4.3. Cranes in tropical forests

4.3.1. Australian Canopy Crane: Getting on top of the World's last biological frontier

Nigel E. Stork & Michael Cermak

Background

The use of industrial cranes in tropical forests has opened up the canopy to exploration by scientists in the same way that the deep-sea submersible gave access to the sea floor. With the installation of a canopy crane in the 'Daintree' rainforest, Australia is now part of an international canopy crane network that is providing new information on a previously unknown part of our rainforests.

The Australian canopy crane (Table 15 and Fig. 66), the first to be erected in the southern hemisphere, was installed section by section by helicopter into the Wet Tropics of Queensland World Heritage - the so called 'Wet Tropics' rainforest in north Queensland, Australia in November 1998. Although today rainforest occupies only about 0.2% of Australia's land mass, some 30 million years ago about one third of the continent was rainforest. These rainforests supported a highly diverse marsupial fauna including flesh-eating kangaroos. As the continent moved northward and became drier the rainforests shrank. Indeed, during the last glacial maxima, these rainforests shrank even further than their current extent. Today about half of Australia's rainforests are in a tropical belt 400 km long and from 2km to 50 km wide where the mountainous Great Dividing Range meets the sea, and hence where the forests meet the World Heritage listed Great Barrier Reef. These forests support about 800 species of vertebrates, many of which are endemic, and about 4-5,000 species of plants at least 1,700 species of which are endemic. These forests are of evolutionary significance as 12 of the world's 19 families of primitive flowering plants are found there and two of these families are endemic. This compares with the Amazon basin where just nine families of primitive flowering plants occur, none of which are endemic. In 1988 these forests were declared the Wet Tropics of Queensland World Heritage Area. This is one of the few areas in the world where the reef meets the rainforest and the only place where two such World Heritage areas sit side by side.

Table 15. Site and crane characteristics of the Australian Canopy Crane.

Variable	Characteristics
Location	Near Daintree National Park, North Queensland, Australia 16°04' S, 145°28' E
Altitude	40m
Mean annual air temperature	25.1°C
Mean annual rainfall	3200-3900mm
Type of forest	Lowland complex mesophyll vine forest
Area of forest accessed by the crane	1.0ha
Canopy height	25-27m
Crane model	Liebherr 91EC, fixed
Height of tower / Length of jib	47.5m/55m
Maximum height reached by the gondola	ca. 40m
Gondola type	Squared, 1.5 x 1.5 x 2.3m
Number of persons carried by the gondola	3
In operation since	1999
Main research topics	• Insect studies • Climate, water and carbon fluxes • Remote sensing
Remarks	The crane site was damaged severely by a category 3 cyclone in 1999. Two years later, the forest had made a substantial recovery
Management	Cooperative Research Centre for Tropical Rainforest Ecology and Management
Contact	Michael Cermak, ACCRF Manager Michael.Cermak@jcu.edu.au
Web site	http://www.rainforest-crc.jcu.edu.au/canopycrane/canopyCrane.htm
List of publications	http://www.rainforest-crc.jcu.edu.au/publications/publications.htm
Fees for researchers	A$60 per hour or A$8,000 for 30 days within 12 months (large project)

Fig. 66. View of Mount Sorrow from the gondola of the Australian Canopy Crane (photo Michael Cermak).

A number of key factors were considered when choosing the location for the crane within the Wet Tropics area: 1) high biodiversity and conservation values since any data that might result from the crane research needed to be relevant to local and national needs; 2) a flat area that was unlikely to flood - a sloping site would make installation difficult and would mean the crane would need to be taller; 3) access to other facilities such as accommodation and tourism ventures for a possible interpretative centre; and 4) most of the lowland forest in North Queensland has been logged in the last 100 years and therefore an area that had not been logged in recent times was needed. About a dozen sites were looked at both within the World Heritage Area and outside. An offer to lease a large area of forest for the crane facilities at almost zero cost was made by the owners of a rainforest tourism resort, Coconut Beach Resort, and this site met the criteria above. One reason for not trying to work within the World Heritage Area and National Parks was due to the restrictions that might be placed on the operation and the possibility that government bureaucracy might slow the process of crane installation.

