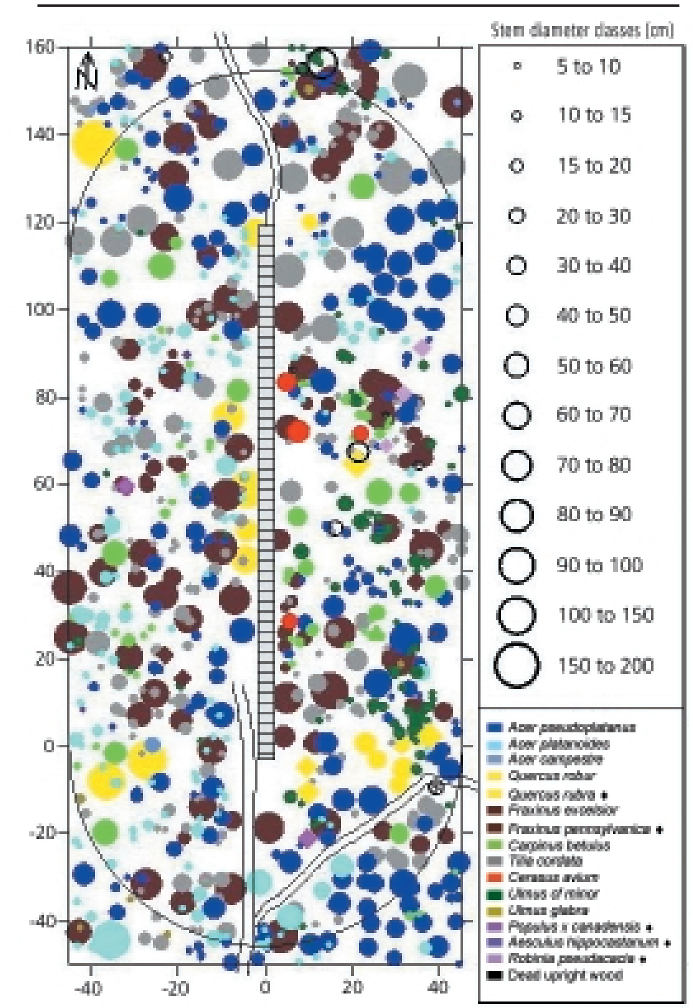


Fig. 36. Distribution of all stem diameters ≥5cm dbh into diameter classes.

Site description and crane details

The climate of the Leipzig area is characterized as intermediate between maritime and continental (mean annual temperature = 8.8°C and mean annual precipitation = 512mm). The soils at the crane site are nutrient-rich loamy floodplain (alluvial) soils. The vegetation is classified as typical floodplain forest of the upper alluvial zone (Querco-Ulmetum). Due to river rectifications and canalization, as well as extensive brown coal mining activities since the early 20TH century, the ground water level in the Leipzig floodplain forests dropped significantly. Thus, the forest suffered a gradual but notable change in species composition, favoring for example Sycamore (*Acer pseudoplatanus*) which today represents the most frequent tree species.

The forest stand at the crane site is characterised by a fairly diverse composition of woody species (17 tree species and 5 shrub species with diameter at breast height (dbh≥1cm), including 4 introduced tree species (neophytes). Table 7 summarizes the inventory of trees in the 1.6ha of forest accessible from the crane gondola.

For means of comparisons and for the dbh class ≥10cm, this corresponds to 389 trees per ha or 43.2 m² basal area per ha. Mean tree height is 25.6±6.9m (SD), with a maximum of 36m.

This species composition (Fig. 35) is a product of centuries of practice of selective logging ('Mittelwaldwirtschaft'), during which old oak trees (*Quercus robur*) were used as timber wood while other species (*Fraxinus excelsior*, *Carpinus betulus*, etc.) were cut much more frequently and used as firewood. This practice ended in 1870. Since that time there have been only minor timber extractions and tree species which were frequently cut in the past grew up to the canopy. Thus, the actual canopy is formed by old oak trees (> 250 years) and younger trees of that species (<130 years). A peculiarity of the stand is its amount of dead wood which provides an important habitat for some rare and endangered insect species, such as wood-boring beetles. These traits make the research site a highly valuable nature sanctuary.

The demography of the whole stand tends to show an inverse exponential curve of stem diameter distribution, typical for many natural forests (Fig. 36). The deviations are so far unexplained. A dendrochronological study is planned.

Main research topics

The interdisciplinary research will address crucial questions about the functional processes that regulate the forest. Cooperation and organization are based on the scheme illustrated in Fig. 37.

The biodiversity investigations are covered by Martin Schlegel and Wilfried Morawetz, whilst plant-animal interactions are studied by Stefan Klotz. Physiological processes, forest structure and genetics, and environmental conditions are investigated by Christian Wilhelm, Andreas Roloff and Christian Bernhofer, respectively.

As far as possible, the data and results will be compared to those of tropical sites, such as Panama (Chapter 4.3.5), Surumoni in Venezuela (Chapter 4.3.4) and Cairns in Australia (Chapter 4.3.1).

The key objectives, with particular emphasis on biodiversity, include answering the following essential questions, which are increasingly complex:

- Species diversity and inventory of canopy organisms.
- Maintenance of biodiversity. Including spatial and temporal structuring, e.g. vertical, horizontal and temporal patterns of canopy organisms.
- Interdependence among organisms and environmental parameters, such as (micro-) climate, water regime, etc.
- Function and functional aspects of selected species and species groups within the forest ecosystem. Identification of keystone organisms or keystone guilds.
- Human impact and its influence on the functional processes identified above. What are the applied issues of our conclusions?

Table 8. Preliminary species richness of organisms investigated in the LAK plot.

Group	No. of observed species	No. of canopy species	No. of exclusive canopy species	No. of expected species*
Trees (≥1cm dbh)	17	-	-	17
Shrubs (≥1cm dbh)	5	-	-	5
Herbs and grasses	37	3	0	>40
Mosses and liverworts	17	17	4	>18
Lichens	20	20	20	>20
Lignicolous macrofungi	56	56	56	>100
Slime moulds (Myxomycota)	15	15	?	?
Water bears (Tardigrada)	3	3	?	?
Butterflies (Lepidoptera)	27	27	?	>100
Ground beetles (Carabidae)	21	23	?	> 23
Wood-dwelling beetles (Coleoptera)	105	105	?	>150
Bugs (Heteroptera)	58	58	?	>70
Ants (Formicidae)	5	5	3	7
Bumble Bees (*Bombus* spp.)	8	8	?	>8
Orb-web spiders (Araneidae)	46	46	?	>100
Amphibians	4	1	0	4
Bats	5	5	?	7

*Rough estimates

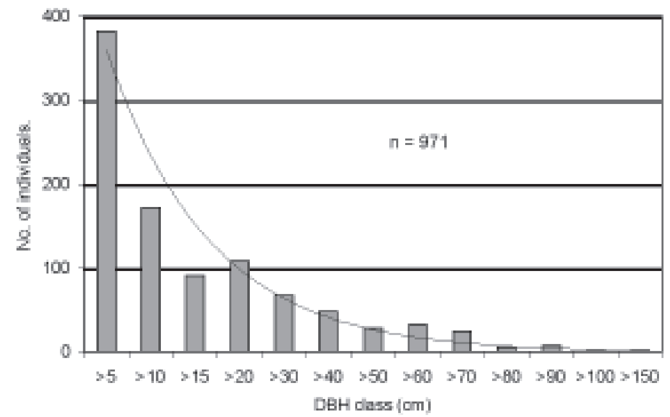


Fig. 36. Distribution of all stem diameters ≥5cm dbh into diameter classes.

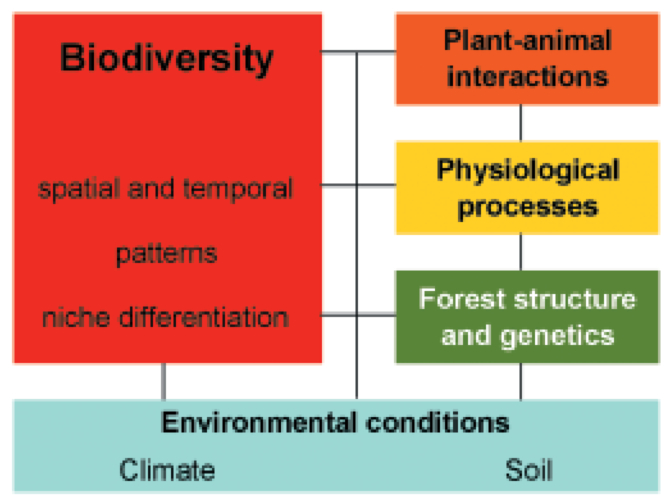


Fig. 37. LAK Project organization scheme.

It is obvious that with increasing complexity there will be a decreasing number of species that can be studied in detail. Nevertheless, we would emphasize the major importance of organismic biology in our project. The main goals of the observation cranes are to allow observations, measurements and sampling *in situ*. All of this information will be databased and linked to a GIS in order to provide reference data for all project participants.

Main findings

Since the crane has recently been established, to date only some, mostly short-term studies have been performed. A first overview of the inventory of forest and canopy biodiversity is given in Table 8.

Surprisingly, observations in the canopy emphasized a rather high diversity in macro fungi (56 spp.), as well as in slime moulds (Myxomycota, 15 spp.) and the re-colonization of formerly very rare and threatened lichen species (11 spp.), clearly indicating improved environmental conditions, i.e. decreasing air pollution.

Some coincidental observations will lead to more detailed studies, and these included:

- the presence of the frog *Hyla arborea* in the upper canopy (first physical proof for Germany),
- the presence of snail species (*Arianta arbustorum*, *Cepea sp.*) foraging on mosses in the upper canopy,
- a bird (*Parus caeruleus*) acting as potential pollinator for a 'usually' wind pollinated tree species (*Fraxinus excelsior*).

Another major research project that was initiated in 2002 was the investigation of tree phenology focusing on the species *Fraxinus excelsior*, *Tilia cordata* and *Quercus robur*. Detailed study of *Fraxinus excelsior* revealed a striking spatial and temporal variability in generative and vegetative phenology, in the distribution of the three flower types as well as in leaf and branching pattern and morphology. The investigation of this focal species will be continued including more detailed studies on reproductive ecology and population genetics. A comparison with the results from the Tomakomai Canopy Crane Project (Chapter 4.2.5) concerning the Japanese tree species *Fraxinus lanuginos*a (Ishida & Hiura, 1998) is planned.

So far, three joint projects with foreign institutes have been initiated, two including visiting researchers. A former co-worker in the Surumoni Canopy Crane Project, Klaus Jaffé (Universidad Simon Bolívar, Caracas, Venezuela) performed a pilot study on canopy ants using baits. This method indicated that the abundance of ants was very low in the canopy, quite unlike that of Surumoni (K. Jaffé *et al.*, unpubl. data).

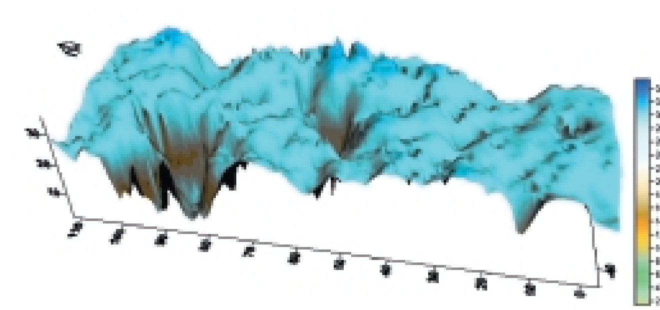


Fig. 38. Surface representation of the canopy topography in the western part of the canopy crane plot, based on a small subset of LIDAR measurements on an area of 45m by 110m. Note the hole (bottom left) a huge gap created in 2002.

Geoffrey Parker (Smithsonian Environmental Research Center, Edgewater, USA) was invited to perform a study of the canopy and understorey topography by means of a laser rangefinder system (LIDAR) to get essential baseline data for all collaborators of the project. The measurements covered a part of the LAK plot. The results for the canopy topography are illustrated in Figure 38.

In fact this represented the first comparison of the same canopy at the same location measured with the same instrument both from above and below. This comparison revealed a notable difference in the arrangement of leaves (Fig. 39).

Whilst leaves are clearly grouped at the outer canopy in order to optimize their position to light no such pattern can be recognized for the leaves and twigs beneath. Overall statistics of height measurements with LIDAR are indicated in Table 9. The standard deviation is a measurement for the roughness of the canopy (G.G. Parker, pers. comm.).

The measurements also permitted the calculation of the mean vertical profile of surface area density (including leaves, twigs and bark; Fig. 40).

David Shaw (Washington University, USA) and Kristina Ernest (Central Washington University, USA) incited the present authors to perform a study on stand level herbivory at LAK. A similar protocol was also applied at various tropical and temperate canopy crane sites in order to obtain global comparative estimates of percent herbivory damage of the whole stand. At 100 randomly selected sampling points, 10 leaves are selected randomly and percent leaf damage is measured for all leaves. In 2002 at LAK, 57 sampling points only (570 leaves) were studied. Based on these data, which were definitely too restrictive for our large study plot (1.6ha) we calculated a percent leaf damage of 1.12%, which appears far below corresponding values obtained for tropical forests. It is planned to repeat this study in 2003, this time collecting *circa* 1,500 leaves at 150 random sampling points.

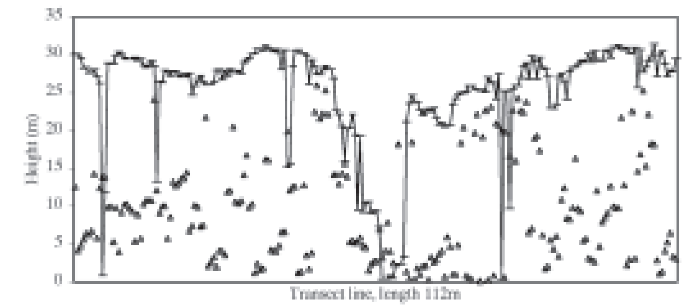


Fig. 39. Comparison of LIDAR measurements (subset) of the outer canopy (small bars connected by line) and "understory height" (triangles; the shortest distance from the ground to the lowest leaf, branch or twig) along the same transect of 112m length.

Table 9. Statistics associated with LIDAR measurements of the height of the canopy surface (outer canopy) and understorey.

Variable	Outer canopy height (m)	Understorey height (m)
Mean	25.6	9.2
Median	27.6	7.6
SD	6.9	7.0

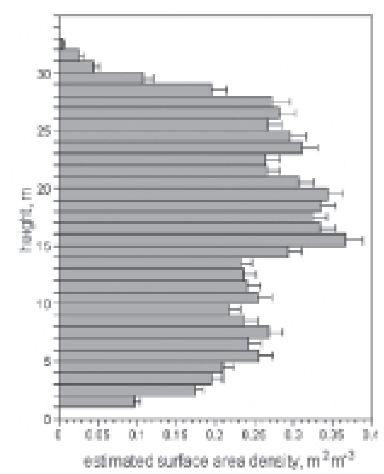


Fig. 40. Mean canopy height profile based on LIDAR measurements with estimated surface area. Error bars represent standard errors.

Future research and collaboration

During this first research phase, the intention was to obtain an overall canopy inventory, but in the future emphasis will be the identification of spatial (particularly vertical) patterns of biodiversity and measuring their environmental correlates, particularly microclimatic parameters. In addition, other studies will be expanded, particularly phenological ones, whilst physiological, biochemical and genetic studies are awaiting funding to be initiated.

A further step will be the replication of the WebFace experiment, currently being performed at the Swiss Canopy Crane by Christian Körner (Chapter 4.2.1). In his experiment, parts of the forest trees are exposed to a CO_2-enriched atmosphere in order to measure the physiological and, ultimately, the ecosystem response. The final aim is to assess the response of the forest to anthropogenic increases in atmospheric concentration of carbon dioxide.

Certain projects are particularly suitable for collaboration with other canopy crane sites. These are the LIDAR and stand level herbivory projects, both so called pathfinder projects of the Global Canopy Programme (see Chapter 2). If possible, they should be replicated at all canopy crane sites.

A pilot study on the spatial and temporal dynamics of thermal properties of the forest stand was performed in 2002 by Jörg Szarzynski and colleagues (Center for Development Research, University of Bonn and Department of Physical Geography, University of Mannheim, Germany). Using a high-precision thermographic camera, thermal scans of the entire forest were generated, from the soil to the canopy. Preliminary results are very auspicious and may yield new insights into the heat balance of vegetation plots. Since spatial data are recorded, this method provides important information for several scientific disciplines, such as bioclimatology, physiology, botany and zoology, or generally to those projects interested in the environmental impact of microhabitat or niche differentiation. Hence, standardized thermographic mapping should be regarded as a method highly suitable to be included in the frame of GCP pathfinder projects.

Another experiment quite amenable to collaboration has been proposed by S. Joseph Wright (Smithsonian Tropical Research Institute, Panama) and already performed in Panama (Chapter 4.3.5, Van Bael). It is intended to exclude predators of arthropods, mainly birds and bats, in order to monitor the response of insect herbivores. This experiment will be replicated in one of the next field seasons.

Since it was rather surprising to find such a high diversity of slime molds (Myxomycota), a collaboration is underway with Martin Schnittler (University of Greifswald, Germany), with the intention of comparing data on this group from several sites (Australia, Costa Rica, USA). A similar effort should be invested into a global comparison of canopy macrofungi.

A collaboration initiated by Andreas Prinzing (University of Mainz, Germany) is planned for 2003 with colleagues from Poland investigating the microfauna, i.e. Acari, Collembola and Tardigrada. These non-flying and less mobile animals are expected to be much more site specific. Hence beta diversity among the microfauna community in the forest canopy is predicted to be higher than among more mobile arthropods. A similar project has been performed by Australian colleagues and appears to be quite stimulating and suitable for a global collaboration.

Finally, in our opinion collaboration is needed for a detailed study of generative and vegetative tree phenology. Therefore, some standard protocol, such as the one used in the stand level herbivory project, needs to be developed.

Many of these collaborations can be facilitated by the Global Canopy Programme and the International Canopy Network. Both provide excellent contacts and databases and we are convinced that a global collaboration is the only way forward to promote canopy research.

4.2.4. Solling, Germany

Michael Bredemeier, Achim Dohrenbusch & Gustav A. Wiedey

Location and site characteristics

The Solling crane is located in the centre of a triangle of roof installations underneath the forest canopy, consisting of three roofs of $300m^2$ surface area each (Figs 41 to 44 and Table 10). This roof facility, part of a European network, was installed in order to perform whole-ecosystem manipulation experiments under field conditions, and it was the only one with a device to gain access to the canopy. In particular, the crane was designed as a device to facilitate physiological measurements in the canopy to investigate tree responses to the experimental manipulations.

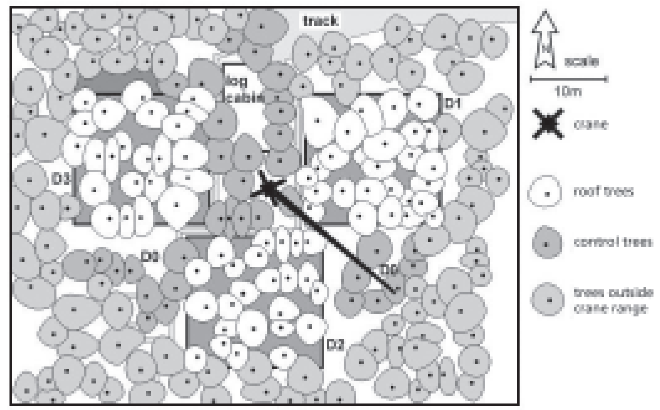


Fig. 41. Ground plan of the Solling roof project.

The roof manipulation facility and the crane were located at Solling since this experimental forest has been a focus of intensive interdisciplinary forest ecosystems research since the 1960s. The site was part of the Man and the Biosphere Programme (MAB) and the International Biosphere Programme (IBP). Therefore, data from former monitoring and research projects were available to be used as baseline information for the ecosystem manipulation study.

The Solling experimental forest is located in central Germany, in a mountainous area which is a part of the Weser river mountain range. The roof manipulation study is run in a 67 year old (2003) stand of *Picea abies* (L.) Karsten (Norway spruce). The site is located at *circa* 500m elevation a.s.l. on a plateau. Average annual rainfall is 1,090mm. The soil is a strongly acidified dystric cambisol (FAO classification) which has developed in a loess solifluction layer overlying sandstone bedrock. Base saturation is 7% or less of cation exchange capacity (i.e., capability of the soil to store nutrient cations) throughout the mineral soil profile.

Fig. 42. View from the gondola to the crane tower and the canopy of the 24m high forest of Norway spruce (photo Achim Dohrenbusch).

The spruce forest is in a state of impaired vitality, with symptoms of needle losses and yellowing, the latter due to severe magnesium deficiency in the highly acidified soil. The roofs were built underneath the canopy with the roof ridge at *circa* 3.5m above the ground. They are permanent timber frame constructions, covered with highly transparent polycarbonate plates. Water falling onto the roofs is collected in a central cabin, processed in various ways and redistributed to the roof plots by a sprinkling system.