Fig. 67. Solar panels permanently attached to the crane tower help power auxiliary equipment (photo Michael Cermak).

The purchase and construction of the Australian crane and associated laboratory and accommodation facilities was funded via an Australian Research Council infrastructure grant with matching funds from a consortium of three universities: James Cook University, Griffith University and the University of Queensland. The total cost was about A$1.6million. Both helicopter time, at about A$150,000 and legal and planning costs associated with getting permission to install the crane, at about A$100,000, were both much higher than had been originally thought.

The Liebherr 91EC crane (figs 67 and 68) is located in forest abutting the Daintree National Park and less than two kilometres south of Cape Tribulation, famous for being where Captain Cook's ship Discovery ran aground on the Great Barrier Reef. This area is home to many of the rare and endangered species of plants for which the region is famous. The crane site is about 40 metres above seas level. The crane is 47.5m tall and has a jib length of 55m providing access to about one hectare of rainforest. The crane is located about 300m from the forest edge and access is via a small walking track.

Fig. 68. The crane has a positioning system designed to allow researchers to accurately and quickly find sites within the canopy (photo Michael Cermak).

Access to the canopy using the crane is via a 'gondola' which is lifted from the ground, raised above the canopy and can be lowered through gaps in the canopy anywhere in the arc of the 55 metre long crane jib. The gondola takes three persons, computer equipment, cameras and any other equipment. One aspect of the canopy crane that surprises first time users is the quietness of the ride since the generator that powers the crane is several hundreds of metres away outside the rainforest. All one may hear is the noise of the insects and birds.

Installing a canopy crane in close proximity to a World Heritage Area presents many unique problems. For example, planning application had to be made to the local council, Douglas Shire Council, showing how the crane would meet the strict regulations with minimal environmental and visual impact. To assess the visual impact of the proposed crane on the region large helium balloons were raised 50m and 100m above the site where the crane was going to be located and photographs were taken from various vantage points up to several kilometres away including photographs from out at sea. These pictures demonstrated that the balloons were not visible or barely visible and that the crane would not have an impact on the visual amenity of the rainforest. Similarly, great efforts were made to ensure that there was minimal impact on the rainforest. A narrow gravel track was constructed providing access for very small digging equipment. A special fabric underlying the gravel surface spread the load of any vehicle that might go up and down the track. One large culvert was built in the track to cover a 30cm wide black bean vine. The route of the track was planned carefully in order to avoid rare and endangered species of plants in the area.

The crane itself was located in a natural gap where there had been an earlier tree fall in order to avoid unnecessary clearing. Four corner concrete pads were laid in the cleared gap and all the other crane parts, totalling 42 separate loads were carefully lowered by helicopter through the gap. We had in mind that at some point in the future the crane might need to be removed and reconstructed elsewhere and therefore the 25 tonnes of concrete at the base of the crane was lowered in more than a dozen pre-set concrete blocks of about 2-3 tonnes each.

We sought the advice of Dr Ken Chapman, the Managing Director of Skyrail, a seven kilometre cable tourist ride near Cairns, and he suggested that from his experience in constructing Skyrail, very few of the helicopter pilots around the world had the necessary skill to construct a crane by helicopter. Therefore, we were limited to only a couple of companies that could do this in the Australasian region. The company we selected, Hevilift, used a Russian Kamov helicopter with counter rotating blades to carry the equipment to the site and lower it into place. The costs of the helicopter time and construction were as expensive as the brand new crane but the skill and speed with which this crane was constructed indicates the necessity of paying this amount.

One of the unfortunate features of using the helicopter was that the down force of the helicopter blades had quite an impact on one part of the canopy and scorched this area quite seriously. When the helicopters lower their loads they come in at an angle to the site and it was in this area the wind damage occurred. Another critical factor was that the helicopter used a 50m line to lower the equipment and since some parts were lowered to ground level this meant that on about twenty occasions the helicopter came within just a few metres of the very top of the rainforest canopy. It was very disappointing to see the damage but all this was put into perspective when the canopy crane was hit by a Category 3 Cyclone 'Rona' in February 1999 as discussed further below!

Safety

The three university partners established the Australian Canopy Crane Pty Ltd to manage the liabilities and risks associated with owning and operating a canopy crane. Management of the company is by senior

executives of the Cooperative Research Centre for Tropical Rainforest Ecology and Management (Rainforest CRC) based at the Cairns campus of James Cook University and they report to the Board of the crane company. There are very strict National and State health and safety regulations and great effort has been taken to ensure that safety standards are of the highest level. A safety manual for the crane site has been produced and approved by the university and government authorities and safety officers regularly visit the site. All those who are visiting or working on the site or are going in the crane gondola are given a safety briefing and sign an agreement to abide by those safety regulations. Those being taken up in the gondola wear a safety harness attached to the gondola frame. Entry to the gondola is only allowed with permission from the crane driver and only once the gondola is on the ground inside the fenced compound at the base of the crane. The company employs an experienced full time crane driver. The canopy crane manager and two crane research assistants have been trained to operate the crane and, after completing hundreds of hours of supervised crane driving time, examinations and practical tests, all three also are now qualified to drive the crane. Usually, the crane is operated by the driver from within the gondola by using a hand-held remote control mechanism.

Site information

There is a strong wet season with most rain occurring from December to April, although rain occurs in all months. The average rainfall for the site is 3.5m a year although in 2000 a total of 6.8m fell. In that year the seasonal creek which runs through the crane site did not dry up. Northern Australia is subject to cyclones in the wet season and their occurrence is unpredictable. On February 14 1999, just two months after installation, a category 3 cyclone, Cyclone Rona, with wind gusts of up to 180kph, hit the coast about five kilometres south of the crane site. The site was damaged severely with perhaps as much as 10% of the trees being brought down and 50% of remaining trees having their tops snapped. Prior to the cyclone canopy cover was almost complete and there were few places to bring the gondola to the ground but the cyclone opened up the canopy enormously. Even though two large trees came down right next to the crane and destroyed the equipment shed, the crane was untouched. Prior to the cyclone about 30-50% of the canopy was covered by vines including lawyer cane, (*Calamus* spp.) but the cyclone brought virtually all vines to the ground making access to the crane site very difficult. The cyclone hit a large area of north Queensland but it is interesting to note that some areas of rainforest were hardly touched, even an area 100m away from the canopy crane, and it was chance that the crane was hit in this way. The cyclone provided a wonderful opportunity to study the natural recovery of the rainforest and now, three years on, it would be very difficult for most people to know that there had been a cyclone through this part of the forest.

A Geographical Information System (GIS) of the site has the identifications, locations, heights and sizes of all trees of trunk diameter larger than 10cm mapped. There are about 600 trees of this size, numbering 80 species. Replication is not a problem as there are three or more individuals for half of these species. The commonest tree with 80 individuals is the black palm (*Normanbya nomanbyi*). The heights and rough dimensions of trees have been plotted on the GIS. Similarly all epiphytes have been named and plotted. No comprehensive survey has yet been undertaken of the vertebrates at the site although a species list has been developed. This includes the Southern Cassowary, Lumholtz tree kangaroo, and feral pigs. A pair of ospreys nest on the ballast weight of the crane jib and have bred there successfully (Fig. 69).

Fig. 69. Our resident Osprey (*Pandion haliaetus*) perched on Steve Turton and Michael Lidell's equipment for measuring water, heat and CO_2 fluxes (photo Michael Cermak).

Fig. 70. Composite Malaise-Flight Interception trap hanging in the mid-canopy (photo Michael Cermak).

Research conducted using the crane

In the last three years more than 20 canopy crane projects have been reviewed and approved by a research committee. The committee carefully reviews these projects in order to ensure that the site and other projects are not affected adversely and to increase collaboration. Funding for research has come from a variety of sources including the Cooperative Research Centre for Tropical Rainforest Ecology and Management (the Rainforest CRC), Australian Research Council, Australian Geographic and Fuchs Oils. Some of the key projects are described below.

A major focus for many of the research projects is the discovery, mapping and identification of the organisms found in the canopy. This includes surveys of mites, insects, fungi and epiphytes. In the last year more of the projects undertaken using the Australian crane are being replicated elsewhere on other cranes.