Installations, experiments and key research topics

The Solling roof project is an interdisciplinary study comprising monitoring of the soil (both chemistry and hydrology), the forest stand (roots and above ground physiology), the ground vegetation and the soil fauna and microflora, as well as micro-meteorological parameters. A detailed listing of installations and monitoring may be found in Bredemeier and Dise (1992).

Fig 43. View up the crane tower (photo Gustav Wiedey).

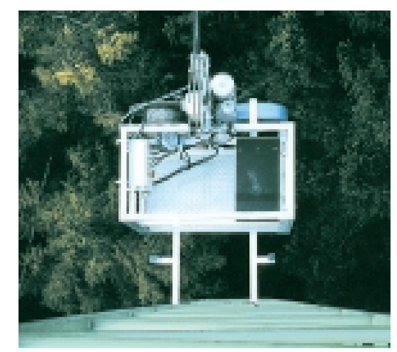


Fig. 44. View down upon the gondola (photo Gustav Wiedey).

The experimental treatments applied in the Solling roof experiment were (Bredemeier *et al.*, 1998):

1. 'Clean rain' roof with simulated pre-industrial throughfall. Water is filtered, de-ionised, adjusted to clean rain - concentrations and redistributed to the plot immediately (designated as site 'D1' or roof 1).
2. Control roof for roof effects alone, without further manipulation. Water is re-sprinkled immediately without changing ion content (site 'D2', roof 2 or control roof).
3. Drought/re-wetting roof, for simulation of strong drought events with subsequent intensive re-wetting. Water is stored in a tank battery during the experimental drought phases and reapplied to the site during the re-wetting phases (site 'D3' or roof 3). The durations of drought periods is in the range of 10-25 weeks, up to 140mm of throughfall can be stored during drought and reapplied in the re-wetting phases. Experimental drought periods were conducted at different times of the year between spring and autumn.
4. Control without roof, consisting of ambient, non-manipulated throughfall (site 'D0' or ambient control).

The composition of the artificially prepared pre-industrial through-fall for the clean rain plot (D1) corresponded to a reduction of sulphur input of circa 65% and a reduction of total nitrogen (ammonium+nitrate) input of 80% relative to the ambient control in the reference years 1990/1991 (i.e., before the activation of the manipulation). The sea salt constituents sodium and chloride are also decreased significantly in the sprinkling solution, since they are considered non-essential for the forest nutrition. Metal nutrient cation contents were only moderately changed in the artificial clean rain solution.

The aim of the drought/re-wetting roof experiment (plot D3) at Solling is to observe the extent of direct drought stress to the forest, but also to detect secondary drought effects in soil water chemistry. With respect to the latter, it has been hypothesised that in phases of re-wetting after intensive drought 'acidification pulses' due to net nitrification would occur (Ulrich, 1983), increasing stress to the ecosystem by adding soil chemical stress to that of drought.

Liquid samples were collected weekly from bulk deposition, throughfall and soil water at several depths (0, 10, 20, 40, 70 and 100cm mineral soil depth) and combined into monthly samples for analysis. In the liquid samples, pH was measured and concentrations of Na, K, Ca, Mg, Al, Fe, Mn, St and Pt were determined, as well as Cl^-, $NO3^-$ and $NH4^+$ concentrations. Litterfall and fine roots from the soil were collected seasonally, pressure-digested and analysed for metal nutrient cations, C, N, S, and P. Suction cup lysimeters were installed at the four sub-plots of the roof experiment in the autumn of 1989, well before the construction of the roofs and the manipulation treatments began. Roofs were closed and sprinkling systems started to operate in September 1991.

In order to investigate physiological responses of the trees to experimental manipulations, it was necessary to gain access to the canopy. In spring 1992 a 33m high crane was installed in the centre of the roofed area. It was equipped with a special transport system for personnel (a gondola with a floor space of 100x70cm) which made it possible to reach the crown area of all of about 100 trees which belonged to the experimental sites. With this method regular physiological measurements of the carbon budget (photosynthesis, respiration) and the water budget (transpiration, xylem water potential, osmotic potential) as well as the shoot elongation and fruiting intensity were performed (Dohrenbusch *et al.*, 2002a). In addition, each year needle samples were taken for element analyses and also an assessment of forest health by visual observation of the needle losses and needle yellowing was performed.

Table 10. Site and crane characteristics of the Solling Canopy Crane.

Variable	Characteristics
Location	Solling mountains, Germany 51°31´ N, 9°34´ E
Altitude	500m
Mean annual air temperature	6.4 °C
Mean annual rainfall	1090mm
Type of forest	Norway spruce plantation
Area of forest accessed by the crane	0.2ha
Canopy height	24m
Crane model	Liebherr modified, based on model 32K/45 (year of manufacture 1977), fixed
Height of tower / Length of jib	33m/25m
Maximum height reached by the gondola	28m
Gondola type	Rectangular, 1.5 x 0.7 x 1.2m, carrying capacity 500kg
Number of persons carried by the gondola	2
In operation since	1992
Main research topics	• Responses of trees to experimental manipulations on roof plots • Precision growth measurements • Precision assessment of vitality status and damages • Photosynthetic capacity and time courses of photosynthesis rate • Trace gas exchange in the canopy
Remarks	Operation by trained personnel only
Management	Dr. Gustav A. Wiedey, University of Göttingen, gwiedey@gwdg.de
Contact	Dr. Michael Bredemeier, University of Göttingen, mbredem@gwdg.de
Web site	http://www.gwdg.de/~fzw/homee/sollingt.htm
List of publications	http://www.gwdg.de/~fzw/homee/publ.htm
Fees for researchers	To be negotiated

Key findings from the crane experiments

Height growth

The course of the annual height growth for all experimental variants showed a development unaffected by treatment. The mean height increment decreased continuously since the beginning of the measurements in 1988 from an average of 37cm on all sites to a minimum in the fifth year of monitoring in 1992 (Fig. 45). At that time the mean shoot growth was only 14cm. Afterwards, up to 1996, a marked increase in height growth was again observed. In the years 1993 and 1994, influence of the drought treatments on the height increment was observed. As a result of the long dry periods during the summer months of previous years the mean height increment on the D3-site was significantly reduced by about 50% compared to the other sites. After 1995, no effects induced by the droughts in previous years could be discerned. By contrast, the effect of the de-acidified precipitation on the height growth of trees at the D-1 site for the total period monitored was not statistically significant (Dohrenbusch *et al.*, 2002b, 2002c, 2002d).

Fructification

Figure 46 shows the average numbers of spruce cones in the years 1992 to 1998. The first count in late summer 1992 showed a large number of cones with an average between 93 and 97 per tree. However, the mean values on an area basis concealed differences between individual trees.

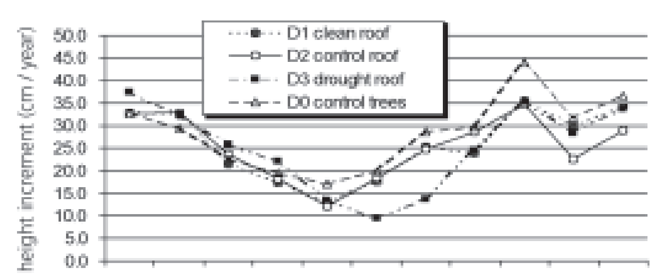


Fig. 45. Development of the annual height growth of the 60 to 70-year-old trees (number of trees per roof: 23-27).

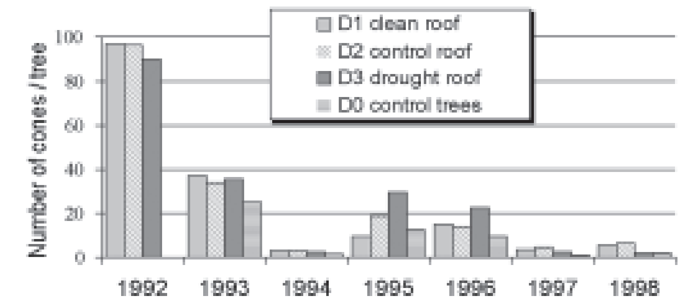


Fig. 46. Cone production during the period 1992-1998.

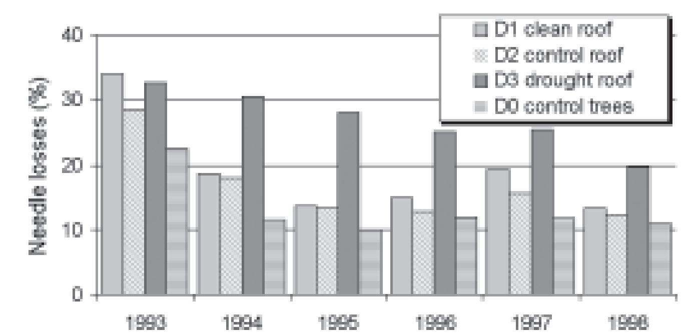
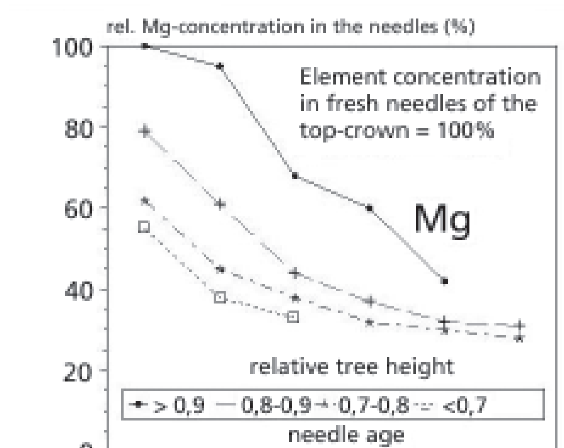


Fig. 47. Observed status of defoliation for the period 1993-1998.



	0	1	2	3	4	5
> 0,9	100	95	68	60	42	
0,8-0,9	79	61	44	37	32	31
0,7-0,8	62	45	38	32	30	28
<0,7	55	38	33			

Fig. 48. Relative concentration of magnesium depending on the position in the crown (relative tree height) and needle age.

Whilst some trees had several hundred cones, others had none. During the following two years the amounts dropped to 30 cones in 1993 or 5 cones in 1994, respectively. After a new increase in the years 1995 and 1996 the number of cones in 1997 attained similar numbers to those of 1994 (Dohrenbusch *et al.*, 2002b, 2002c, 2002d).

Tree vitality and visual appearance of the crown

From 1993 onwards, needle loss and yellowing were monitored for the trees of the roof and control areas. This assessment of the crown was performed from the crane by the same person every year. However, comparisons between years have to be viewed with caution. Therefore, for almost all the trees, photographs of the crown were taken from the same perspective, to optimise the annual damage assessment. During the observation period the tree vitality increased continually. This development was perceived on all of the roofed plots (Fig. 47). The effect of experimental treatment was particularly distinguishable on the trees in the drought experiment, which exhibited particularly high needle loss (Fig. 47) and severe yellowing of needles (Dohrenbusch *et al.*, 2002c).