Studies on insects are concentrated on the way these organisms interact with each other and with plants, their diversity and distribution, and their role in canopy processes. We are looking at how many species of insects there are in this forest and what proportion are found in the canopy (N.E. Stork & M. Cermak, unpublished data). Some researchers believe that the canopy is twice as rich in insect species as the ground but this has yet to be tested. At four locations on the canopy crane site and at one location 100 metres away, pairs of combined Malaise-Flight Interception Traps have been placed in the canopy and directly below on the ground (Fig. 70). These traps catch flying insects, some flying up into the top part of the net where they are caught in a bottle and some dropping into a water trap at the bottom of the net. Sampling two weeks a month, these traps have caught about 10,000 beetles that are being sorted to species.

Other projects include Professor Roger Kitching's and collaborators from the University of Leipzig study of the dynamic interactions between the flowering cycle of the principle trees and vines on the crane plot and the assemblage of canopy arthropods that occur in and around the inflorescences. Currently a complete year of data is being assembled on the arthropods on inflorescences with spin-off information on flowering

Fig. 71. Romina Rader and Richard Cooper setting up mammal traps in the canopy (photo Michael Cermak).

phenology, pollen structures and casual visitation of flowers by larger insects. The assemblages of arthropods associated with flowers will be sorted into guilds and their roles as potential pollinators, nectarivores, anthophages, predators and so on, assessed. Hypotheses derived from these phenomenological studies will be further tested using exclusion experiments.

Nico Blüthgen, a PhD student from the University of Bonn, was looking at the use of plant food resources by ants. He has found that 40% of the tree species have extrafloral nectaries which are used by ants. He is also examining the preferences of ant species for different sugars, particularly those of the dominant ant species on the site, *Oecophylla smaragdina*, which also tends Hemiptera. This study will help determine whether ant mosaics occur in natural tropical rainforests (N. Blüthgen *et al.*, unpubl. data). Blüthgen also investigated the trophic interactions between *Oecophylla smaragdina* and homopterans, trees and lianas (Blüthgen & Fiedler, 2002).

The mammal fauna of Australia's tropical forests are relatively well-known with many canopy species such as a number of possum species being restricted to the upland forests. A canopy crane study of the arboreal mammals by MSc Student Romina Rader has shown that a number of ground based mammals frequently use the canopy for foraging (Fig. 71). It has also become evident, that the Prehensile-tailed Rat *Pogonomys* sp. is frequenting the very tops of rainforest trees (30 to 35m). Using standard techniques, this species has never been trapped before at the ground level and, if it were not for the canopy crane, the foraging patterns of this species would still remain relatively unknown.

A second major focus for the canopy crane relates to the broad issue of tropical rainforests and their role in photosynthetic processes and climate. A team of researchers (Associate Professor Turton and Drs Franks, Liddell, and Tapper) are studying how carbon, heat and water fluxes change over time as the canopy recovers from the cyclone. They are also trying to resolve which are the main species responsible in shifting the carbon balance. This research is comprised of three components: 1) ecosystem-level CO_2 heat and water flux (eddy covariance) measurements, 2) meteorological and micrometeorological measurements, 3) leaf-level leaf canopy photosynthesis measurements, and 4) soil CO_2 flux measurements. Cyclone Rona dramatically altered the micro- and meso-climate of the area by removing almost all foliage and bringing the canopy boundary layer almost to ground level. Over the last three years, regrowth of the canopy has resulted in an increased difference between the maximum temperature at the canopy and ground levels. A data collection module has been designed, which can be suspended from the crane's gondola to any level of the forest. This devise improved the method of obtaining measurements of microclimates in dense rainforest canopies (Siegenthaler *et al.*, 2000).

A proposal to measure diurnal and seasonal energetics above and within a lowland tropical rainforest canopy has been submitted (Turton *et al.*, 1999). A regression model, which estimates monthly averages of daily peak sun hours in the region, was produced by JCU researchers (Curtis & Turton, 2002). The canopy crane is also being used by Dr Stuart Phinn (University of Queensland) and Dr Alex Held (CSIRO) to assist the development of operational methods for monitoring of the condition of tropical rainforests. In particular the crane is being used to provide access to the canopy to test the different signals from various new remote sensing technologies. More recently, G.G. Parker from the Smithsonian Environmental Research Centre, used a portable laser rangefinding system to make dense measurements of the location of canopy elements. He assembled these into high-resolution views of structure in three dimensions. A PhD student from University of Melbourne is investigating the seasonal variation in concentrations of secondary metabolites in rainforest trees. Dr. Martin Freiberg from University of Ulm in Germany studied the interrelationship between epiphytes, humus accumulation and microclimate in the rainforest canopy (Fig. 72). The research concentrated on the effect of seasonality, so highly pronounced in Northeast Australia.