Nutritional status of the trees (mineral element concentrations)

To determine the element concentrations in needles from 1992 onwards, needle samples were taken from all trees of the roof and control sites. Sampling took place in September from the sun crown of the trees (6th whorl from the top). Only green branches were harvested, and only needles of the two most recent years were investigated. In order to estimate the nutrient concentration for the whole tree, detailed investigations into the variation of nutrient concentration in the crown have been made. The crane with the transportation system permits the access to all parts of the tree crown. Needle samples were obtained from each year and different crown levels (tree heights). Figure 48 shows as an example the trend of magnesium concentration according to crown position and needle age (Dohrenbusch *et al.*, 2002c).

Conclusions from the Solling crane measurements

The crane at Solling was used to measure above ground responses of the spruce stand to the experimental manipulations in the roof project as described above. In the clean rain experiment, above ground effects were generally weak, while the effects of the altered input on soil water chemistry were rapid and strong. Also the root system responded by increased fine-root growth and an improved morphology, but with a time lag of several years. The measurements from the crane are being continued at a lower level of intensity, in order to check whether responses in the canopy will occur with an even longer time lag. In contrast to the clean rain manipulation, canopy level responses in the drought/re-wetting experiments were strong: height growth declined significantly in years following experimental drought phases, and photosynthetic parameters decreased during drought treatments. However, all these parameters also exhibited relatively fast recovery after the end of the experimental manipulations.

4.2.5. Tomakomai Experimental Forest, Japan

Masashi Murakami & Tsutom Hiura

Background

The Tomakomai canopy crane was installed in November 1997 in the 2,715ha Tomakomai Experimental Forest (TOEF), situated near the town of Tomakomai in Japan (Table 11). The forest is adjacent to the Utonai bird sanctuary in the Yufutsu marsh. The crane was funded by the Ministry of Education, Science, Sports and Culture of Japan, through the programme "An integrated study on biodiversity conservation under global change and bio-inventory management system". It is managed by the Tomakomai Research Station, a unit of the Hokkaido University Forests. The University forests were established in 1901 and total 70,000ha, including a tree breeding station, a tree nursery, two experimental stands, and six regional forests, including TOEF. TOEF hosts 150 visiting scientists each year, facilitating their work by providing laboratories, housing, libraries, and research permits. Dormitories are available for visiting researchers and students using the station for educational and research purposes, with the Director's permission. Long-term dormitories with kitchen can accommodate a maximum of 20 people, whilst short-term dormitories can accommodate 42 people.

Table 11. Site and crane characteristics of the Tomakomai Canopy Crane.

Variable	Characteristics
Location	Tomakomai Experimental Forest, Hokkaido island, Japan 42°40' N, 141°36' E
Altitude	90m
Mean annual air temperature	6.1°C
Mean annual rainfall	1254mm
Type of forest	Temperate deciduous broad-leaved forest
Area of forest accessed by the crane	0.5ha
Canopy height	20m
Crane model	Ogawa Industries, OTH-80N, fixed
Height of tower / Length of jib	25m/41m
Maximum height reached by the gondola	20
Gondola type	a: Cylindrical, 2.1 x 0.7m b: Cylindrical 2.4 x 1.2m
Number of persons carried by the gondola	a: 1 person b: 5 persons
In operation since	1997
Main research topics	• Forest structure and species richness • Diversity and productivity in the forest ecosystem • Carbon and nitrogen dynamics of a deciduous broad-leaved forest • Climate change • Seasonal exchange of leaf-level characteristics in relation to successional traits • Mechanisms of masting in relation to storage reserves in tree species • Relationships between the three-dimensional structure of the forest and insect diversity • Other research topics as detailed in the text
Remarks	Located in an experimental plot of 9ha in which a large scaffolding unit also stands
Management	Tomakomai Research Station, Hokkaido University Forests
Contacts	Prof. Tsutom Hiura, Director, Hokkaido University, hiura@exfor.agr.hokudai.ac.jp Prof. Masashi Murakami, Hokkaido University, masa@exfor.agr.hokudai.ac.jp Prof. Naoki Agetsuma, Hokkaido University, age@exfor.agr.hokudai.ac.jp
Web site	http://pc3.nrs-unet.ocn.ne.jp/~exfor/toef/toef.html
List of publications	http://pc3.nrs-unet.ocn.ne.jp/~exfor/toef/toef.html
Fees for researchers	Dormitory fees only

Fig. 49. The TOEF Canopy Crane in summer, in use to count leaves (photo Tsutom Hiura).

Canopy Crane

The crane is located in a mature deciduous forest with *Ostrya japonica*, *Acer mono*, *Cercidiphyllum japonicum*, *Quercus crispula* and *Tilia japonica* among the most common species (Fig. 49). The crane can reach 20 species of trees and 6 species of liana. The crane perimeter covers an area of 0.5ha and is part of an experimental plot of 9ha in which all individuals of 10cm diameter at breast height (dbh) or greater have been measured, mapped and identified. One ha of this forest includes 458 stems larger than 10cm in diameter, so that the total basal area is 27m^2 per ha. TOEF is situated on a deep layer of volcanic material (2m in depth), originating from the last eruption of Mt. Tarumae in 1739. The slope of this forest is rather moderate (from flat to 10°).

The Japanese archipelago is located along the green belt of the western Pacific and Asia, where a humid climate extends from northern Siberia to southern New Zealand. It is an area with high biodiversity and productivity. TOEF is a core site for several international programs, including DIWPA-IBOY (International Biodiversity Observation Year) and DIVERSITAS. In these programmes, the diversity of forest plants, vertebrates, and invertebrates are monitored to study functional aspects of the ecosystem. The diversity of targeted organisms is determined using standardized methods (Nakashizuka & Stork, 2002). TOEF welcomes collaborative research on any field of canopy ecology and biology.

Below, we present the main research topics and results of TOEF projects with respect to (a) forest structure, productivity and climate changes; (b) plant resources in the forest; (c) arthropod diversity and forest structure, and (d) animal-plant interactions.

Forest structure, productivity and climate change

Relationships between diversity and productivity

Forest ecosystems include a large number of species and are the greatest reservoir of carbon of terrestrial ecosystems on Earth. However, anthropogenic activity is raising the level of carbon dioxide in the air and reducing biodiversity. Recent experiments on microcosms and grasslands have shown that as the number of plant species increases, the net primary productivity and nutrient cycling in these systems also increases. However, no empirical tests of this result have been attempted in forest ecosystems, due to the difficulties in either manipulating the forest experimentally or selecting appropriate fields that have uniform environmental conditions to test this controversial hypothesis. In this study, we used an ideal forest ecosystem, in which environmental conditions were uniform among the stands, to show that ecosystem productivity in 40 forest plots increased significantly with an increase in tree diversity. The results of this study imply that the preservation of biodiversity is essential for the well-functioning of carbon cycle in forest ecosystems (Ishii *et al.*, in press; Hiura, in press).

Carbon and nitrogen dynamics of a deciduous broad-leaved forest

Seasonal changes in the soil respiration rate and litter production were measured in TOEF. Soil respiration rate was detected monthly by an open-ended soil respiration chamber and was significantly correlated with soil temperature, at about 10cm depth. Litter fall was monitored with twelve 0.88m^2 traps, which were installed at random within the forest. Green litter was observed in summer as a result of the action of strong winds. Based on the dynamics of carbon and nitrogen, we will shortly estimate carbon flux in the forest ecosystem, as a function of nitrogen flow through the plants.

The size-dependent decline in the productivity and hydraulic conductance of canopy trees was also examined. In the forest, canopy trees have higher primary productivity than that of other plants, but hydraulic conductance may decrease as tree size increases. The decrease of hydraulic conductance may reduce photosynthesis of canopy leaves. Therefore, we hypothesized that within single species, photosynthesis of canopy leaves declines as tree size increases due to the increase of hydraulic limitation, resulting in a size-dependent decline in the productivity of canopy trees. However, maximum sizes differ among species. Hence, among species, canopy trees with similar sizes may have different hydraulic conductance. A different hypothesis implies that, among species, canopy trees with smaller maximum size have stronger hydraulic limitation to photosynthesis of their canopy leaves. These two hypotheses are being tested on sympatric species of Acer, including *A. mono*, *A. palmatum* and *A. japonicum* (Suzuki & Hiura, 2000).

Climate change

To infer the responses of plants to changing environments at a large scale, it is important to be able to make predictions about processes at a smaller scale, and to classify plants among functional types with respect to these responses. To understand the factors influencing the seasonal changes of photosynthesis, forest ecologists at the Hokkaido University simultaneously measured a suite of environmental conditions surrounding leaves of 20 tree and liana species. In doing so, they quantified the species-specific sensitivity to environmental conditions as they change throughout the growing season. Seasonal patterns of leaf-level photosynthesis appear to consist of interactions between the suite of ambient environment conditions and the species-specific sensitivity to this combination of factors. Furthermore, to investigate the response of forest productivity to climate changes, the three-dimensional leaf structure in a forest patch was examined in detail (480,399 leaves were counted and mapped in total). A production model will be constructed shortly, using the data obtained in measurements of photosynthesis and forest structure (contact: Tsutom Hiura).

Seasonal change of leaf-level photosynthetic characteristics as related to successional traits

Changes in solar radiation, air temperature, and vapour pressure deficit through the growing season lead, in part, to seasonal differences in photosynthetic rate, particularly in the forest canopy. To understand the factors influencing seasonal changes in photosynthetic rate, we simultaneously measured a suite of environmental conditions surrounding leaves to quantify the species-specific sensitivity to changing environmental conditions throughout the growing season. In particular, we observed species-specific seasonal patterns in photosynthetic rates in the canopy.

Fig. 50. Measurement of the photosynthetic activity of *Quercus crispula* in the forest canopy (photo Tsutom Hiura).

Fig. 51. Flowers of *Styrax obassia*. This species produces mast-flowering with intervals of *circa* 5 years (photo Yuko Miyazaki).

In late successional species, such as maple and sub-canopy hornbeams, the stable period of light-saturated assimilation rate (A_{max}) was longer than other species, whilst light-demanding birch and several species of gap-specialist magnolias indicated temporal depression of A_{max} in summer. A_{max} of mid-successional species, such as hop hornbeams and oak, reached their maximum value in July, and declined gradually through the season. Thus, we confirmed that seasonal changes in photosynthesis rates were limited by both stomatal and non-stomatal factors, such as stomatal closure and reduction of photochemical activity. In other words, seasonal patterns of leaf-level photosynthesis consist of interactions between the suite of ambient environment conditions and the species-specific sensitivity to the combination of those factors (Fig. 50) (contact: Tsutom Hiura).