Fig. 72. Dataloggers used in microclimate experiments (photo Michael Cermak).

Although the Australian Canopy Crane Research Facility has been operating only for three years, a wide range of research topics has been addressed and results published. Already, we have established several collaborative ventures with international institutions, the most recent one being an official signing of Memorandum of Understanding with the University of Leipzig. We are envisaging an increase in international collaborative research through the Global Canopy Program and the International Canopy Crane Network and we are keen to invite any interested parties, be it scientific and teaching institutions or individual researchers to contact us for further information. Please visit our web site: www.canopycrane.jcu.edu.au

4.3.2. COPAS, French Guiana
COPAS: a new permanent system to reach the forest canopy

Pierre Charles-Dominique, Gerhard Gottsberger, Martin Freiberg & Albert-Dieter Stevens

In the 1990's there were several systems available for gaining access to the crown and canopy strata of tropical forests, including the single rope technique (SRT) and construction cranes. The SRT, extensively used by one of us (M. Freiberg), was designed to work in the canopy but, by going to the same spot repeatedly, inevitably caused some damage. Construction cranes overcame this problem, but their immobility and rigid structure was not ideal for research in tropical forests. There were few means available by which the area reached by the crane could be enlarged and its erection to avoid forest damage was difficult and costly.

To overcome those problems, a new canopy access system, COPAS (Canopy Operation Permanent Access System; Gottsberger & Döring, 1995; Table 16) was developed. COPAS consists of three towers, emergent from the canopy, arranged at the apices of a regular triangle (Fig. 73). Cables from the base of each tower lead to their apex and are connected at a junction knot, with a gondola connected to this point. The three cables provide movement in the horizontal plane, the gondola itself moving vertically. The requirement of having the lowest impact possible on the forest led to the design of towers, which can be erected by hand (Fig. 74). Such towers, however, would not have been strong enough to carry the forces by the gondola and its load. The solution for this was the introduction of a helium balloon pulling the junction knot of the three guiding cables vertically upwards.

Table 16. Site and crane characteristics of the COPAS project.

Variable	Characteristics
Location	5.5km from the CNRS station Les Nouragues, French Guiana 4°2' N, 52°40' W
Altitude	25-180m
Mean annual air temperature	22°C
Mean annual rainfall	3000mm
Type of forest	Lowland evergreen wet forest
Area of forest accessed by COPAS	1.4ha, can be extended with additional masts and balloons to 8.4ha
Canopy height	ca. 40m
Height of masts / distance between masts	ca. 45m/180m
Maximum height reached by the gondola	200m
Gondola type	aluminium case, base 1m x 1m
Number of persons carried by the gondola	2 persons
In operation since	Public operation envisaged for October/November 2003
Planned research topics	• Mechanisms of tree growth; photosynthesis • Microclimates and microhabitats of the canopy • Pollination systems • Pre- and post-dispersal seed predation • Ant-plant relationships • Biodiversity of canopy invertebrates • Interactions between arboreal vertebrates • Medical entomology
Management	Centre National pour la Recherche Scientifique (CNRS), France
Contacts	Prof. Pierre Charles-Dominique, CNRS, Pierre.Charles-Dominique@wanadoo.fr Prof. Gerhard Gottsberger, Universität Ulm, gerhard.gottsberger@biologie.uni-ulm.de Dr Martin, Freiberg, Universität Ulm, martin.freiberg@biologie.uni-ulm.de
Web site	http://www.cnrs.fr/nouragues/Nourcopas.htm http://www.biologie.uni-ulm.de/copas/index.html
Fees for researchers	Not yet known. Station fees (accomodation and food) *circa* USD 20 per day