Plant resources in the forest

Masting and its relationship to storage reserves

Perennial plants allocate a significant fraction of their photosynthetic output to long-term storage. The continued oversupply of photosynthate suggests that stored reserves have some important ecological roles. Masting is an intermittent production of large seed crops. Most studies of this phenomenon deal with the evolutionary advantages of masting, and not with the mechanism of masting. This study will investigate the mechanism of masting and its relationships to storage reserves in different tree species. We propose to measure the stored reserves with microscopic observations of plant cells surveyed from trunks and branches of trees at different heights (0.3m, 1.3m and 4m), from various phenological stages (Miyazaki *et al.*, 2002; Miyazaki *et al.*, in press; Fig. 51).

Variation of tree sex-ratio during forest succession

In androdioecy (gender expression of male and hermaphrodite trees), the equilibrium frequency of males depends on their average pollen fitness relative to the average pollen fitness of hermaphrodites. In a wind-pollinated androdioecious species, selection favours a hermaphrodite-biased sex ratio and self-fertility in low-density stands, but male frequency increases with increasing population density due to the increment in the efficiency of wind pollination. To test this hypothesis, the frequency of males was determined for ten populations of a wind-pollinated androdioecious ash (*Fraxinus lanuginosa*) and these frequencies were related to stand structure. Male frequency correlated significantly with the density of the ash and the existence of sex-labile trees, indicating an environmental component in sex determination. The average fruit set in a mass-flowering year was positively correlated with forest productivity. The sex ratio converged on a consistent value in accordance with the prediction of the model of sex ratio for androdioecy as the forest achieved a dynamic equilibrium. The results showed that environmental fluctuations and community structure were important in the maintenance of the androdioecious tree (Ishida & Hiura, 1998, 2002; Fig. 52).

Arthropod diversity and forest structure

Diversity and vertical distributions of flying insects

Many scientists have used the canopy crane to study insect herbivores and pollinators, and their diversity. Entomologists at the Hokkaido University collected drosophilids, beetles, moth larvae and bumblebees from the canopy using the crane and other techniques during three years. In total, 402 species of small beetles, 3,908 bumblebee individuals and huge numbers of drosophilids and moth larvae were collected. The entomologists investigated the seasonal habitats and three-dimensional distribution of insects in the

Fig. 52. Paper bags installed in ash (*Fraxinus lanuginosa*) to monitor self-incompatibility (photo Tsutom Hiura).

forest. Common winged insect species were distributed vertically in a specific way in close relation to the stratified structure of the forest vegetation. Even on a rather small spatial scale (18x18x22m), a stratified distribution was prominent for most insect species flying above the ground in the forest. Regardless of the variation in foliage density and tree species among grid-cells at the same height, each insect species tended to be distributed rather evenly within a particular stratum. Thus, the stratification of vegetation plays a major role in promoting the diversity of flying insects in forest ecosystems (Fukushima *et al.*, 1998).

Along the Asian Green Belt, the diversity of the regional species-pool, which has largely been determined as a historical product of the past geological and biological processes, decreases in parallel with the decline in complexity of forest structure from the tropics to the polar regions. In order to evaluate the effects of forest structure itself on the diversity of forest animals, it is necessary to compare animal

Fig. 53. Moth larvae of a species of Saturniidae. In TOEF, moth inventory is on-going, and collections have so far included 27,966 specimens from 55 families and 2,072 species. This corresponds to 75% of the 2,780 species recorded in Hokkaido (photo Masashi Murakami).

communities among structurally different forests within the same regional species-pool. We installed vertical collecting devices with various types of traps for flying insects in natural and secondary forests of TOEF. Sampling devices included interception traps (Malaise and window traps) and bait traps. These traps were easily surveyed and enabled non-destructive, continuous sampling (day and night, and throughout the year). Those traps were set at approximately 5m intervals from the ground to over the canopy. Samples were collected weekly throughout the active season. In combination with a rope system, the traps yielded samples from different strata of forest vegetation. The material was first sorted at the order level, and species identification is now on-going. The two types of interception traps yielded samples quite different in the composition of insect species: samples from Malaise traps were dominated by weak fliers such as small dipterans and parasitoid wasps, whilst those from window traps were dominated by strong fliers such as large bumblebees, halictine bees, vespids, and beetles. Common winged insect species were distributed vertically in a specific way in close relation to the stratified structure of the forest vegetation (contact: Masanori Toda, hutian@pop.lowtem.hokudai.ac.jp).

Three-dimensional distribution of foliage and flying insects

The microdistribution of insects, mainly drosophilids, flying above the ground within the forest was examined in relation to the three-dimensional distribution of foliage within a relatively small spatial scale. With the aid of a canopy-access system, which divided a space of 18mx18mx22m of forest into a grid of 1.83m³ 'cubes', a total of 80 banana-bait traps were installed in a checkered fashion at 3.6 m intervals. The amount of foliage was measured for each tree species and for each 'cube' of the grid. Drosophilid samples were collected every 5 days during the summer from mid July to mid August. Even within this relatively small spatial scale, the vertical distribution of insects flying above the ground was stratified for most species. Regardless of the variation in foliage density and tree species among grid-cells

Fig 54. Counting the number of flowers on the ash *Fraxinus lanuginosa* (photo Tsutom Hiura).

at the same height, each insect species tended to occur within a particular stratum. Thus, the stratification of vegetation plays a major role in promoting the diversity of flying insects in forest ecosystems (Tanabe, 2002).

Animal plant interactions

Spatio-temporal variation in the moth larval community associated with oak
Trees provide animals with both habitats and food. The amount and quality of these food resources also exhibit spatio-temporal variation. For example, the quantity and quality of leaves as food for herbivores change both between seasons and between conspecific trees growing in the canopy and understorey (mature trees, saplings and seedlings). Such spatio-temporal variation in the food resources provided by trees should affect the composition and the diversity of the communities of animal consumers. Moth larvae were hand-collected from sunlit and shaded leaves of canopy oak trees and their saplings, during the spring and summer. Several physical properties of the habitats and physico-chemical properties of the leaves sampled were measured. Preliminary results suggest that during spring, oak sapling leaves were toughest, followed by shaded and sunlit canopy leaves, reflecting the order of leaf sprouting. However, during summer the order of leaf toughness was reversed: sunlit canopy leaves > shaded canopy leaves >> sapling leaves. Such food resources provided by the same host plant but varying spatio-temporally in quality supported different communities of consumers during different seasons and at different locations within the forest. As a result, even a single tree species may accommodate diverse communities of herbivores within a structured forest and in seasonally fluctuating environments (Wada *et al.*, 2000; Fig. 53).

Effects of herbivory and resource availability on induced defenses in oak
Plants have evolved many defenses against herbivores. Among them, plant secondary metabolites could have evolved as one of the main active defenses against herbivores. Often, these are produced in response to foliar damage. Since they are by-products of metabolism and only produced under certain physiological circumstances, their production may be constrained by the availability of plant nutrients. However, it is still unknown how nutrient availability and foliar damage affect plant chemistry. This study will examine the response of oaks to herbivory, using saplings and canopy trees at the crane site, under different light and soil conditions. Leaf mass per area (LMA) and leaf tissue concentrations of carbon, nitrogen, total phenolics, and tannins are being measured as plant defenses. Preliminary data show significant relationships among height, light availability, herbivory and LMA (contact: Masashi Murakami).

Variation in resource allocation in trees and its effect on canopy herbivores
The relationships between community structure (abundance and diversity) of herbivores and seasonal changes in leaf characteristics are being examined. Leaf toughness, nitrogen and tannin content were measured on 10 canopy tree species. Arthropods were collected by beating. Patterns in resource seasonality (i.e., allocation of nitrogen and carbon) differ considerably among tree species, according to either their pattern of leaf-flush or their mechanisms of defenses against herbivores. Seasonal trends in the allocation of nitrogen and carbon and the patterns of distribution of herbivore communities are being compared among tree species in the canopy. For example, two conspicuous and seasonal peaks in abundance were observed when studying the dynamics of populations of caterpillars in the canopy of the oak *Quercus crispula*. Our aim is to derive general patterns involving herbivore-plant interactions and the nitrogen dynamics within the forest canopy (contact: Masashi Murakami).

Fluctuation of tree flower abundance and its effects on the population dynamics of bumblebees and on fruit production of understorey herbs

The goal of this study was to understand the yearly dynamics of the pollination system within the forest. Bumblebee populations require abundant flower resources throughout the year. In temperate deciduous forest, the abundance of flowers from tree species pollinated by insects fluctuates significantly between years. Hence, the availability of flower resources in trees may affect the population size of bumblebees greatly. In turn, bumblebee abundance may affect the pollination of understorey herbs. Thus, we examined the relationship between flower abundance of trees, population size of bumblebees and fruit production of understorey herbs.

Both visiting insects and the flowering phenology of trees were studied. For ten tree species, we counted the number of inflorescences on 10 individual trees. We calculated the relationships between breast height diameter and the number of inflorescences per tree, fitted the resulting function to all trees of a 4 ha plot, and summed these estimations. Fluctuations of the population size of bumblebees were recorded by installing window traps at various heights in the forest. The visiting pollinators and fruit production of some understorey herbs pollinated by bumblebees were also examined. Our preliminary results indeed suggest that the fruit production of understorey herbs is affected by the flowering intensity of canopy trees via the activities of pollinators (Fig. 54; contact: Tsutom Hiura).

4.2.6. Wind River Canopy Crane Research Facility, USA

David C. Shaw, Frederick C. Meinzer, Ken J. Bible & Geoffrey G. Parker

Background and management system

The Wind River Canopy Crane was erected in April of 1995 by the University of Washington, in cooperation with the United States Department of Agriculture, Forest Service, Pacific Northwest Research Station (Portland, Oregon), Wind River Experimental Forest (Skamania County, Washington) and Gifford Pinchot National Forest (Vancouver, Washington). The crane is owned and operated by the University of Washington. The Director is Prof. Jerry Franklin (Univ. Wash.). Dr. Rick Meinzer (USFS) is Co-PI and Canopy Team Leader at the Pacific Northwest Research Station. Funding for the project comes from the USDA Forest Service, Pacific Northwest Research Station and the University of Washington.

Fig. 55. Wind River Canopy Crane (photo Jerry Franklin).

The crane is 74.5m tall at the jib, with an arm of 85m (Figs 55 and 56). The surrounding forest attains a maximum height of 63m, and the crane can gain access to 320 canopy trees in the 2.3ha perimeter. There are seven conifer and two angiosperm tree species in the crane perimeter. The crane was placed off an abandoned haul road through the old-growth forest using a mobile crane. Power is provided from access to line systems approximately 1.5km distant.

Fig. 56. Wind River Canopy Crane (photo Jerry Franklin).

The crane research facility is managed by the Director with support from a two tiered committee system; an Operations Committee which meets bi-monthly to direct day to day management of the research facility and evaluate proposed research, and a National Scientific Advisory Committee which meets once a year to provide scientific review of the overall management and mission. Facilities at this field station include office, shop, and storage buildings, and two bunk houses that can accommodate 12 and 8 people. There are five full time staff on site: Research Manager (D.C. Shaw), Research Coordinator, Program Coordinator, Research Tower Crane Operator, and Field Meteorological Scientist. The Director is based in Seattle at the University of Washington. Co-PI is located in Corvallis, Oregon at the Pacific Northwest Research Station, Forestry Sciences Laboratory.

The Wind River Canopy Crane Research Facility (WRCCRF) is managed as a user facility. Researchers and educators make proposals via our web site (http://depts.washington.edu/wrccrf). Research proposals are reviewed by a sub-group of the Operations Committee. Education proposals, usually requesting an 'educational lift' (i.e., an educational tour into the canopy), are handled by the Research Manager. Educational lifts are provided for college classes, academic and professional societies, agency personnel, and the general public through adult education classes. Our web page provides researchers, academics, and others access to information regarding the research facility, our program and some research findings. The WRCCRF is not generally accessible to the public, although an interpretative trail does go near the border of our research area, and there is a place to view the crane through the canopy, along with an interpretative sign.

Description of the site

The canopy crane is located in the Thornton T. Munger Research Natural Area (Table 12, Figs 57 and 58), a 478ha old-growth (500yr) forest. This low elevation (335-610m) *Pseudotsuga menziezii* (Douglas-fir) / *Tsuga heterophylla* (western hemlock) forest was designated for non-destructive research by the US Forest Service in 1934 to represent the typical forest type that originally covered many valleys in western Washington's Cascade Mountain Range. The Research Natural Area is located in the Wind River Experimental Forest, managed by the US Forest Service Pacific Northwest Research Station. The Experimental forest (4,208ha) has a range of forest ages and cutting regimes and is the site of chronosequence studies linking the canopy crane old-growth to younger forest types.

Table 12. Site and crane characteristics of the Wind River Canopy Crane Research Facility.

Variable	Characteristics
Location	T. T. Munger Research Natural Area, Gifford Pinchot National Forest, Washington State, USA, 45°49' 13.76" N, 121°57' 06.88" W
Altitude	335m
Mean annual air temperature	8.7°C
Mean annual rainfall	2197mm
Type of forest	Temperate coniferous seasonal rainforest
Area of forest accessed by the crane	2.3ha
Canopy height	Max. 63m
Crane model	Liebherr 550EC, fixed
Height of tower / Length of jib	74.5m / 85m
Maximum height reached by the gondola	ca. 67m
Gondola type	a: Squared, 1.2 x 1.2 x 2.2m, max. load 454kg b: Rectangular, 2.7 x 1.3 x 2.2m, max. load 908kg
Number of persons carried by the gondola	a: 4 persons b: 8 persons
In operation since	1995
Main research topics	• Forest structure and diversity • Biodiversity • Parasitic plants • Tree physiology • Climate change and carbon dynamics
Remarks	Educational crane lifts may be provided for academic and professional societies, and for the public through adult education classes
Management	University of Washington
Contact	David C. Shaw, University of Washington E-mail dshaw@u.washington.edu
Web site	http://depts.washington.edu/wrccrf/
List of publications	http://depts.washington.edu/wrccrf/
Fees for researchers	USD 182 per hour, negotiable

Climate

The canopy crane is located in a temperate coniferous seasonal rainforest (Shaw *et al.*, in press) with four distinct seasons (Table 13, monthly averages). Average annual precipitation is 2,197mm, with a distinct dry period occurring during June, July and August. This 'summer drought' is an important characteristic of Pacific Northwest climate, since it affects summertime tree growth and productivity. Average annual temperature is 8.7°C. Much of the winter precipitation falls as snow (average snowfall 2,330mm), and we experience rain-on-snow events commonly during the winter months.

The WRCCRF is located on the crest of the Cascade Mountain Range where continental climates dominate to the east, while maritime climate dominates to the west. Winter weather is typically maritime, whilst summer weather is typically continental. Fifteen kilometers to the south is the Columbia River Gorge, which has dramatic weather patterns caused by dynamics of deserts in the east and ocean to the west. In winter, freezing rains, rain-on-snow, and hail events are common.

Forest history

It is probable that the forest stand in the T.T. Munger RNA originated after a fire or series of fires about 500 years ago. *Pseudotsuga menziesii* (Fig. 59) dominated the young forest for the first 200 years, after which, the shade tolerant *Tsuga heterophylla* (Fig. 60) and *Thuja plicata* (western redcedar) began to move into the understorey. *Pseudotsuga menziesii* still maintains dominance in basal area, wood volume and height. The forest is unusually diverse for the Cascade Mountains with eight coniferous species, including *P. menziesii* (Pinaceae), *T. heterophylla* (Pinaceae), *T. plicata* (Cupressaceae), *Taxus brevifolia* (Pacific yew, Taxaceae), *Abies amabilis* (Pacific silver fir, Pinaceae), *A. procera* (noble fir, Pinaceae), *A. grandis* (grand fir, Pinaceae), and *Pinus monticola* (western white pine, Pinaceae).

Flora and fauna

Vascular and non-vascular plant, lichen and macrofungi species diversity surveys of the 4 ha site under the crane have been completed or are in progress. To date, we have identified 75 vascular plant species, including 10 trees (8 conifers, 2 angiosperms), 14 shrubs, 40 herbs, 5 graminoids, and 6 ferns. In addition there are roughly 52 mosses, 7 liverworts and 113 (+) lichens. The epiphytic plant community is exclusively non-vascular plants, bryophytes and lichens. There is a strong stratification of the epiphytic community with bryophytes dominating the lower canopy, cyanolichens (nitrogen fixers) dominating the mid canopy, and green-algal-foliose and alectorioid lichens dominating the upper canopy. Highest bryophyte diversity is on the forest floor and on fallen timber. Interestingly, the only angiosperm above 15m is *Arceuthobium tsugense* (hemlock dwarf mistletoe, Viscaceae), a parasite on *T. heterophylla* that is common over about 1ha of the 4ha plot. The genus *Arceuthobium* differs from other mistletoes in that it spreads by explosively discharged seed, rather than bird dispersal, which makes the composition and structure of the forest a controlling influence on its spread.

Thirty-three plant families are represented in the vascular plants, 18 of which have only one species, and 7 families have 2 species. Dominant plant families include Ericaceae (8 spp.), Liliaceae (7 spp.), Pinaceace

Fig. 57. Wind River Canopy Crane looking west over T.T. Munger Research Natural Area. The crane is in the lower right corner (photo David Shaw).

Fig. 58. Wind River Valley looking south. The crane is in the centre of the photo, just this side of the brown agricultural fields. Mt. Hood is in the back left (photo David Shaw).

Table 13. Long-term microclimate summary for the WRCCRF derived from data collected between 1978 and 2001, inclusive, at the Carson Fish Hatchery, a National Oceanic and Atmospheric Administration (www.ncdc.noaa.gov) meteorological station located 5.7 km NNW from the canopy crane.

Monthly	Dec	Jan	Feb
Precipitation			
mean total rainfall (mm)	377.9 (182.2)	336.7 (162.7)	320.6 (151.6)
Air temperatures			
mean daily (C)	0.2 (1.9)	0.2 (2.2)	1.8 (1.9)
mean daily minimum (C)	-2.7 (2.3)	-2.9 (2.7)	-2.2 (2.0)
mean daily maximum (C)	3.0 (1.6)	3.3 (1.9)	5.7 (2.1)
	Mar	**Apr**	**May**
Precipitation			
mean total rainfall (mm)	224.7 (103.1)	163.0 (86.3)	84.2 (44.4)
Air temperatures			
mean daily (C)	5.1 (1.3)	8.0 (1.2)	11.6 (1.3)
mean daily minimum (C)	-0.5 (0.9)	1.5 (1.1)	4.5 (1.1)
mean daily maximum (C)	10.6 (2.1)	14.4 (1.7)	18.6 (2.2)
	Jun	**Jul**	**Aug**
Precipitation			
mean total rainfall (mm)	57.7 (36.8)	20.5 (21.2)	22.9 (23.2)
Air temperatures			
mean daily (C)	14.7 (1.4)	17.6 (1.5)	17.8 (1.2)
mean daily minimum (C)	7.2 (1.0)	8.9 (1.3)	8.4 (1.3)
mean daily maximum (C)	22.1 (2.2)	26.3 (2.5)	27.1 (1.6)
	Sep	**Oct**	**Nov**
Precipitation			
mean total rainfall (mm)	71.3 (5.4)	162.4 (106.9)	365.5 (172.4)
Air temperatures			
mean daily (C)	14.5 (1.5)	9.1 (1.2)	4.1 (2.1)
mean daily minimum (C)	5.8 (1.2)	2.0 (1.4)	0.3 (2.5)
mean daily maximum (C)	23.4 (2.3)	16.1 (2.1)	7.8 (1.9)
Annual			
Mean total rainfall (mm)	2196.7(488.2)		
Mean air temperature (C)	8.7 (0.8)		

standard deviations in parentheses

Fig. 59. *Pseudotsuga menziesii* new foliage flush from above (photo Jerry Franklin).

Fig. 60. Snow on *Tsuga heterophylla* (photo Andrew Baker).

Fig. 61. *Acer circinatum* in the understorey (photo Jerry Franklin).

(6 spp.), Polypodiaceae (5 spp.) and Roseaceae (5 spp.). Understorey vegetation cover and frequency were quantified on sixty-four 25x25 m plots in the 4 ha study area. Prominence values (pv) were determined by multiplying the average percent cover by the % frequency. The dominant understorey species were *Acer circinatum* (Aceraceae, pv 25.5, Fig. 61), *Gaultheria shallon* (Ericaceae, pv 16.0), *Berberis nervosa* (Berberidaceae, pv 14.2), *Achlys triphylla* (Berberidaceae, pv 4.4), *Vaccinium parvifolium* (Ericaceae, pv 4.2), *Vancouvaria hexandra* (Berberidaceae, pv 1.4) *Pteridium aquilinum* (Polypodiaceae, pv 1.4), *Linnaea borealis* (Caprifoliaceae, pv 1.1), and *Xerophyllum tenax* (Liliaceae, pv 1.0). No other plant species had a pv of 1 or greater.