The principle of COPAS

COPAS has been erected provisionally and tested in the Botanic Garden of the University of Ulm in July 2000 (Fig. 75). The winches at the bases of the three towers have cables long enough to allow the coverage of a regular triangle with a base line of 180m. Thus the area covered is 1.4ha. The use of a triangle makes it possible that this area can be doubled in the future by simply adding another tower. With the use of one central tower and six towers (and balloons) in the periphery, therefore, six regular triangles would cover 8.4ha, etc. All towers are equipped with ladders and have platforms on top, which are 3m in diameter and which provide additional space for observations and installing various equipment. The towers are made up of 3m long elements, mounted one above the other and secured with bolts. With 45m the towers are a few metres higher than the surrounding forest canopy at the site in French Guiana. Each element can be installed manually and hoisted with a winch placed on the highest element already fitted. Therefore, a canopy opening at the site of a tower of 5m in diameter is enough to erect the tower.

Retracting and extending the cables of the three winches facilitates the horizontal movement of the junction knot above the canopy. If one winch is retracting a cable, at least one other winch needs to extend its cable. For security reasons and to use as easy operating commands in the gondola as possible, the cable forces of all three winches are measured permanently by a central computer unit which controls the movement. The gondola pilot just pushes or pulls the gondola navigation joy stick towards the desired direction and the gondola then follows this movement. This automatic mechanism is working permanently and instantaneously corrects additional wind forces affecting the balloon or the cables.

The helium-filled balloon has a diameter of 11m and carries the weight of the gondola and two passengers, or the gondola with one passenger plus equipment. The passengers are secured with harnesses at the ladders, on the platforms and in the gondola at all times. The balloon hovers 50m above the canopy and is connected to the junction knot via a cable. Even if the balloon is moving, this junction is kept in place horizontally by the guiding cables controlled by computer. The balloon can be pulled to the ground by means of another winch which is mounted on a small movable caterpillar. For climate measurements or mapping purposes, etc. it is possible to use only this winch with the balloon and the gondola and ascend 180m above the canopy. The parking zone of the balloon at the foot of one of the towers needs to be cleared for 15m in diameter, but this clearance can be made some metres outside the investigation plot itself by using the movable winch. Therefore, the plot sustains

Fig. 73. COPAS as envisioned in French Guiana.

Fig. 74. Manual erection of the COPAS masts in Ulm.

Fig. 75. Test of COPAS in the Botanical Gardens of Ulm.

negligible damage during the erection or maintenance purposes of the system.

The vertical movement of the gondola is facilitated by another winch within the gondola. The gondola is connected to one side of the cable of this winch, the junction knot above the canopy being connected to the other. The electrical power for the motor is provided by a rechargeable battery pack inside the gondola. Power is only needed for upward movement, while the power generated in the motor by downward movement recharges the battery.

Time schedule

A long period elapsed between the first precise ideas to translate the COPAS idea into action (in 1995) and its demonstration installation in Ulm (in 2000). This interval was necessary to convince entrepreneurs and to develop a device well adapted to tropical conditions. The system was transported from Germany to Cayenne harbor in French Guiana in January 2002. The material will be brought to the site of erection in April/May 2003 and then erected. The whole system is expected to operate fully by October/November 2003.

Location of COPAS

A majority of the 150,000 inhabitants In French Guiana live along the coast and 85% of the land is covered by primary forest. This, together with the excellent French-German partnership in science, led to the selection of French Guiana for the implementation of the first COPAS project. COPAS will be erected in the 1,000 km² Les Nouragues Strict Nature Reserve. Les Nouragues is located in a totally uninhabited area, 100km inland from the coast. The COPAS site (4°2’212 N, 52°40’654 W) was selected inside this reserve, close to the Saut Pararé rapids of the Arataye river (‘Pararé-station’) and 5.5km from the Les Nouragues Research Station of the CNRS (‘Comité National de la Recherche Scientifique’).