Fifty species of birds have been identified in on-going avian research. Seventeen of these are Neotropical migrants, while the remainder are residents or regional migrants. The most common residents are *Troglodytes troglodytes* (Winter Wren), *Poecile rufescens* (Chestnut-backed Chickadee), *Certhia americana* (Brown Creeper), *Perisoreus canadensis* (Gray Jay), *Turdus migratorius* (American Robin), and *Regulus satrapa* (Golden-crowned Kinglet). The most abundant neotropical migrants are *Empidonax difficilis* (Pacific-slope Flycatcher), *Catharus guttatus* (Hermit Thrush), *Chordeiles minor* (Common Nighthawk), *Catharus ustulatus* (Swainson's Thrush), and *Dendroica occidentalis* (Hermit warbler). Larger birds using the site include *Dryocopus pileatus* (Pileated Woodpecker), *Corvus corax* (Raven), *Strix varia* (Barred Owl), and *Accipiter gentilis* (Goshawk). *Strix occidentalis* (Spotted Owl) has apparently been displaced by *S. varia*. *Sturnus vulgaris* (European Starling) have been nesting on the crane, which we attempt to control.

Reptiles are rare in this forest type, and include two snakes *Thamnophis sirtalis* (Common Garter Snake) and *Charina bottae* (Rubber Boa). Amphibians include *Ensatina escholtzii* (Ensatina), *Ambystoma macrodactylum* (Long-toed Salamander), *Ambystoma gracile* (Northwestern Salamander), *Taricha granulosa* (Roughskin Newt), *Rana aurora* (Red-legged Frog), and *Hyla regilla* (Pacific Tree Frog).

Thirty-nine species of mammals are thought to occur in the area around the Research Natural Area, in 6 orders, including Insectivora (5 spp.), Chiroptera (9 spp.), Lagomorpha (1 spp.), Rodentia (13 spp.), Carnivora (9 spp.), and Artiodactyla (2 spp.). Most notable of these is *Cervus canadensis* (elk), *Felis concolor* (cougar), and *Ursus americanus* (black bear). There are no exclusively arboreal mammals in this forest, the most 'arboreal' of the mammals are *Glaucomys sabrinus* (northern flying squirrel), *Tamiasciurus douglasii* (Douglas' squirrel), *Neotoma cinerea* (bushy-tailed woodrat), *Tamias townsendii* (Townsend's chipmunk), *Erethizon dorsatum* (porcupine), *Martes americaana* (martin), and *Martes pennanti* (fisher).

Stand characteristics

The forest stand has been characterized on a 4ha plot, which has been expanded to a 12ha plot. However, data presented here are based on the 4ha plot directly under and around the canopy crane, with all trees with diameter at breast height (dbh) ≥ 5cm mapped. The basal area is 82.8 m^2/ha, while trees average 428 stems/ha. For trees with dbh ≥ 10cm, density is 309 stems/ha, while for trees with dbh ≥ 20cm, density is 194 stems/ha. It is a classic late-successional forest with a population of large and relatively evenly aged *P. menziesii* dominating the forest in terms of height, wood volume and basal area. These trees are dying out of the stand slowly and there is no reproduction of these shade-intolerant trees in the understorey. *T. heterophylla*, *T. plicata*, and *A. amabilis* are shade tolerant, dominate the smaller diameter classes, and represent the primary reproducing species (Fig. 62). *Taxus brevifolia* is an important understorey, small stature tree, averaging 89 trees/ha. The density of trees in 5cm diameter classes is summarized in Table 14, and reflects the abundance of small diameter trees in this uneven aged old-growth forest. Height distributions are summarized in Figure 63. Average height of *P. menziesii* is 52.2m (tallest tree is 65m), whilst *T. heterophylla* averages 19.0m (tallest tree is 55m). *Pseudotsuga menziesii* has only 8.5% of the stems present but 43.3% of the basal area, 47.9% of the stem wood volume, and 33% of foliage. However, *Tsuga heterophylla* has 51.7% of the stems, with 31.4% of the basal area, 32.4% of the stem wood volume, and 45.7% of the foliage. *Thuja plicata* has 6.9% of the stems, 19.9% of the basal area, 17% of the stem wood volume, and 15.4% of the foliage.

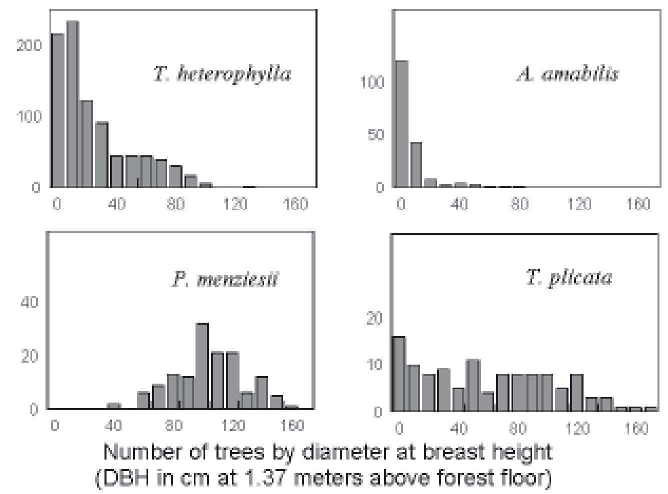


Fig. 62. Number of trees by diameter class for the 4ha plot around the Wind River Canopy Crane.

Table 14. Total number of trees (all species) in 5cm diameter classes.

dbh		
From	To	Trees/ha
5.0	9.9	119.3
10.0	14.9	74.3
15.0	19.9	41.3
20.0	24.9	28.0
25.0	29.9	16.8
30.0	34.9	16.0
35.0	39.9	13.3
40.0	44.9	8.8
45.0	49.9	7.0
50.0	54.9	7.5
55.0	59.9	8.5
60.0	64.9	7.8
65.0	69.9	7.0
70.0	74.9	7.3
75.0	79.9	7.0
80.0	84.9	7.3
85.0	89.9	6.8
90.0	94.9	4.3
95.0	99.9	4.8
100.0	104.9	4.8
105.0	109.9	5.8
110.0	114.9	4.5
115.0	119.9	3.3
120.0	124.9	3.3
125.0	129.9	4.5
130.0	134.9	1.5
135.0	139.9	1.3
140.0	144.9	2.3
145.0	149.9	1.5
150.0	154.9	0.8
155.0	159.9	0.8

Main research topics studied at the site

a) Forest carbon, water and nutrient cycles (biogeochemical cycles)

Developing science-based strategies for managing biogeochemical cycles will require much additional work to increase our understanding of them, the controls on them, interactions among them, and how they are being perturbed by human activities. Quantifying sources and sinks for carbon is particularly important from the standpoint of predicting and ameliorating carbon dioxide-driven global climate change. Since the carbon cycle is linked inextricably with the water and nutrient cycles, these cycles must be studied concurrently in order to arrive at a full understanding of factors controlling the magnitude of carbon dioxide sources and sinks.

Relevant research at the WRCCRF includes a major interdisciplinary initiative supported by the Western Region of the National Institute for Global Environmental Change. Multiple teams of investigators are employing independent approaches to determine the magnitude of carbon and water fluxes and to characterize the mechanisms that control them. These activities have resulted in Wind River being designated as an official Ameriflux site (part of the FLUXNET network, see Chapter 2). In the Ameriflux network, a micrometeorological technique known as eddy covariance is being used to measure canopy level fluxes of carbon dioxide and water vapour continuously in a range of vegetation types. These measurements will help identify major carbon sources and sinks.

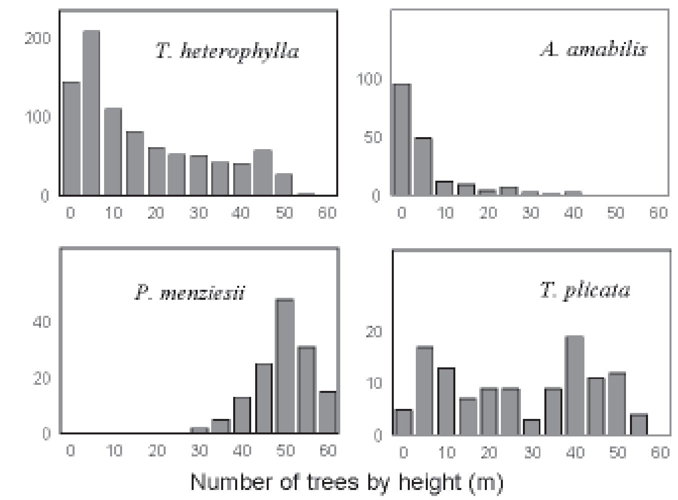


Fig. 63. Number of trees by height class for the 4ha plot around the Wind River Canopy Crane.

Whole stand estimates of tree water use are being attempted using sap flow sensors. This will provide data on quantities of material transfer with the atmosphere. Nitrogen cycling is being studied below ground and at multiple canopy levels.

b) Biological diversity and ecosystem functioning

The maintenance of biological diversity is a key goal of the US Forest Service. Biological diversity is known to affect ecosystem functioning, with rare and endangered organisms being considered potential indicators of problems. The spatial and temporal organization of biological organisms within a forest community is a key factor in understanding how its biological diversity may be sustained.

The WRCCRF is a major new tool being used to investigate how biological organisms are organized in a tall stature, old-growth conifer forest. Organisms being studied include insects, fungi, birds, bats, small mammals, lichens, and mosses. Ecosystem processes dependent on biological diversity that are being studied concurrently include nitrogen fixation, forest hydrology, avian controls on leaf herbivory, dwarf mistletoe disease development, and food resources for vertebrates.

c) Forest health and protection (plant pathology and disease)

Forest health is a major societal concern, and keeping forests healthy is a goal of the US Forest Service in its management of forest lands. For example, the Forest Service has determined that dwarf mistletoe has a greater impact on productivity in western forests than insects and diseases combined.

The WRCCRF has provided a unique opportunity for scientists to study crown-dwelling pest organisms that would be difficult to survey. Since old-growth forests in western Washington and Oregon are known for their lack of defoliating insect outbreaks, researchers at the canopy crane are studying what controls herbivory by insects in the Wind River old-growth forest. A major research initiative on dwarf mistletoe epidemiology has also been conducted at the canopy crane since it was installed. Finally, the WRCCRF has partnered with the Swiss Needle Cast Cooperative, and the canopy crane is now used as a reference site to study and monitor a natural population of Swiss Needle Cast (*Phaeocryptopus gaumannii*), a fungi causing early needle loss and reduced growth of Douglas-fir in the coast range of Oregon and Washington.

d) Monitoring of climate and climate variability

Assessing and predicting the impact of climate variability on forests requires continuous monitoring of both basic climate variables and forest response variables. Basic climatic monitoring at the WRCCRF is accomplished with an open field meteorological station and a vertical array of sensors on the crane tower for characterizing the microclimate at different depths in the forest canopy. Forest response variables being measured include phenology, diameter growth, annual mortality, cone crops, and needle longevity.

e) Validation and testing of new remote sensing technology

The development of remote sensing technology has great potential for facilitating rapid and frequent assessment of the status of forest stands with regard to important variables such as health and productivity. However, ground-truthing of remote sensing interpretation has been hampered by difficulty in accessing the forest canopy, which contributes most of the reflected light detected by remote sensing devices. Canopy access tools such as cranes are playing an important role in overcoming this impediment.