This research station, active since 1986, permitted the launch of the COPAS project in a forest which had been studied relatively extensively. Several factors were considered in the selection of a site some kilometres away far from the present research station (‘Inselberg-station’): (1) the relatively large diversity and abundance of epiphytes at the new site in comparison with other sites in French Guyana; (2) the selected site is located 800m downstream from a section of rapids, the Saut Pararé, where it will be possible to install a small water turbine to produce hydroelectric power; (3) most transport between Cayenne and the Les Nouragues Research Station currently takes place by helicopter but, for large loads in particular, river transport is generally cheaper. The development of two research sites a few kilometres apart will lessen the human impact on both of them (2 1/2 to 3 1/2 hours are needed to walk the 7.5km footpath). Moreover, the two sites are complementary in terms of habitat diversity, since the Inselberg-station is located at the foot of an inselberg and the second one (the Pararé site) lies on the banks of a river; therefore, this arrangement will enable researchers to survey a wider range of biotopes.

Management and research programmes

The construction of COPAS is placed under the responsibility of the University of Ulm, whereas the setting up of the base camp, the transport and the on-site assembly of COPAS are under that of ECOFOR (a group of several French scientific bodies involved in forest research). The CNRS, which also manages the Inselberg-Station, will be in charge of the management and running of COPAS.

Initially, the Les Nouragues Research Station operated around a few French research projects focused on forest regeneration and seed dispersal by fruit-eating vertebrates. Relatively recently, other topics of study were developed, partly as a result of collaboration with scientists from other countries (mostly from Europe and North America). The Web site www.cnrs.fr/nouragues provides information on the station and its activity, as well as on the COPAS project. The book on Les Nouragues, by Bongers *et al.* (2001), summarizes research undertaken at the station over a dozen years.

COPAS is part of a large scale research project on the Guianan tropical rainforest ecosystem and, through linkages with other research stations worldwide, of the global scientific programmes that focus on tropical rainforests in general. The new COPAS operative unit should allow the further development of ongoing programmes as well as the launching of new research projects. COPAS will be open to the international scientific community depending on the approval of an already working selection committee, with the aim of enhancing collaboration with other canopy study sites worldwide. During workshops in Paris and Ulm, the following topics were selected, based on incoming project proposals:

- The mechanisms of tree growth in height and diameter, coupling *in situ* observation with laser measurements; dynamics of tree crown growth; productivity, biomass of root-climbers and hemiepiphytes;
- Investigations on sunlight characteristics; influence of the canopy on the lighting of the different forest strata; consequences on the evolution of coloured signals, on biomass and on biodiversity;
- Microclimates and microhabitats of the canopy; water and nutrient cycles (storage in the atmosphere); the role of epiphyllous organisms in the fixation of atmospheric nitrogen;
- The mechanisms of photosynthesis; correlations with microclimate and transpiration; C3 (trees) and C4 (epiphytes and stranglers) photosynthesis; the mechanisms of gas exchanges within the canopy and in the underlying strata (carbon isotopic discrimination, sap flows, stomatal conductance of water vapour, balance of CO_2 and H_2O flows, $\delta^{13}C$);
- Survey and ecology of a number of plant families (Annonaceae, Araceae, Arecaceae, etc.);
- Pollination systems; the roles of the different insect and nectarivorous vertebrate communities; pollination syndromes; flowering and fruiting phenology;
- The study of predation of immature fruit; the role of arboreal rodents, parrots and seed-eating insects (biomass produced, timing of metabolite mobilisation in developing seeds, production of toxic secondary compounds);
- Seed dispersal by the fruit-eating community;
- Ant-plant relationships (selection of nesting sites, feeding behaviour, the function of venoms, conflicts of interest between entomophilous pollination and ant-based protective systems);
- The biodiversity of canopy invertebrates: Lepidoptera and relationships with their host-plants, Heteroptera, ants, termites, coprophagous Coleoptera, etc.; food resources and timing of reproduction; invertebrate movements from one tree crown to another;
- The sharing of resources and space between communities of arboreal vertebrates (rodents, primates, bats, sloths, birds, amphibians);
- Medical entomology: investigations on the insect vectors of yellow fever, malaria, leishmaniasis and Chagas' disease; seasonal cycles of vectors and parasite infections;
- Survey of the reservoirs of plant trypanosomes.