At the WRCCRF a multi-institutional team has been exploring ways of linking forest properties with remotely sensed spectral data. This ground-truthing effort will be instrumental in attaining the ultimate goal of using remote sensing data to provide stand level, regional, and global assessments of the status of forests and other vegetation.

f) Tree physiology and growth

Due to their large size and logistical difficulties in gaining access to their crowns, physiological processes in trees have traditionally been studied at a single scale or over a limited range of scale. The availability of large canopy cranes, has presented new opportunities for studying large trees as whole, integrated organisms. An understanding of how processes such as photosynthesis (Fig. 64) and water use are integrated at the whole-tree level is essential for linking different scales in ecological process models effectively and for a seamless understanding of how processes are controlled as we move along a continuum of scale from leaves to ecosystems.

Fig. 64. William Winner and Sean Thomas measuring photosynthesis from gondola (photo Andrew Baker).

Research on tree physiology at the WRCCRF has concentrated on control of water uptake, transport and loss along the soil-to-atmosphere continuum, seasonal, spatial and leaf age-related patterns of canopy photosynthesis, and relationships between tree architecture and growth. Future work will concentrate on tree physiological behaviour along a chronosequence of forest age in the Wind River Experimental Forest.

Major findings

a) Forest carbon, water and nutrient cycles (biogeochemical cycles)

The total store of carbon in living plants at the Wind River site was 39,800g C m^{-2} (Harmon *et al.*, in press). Long term, the site is considered a slight sink for carbon dioxide, yet contrary to conventional wisdom, continuous measurements of canopy carbon dioxide flux at the WRCCRF have shown that old-growth coniferous forests can be significant carbon dioxide sinks in certain years (Paw U *et al.*, in press). The fact that old-growth forests can function as carbon storehouses rather than carbon sources has far-reaching implications for managing forests to improve carbon sequestration. Future work at WRCCRF and surrounding Wind River Experimental Forest will concentrate on carbon sequestration as a function of forest age.

A special issue of the journal 'Ecosystems' will focus on the carbon program and these papers are in press (Suchanek *et al.*, in press, lead paper). A special issue of the journal 'Tree Physiology' (Vol. 22 No. 2 and 3) included many papers that have focused on connecting the canopy crane site to younger forests in a chronosequence (Bond & Franklin, 2002, lead paper).

b) Biological diversity and ecosystem functioning

Work on biodiversity and ecosystem functioning has identified specific elements of forest structure that contribute to biodiversity. For many types of organisms, biodiversity in the old-growth forest at the WRCCRF has a strong vertical component that outweighs other structural features of the forest. For example, lichen diversity increases but moss diversity decreases with increasing height in the canopy. A unique, previously undescribed lichen community associated with dead tops and roosting posts of birds has been discovered in the upper 2m of the canopy (McCune *et al.*, 2000). Conversely, arthropod diversity is determined largely by the species of the host tree. A unique arthropod community dominated by mites and spiders is associated with western red cedar (Schowalter & Ganio, 1998). This result implies that forests managed for fewer tree species eliminate important components of arthropod diversity. Vertically stratified avian surveys have shown that during March - October there are equal numbers of birds detected in the lower, mid, and upper canopy, but during November - February (winter) there is a distinct shift in detections to the upper canopy. This implies that the structure and resources of the upper canopy of old-growth forests are more important for birds than previously realized (Shaw *et al.*, 2002).

c) Forest health and protection (plant pathology and disease)

Research on hemlock dwarf mistletoe (*Arceuthobium tsugense*, Viscaceae) epidemiology is ongoing at WRCCF and has shown that vertical structure of the canopy and species composition of the forest are the major factors controlling the intensification and spread of infection. Plants tend to be clumped into infection centres that are expanding as western hemlock increases in abundance and importance. Herbivory research has shown that in the overstorey conifers leaf area loss to insect herbivores is less that 2%, while in understorey vine maple (*Acer circinatum*) it was 10% (Braun *et al.*, 2002). Research on Swiss needle cast at WRCCF is employing an assay that allows total fungal biomass to be estimated based on extraction of mitochondrial DNA from infected needles. This assay will facilitate rapid assessment of the severity of Swiss needle cast infection, whilst current research is attempting to quantify the impacts of this disease on carbon dynamics of Douglas-fir.

d) Monitoring of climate and climate variability

The continuous records of vertical microclimate being obtained probably represent the only such data available for old-growth coniferous forests. These data are valuable to researchers working on biological diversity, forest health, and other topics, and will help us understand the influence of forests on local and regional climate. The data are available to all researchers via the Internet (http://depts.washington.edu/wrccrf).

e) Ground validation and testing of new remote sensing technology

The vertical structure of the forest canopy, as well as all the traditional aspects of forest structure (dbh distribution, basal area, heights) have been quantified in a core 4ha plot around the canopy crane. This uniquely detailed information on forest structure has allowed the canopy crane forest to serve as a major site for validation of data quality (Freeman & Ford, 2002), forest mistletoe surveys (Shaw *et al.*, 2000) and new remote sensing technologies being developed and field-tested in the United States today (Parker *et al.*, 2001; Lefsky *et al.*, 2002). Ultra-lights, airplanes, and satellites have overflown the site, and even the canopy crane structure itself has had remote sensing instrumentation attached to it 15m above the forest canopy. These validations either would not have occurred at the WRCCRF, or in many cases, would not have been possible at all without the availability of the crane.

f) Tree physiology and growth

Research on water uptake and utilization by trees has shown that Douglas-fir roots are able to redistribute hydraulically water from wetter to drier portions of the soil profile (Brooks *et al.*, 2002) and that large trees rely on rechargeable stem water storage for a larger fraction of their daily water use than small trees (McDowell *et al.*, 2002). Both of these findings have important implications for adaptation of Douglas-fir to summer drought, for ecosystem-level hydrology, and, therefore, yield of watersheds occupied by stands of different ages. Needle-level light response of photosynthesis across a vertical light gradient has shown that mean light-saturated photosynthetic rates, light compensation points, and respiration rates declined from upper crowns to lower crowns in overstorey Douglas-fir and western hemlock. Increasing light-saturated photosynthetic rates in the canopy top increased carbon uptake at high photosynthetic photon flux density (PPFD) relative to lower canopy needles. Reduced respiration rates in lower canopy needles relative to upper canopy needles increased carbon uptake at low PPFD by reducing the light compensation point (Lewis *et al.*, 2000).

With regard to growth, about 20 to 70 per cent of the foliage on old-growth Douglas-fir trees is found on epicormic branches. These are non-primary branches that sprout from dormant buds in the trunk and on other branches. This branching behaviour is a major factor contributing to the longevity of Douglas-fir (Ishii & Ford, 2001). The leaf area index (LAI) of this forest is estimated at 8.61, while 20% (1.69) is in the understorey vegetation (Thomas & Winner, 2000). The canopy crane was used in a novel fashion to estimate this LAI.

g) Forest structure

The development of forest structure and its influence on microclimate have a controlling influence on the productivity and biodiversity of forest ecosystems. The Wind River old-growth forest is 'bottom heavy' with structure, meaning the largest amount of material is located below 30m (Parker, 1997). The light environment has been divided into three zones, a bright zone, where high light dominates, above 40m, a transition zone, where the mean light transmittance changes rapidly with height (40-12m), and a dim zone which is characterized by low transmittance (< 12m; Fig. 65). When compared to stands in a chronosequence, the bright zone is wider and dim zone is narrower in old-growth than younger forests (Parker *et al.*, 2002). The vertical stratification of species in the Wind River old-growth forest allows Douglas-fir to maintain dominance and longevity (Ishii *et al.*, 2000), whilst tree age is significantly related to the development of crown structural parameters (Ishii & McDowell, 2002).

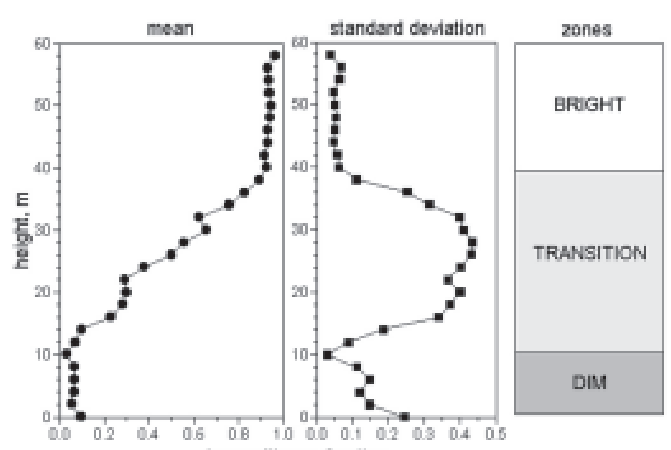


Fig. 65. Variation in PAR transmittance profiles with height in the old-growth forest under the Wind River Canopy Crane.

Future visions and collaboration with the ICCN

The Wind River Canopy Crane will continue to be an ecosystem observatory, a research tool for a broad array of scientists, and a facilitator for education. We hope the research program broadens to include forests of all ages (chronosequence) and structures (land management regimes) in an attempt to understand forest ecosystem processes at all scales and provide context for the Wind River old-growth forest and canopy crane research program. Climate change and carbon dynamics will be a major focus of long term research, which will integrate nutrient and water cycles. We hope to integrate other research more closely with National and International environmental observation networks, which are critical to understanding global change. Whole forest processes, such as controls on net primary productivity, carbon cycling, photosynthesis, and water use will continue to be central to our research program. Finally, understanding the foundations of biodiversity in forests, particularly the role of the hard-to-access upper canopy, will continue as a central topic of research.

Opportunities to collaborate with the International Canopy Crane Network are numerous, and at various scales. Collaboration may be as simple as hosting visiting researchers who are also doing research at other canopy cranes, or as complex as joint research grants or programs. Several areas stand out, including linking the canopy cranes into an observation network, addressing key scientific questions about biodiversity and ecosystem process, testing hypotheses at multiple crane sites, and elucidating 'universal rules' that apply to tree physiology, canopy processes and forest health across multiple forest biomes.