Acknowledgments

G. Gottsberger designed COPAS, initially together with J. Döring from the University of Giessen and later on with E. and M. Freiberg, A. and R. Lücking and A.-D. Stevens from the University of Ulm and with the German companies Ballonbau Wörner in Augsburg, Stahlbau Glocker in Ehingen, A. Hammerl engineer's office in Ellgau, R. Conradt Mess- und Regeltechnik in Allensbach, J. Kuder Industriedienstleistungen in Friedberg and the Luftfahrt-Bundesamt in Braunschweig. The final success of the project was secured by receiving the Körber European science award in 1996 by the two project coordinators G. Gottsberger (Abteilung Systematische Botanik und Ökologie, Universität Ulm, Germany) and U. Lüttge (Institut für Botanik, Technische Hochschule Darmstadt, Germany), and P. Charles-Dominique (Laboratoire d'Ecologie du Muséum National d'Histoire Naturelle et Station de Recherche des Nouragues UPS 656, CNRS, France), A. Cleef (Hugo de Vries Laboratory, University of Amsterdam, The Netherlands), B. Hölldobler (Lehrstuhl Zoologie II, Universität Würzburg, Germany) and K. Linsenmair (Lehrstuhl für Tierökologie und Tropenbiologie, Universität Würzburg, Germany). Other sources of funding came from the University of Ulm and the State of Baden-Württemberg, Germany, as well as from the CNRS, the Ministry of Scientific and Technical Research and the Regional Council of French Guiana, France.

4.3.3. Lambir Hills National Park Canopy Crane, Malaysia

Tohru Nakashizuka, Shoko Sakai & Lucy Chong

Background

In 1992, Drs. Tamiji Inoue (Center for Ecological Research, Kyoto University), Kazuhiko Ogino (Shiga Prefectural University), Takuo Yamakuara (Osaka City University), and Isamu Yamada (Kyoto University) installed two canopy towers and a walkway system at the 6,800ha Lambir Hills National Park, northern Sarawak, Malaysia. The Canopy Biology Program (CBP) at Lambir Hills was initiated with local collaborators, Dr. Lee Hua Seng (Forest Department Sarawak) and Mr. Abang Abdul Hamid (Forest Research Center, Sarawak). Around 1996, the late Dr. Tamiji Inoue planned to install a canopy crane at Lambir Hills National Park. In 1998, the Japan Science and Technology Agency (JST) funded ‘Research and Observation on the Mechanisms of Atmosphere-Ecosphere Interaction in the Tropical Forest Canopy’ (PI: Dr Tohru Nakashizuka), as part of their Core Research for Evolutional Science and Technology Project (CREST). The canopy crane represented a key device in order to facilitate the research project, and the installation of the second crane funded by Japan (see Chapter 4.2.5 for the first one) was completed on April 20, 2000 at Lambir Hills (Table 17).

Table 17. Site and crane characteristics of the Lambir Hills National Park Canopy Crane.

Variable	Characteristics
Location	Lambir Hills National Park, northern Sarawak, Malaysia 4°2’N, 113°50’E
Altitude	150 - 465m
Mean annual air temperature	26.7°C
Mean annual rainfall	2700mm
Type of forest	Old-growth lowland rain forest (lowland dipterocarp forest)
Area of forest accessed by the crane	1.77ha
Canopy height	50-55m
Crane model	Liebherr, Model 245 EC-H6
Height of tower / Length of jib	85m/75m
Maximum height reached by the gondola	Hook height = 81.7m
Gondola type	a: 2.4 x 0.5m b: 2.4 x 1.2m
Number of persons carried by the gondola	a: 1 person b: 5 persons
In operation since	2000
Main research topics	• General flowering • Plant-animal interactions • Carbon budget • Remote sensing
Remarks	An other canopy access system exists in the park, consisting of two towers and walkways
Management	Kyoto University (Japan), Research Institute for Humanity and Nature (Japan) and Forest Research Center (Sarawak, Malaysia)
Contact	Tohru Nakashizuka, Research Institute for Humanity and Nature, toron@cikyu.ac.jp
Web site	http://www.tropicanopy.org/project/projtop.html http://www.forestry.sarawak.gov.my/forweb/research/fr/ip/eco/bccrane.htm
List of publications	http://www.tropicanopy.org/results/list.htm
Fees for researchers	Please contact the project leader, Tohru Nakashizuka

Researchers from different Japanese organizations and the Forest Research Center in Sarawak coordinate the research at the crane site. The crane is administered via an agreement between the Forest Department

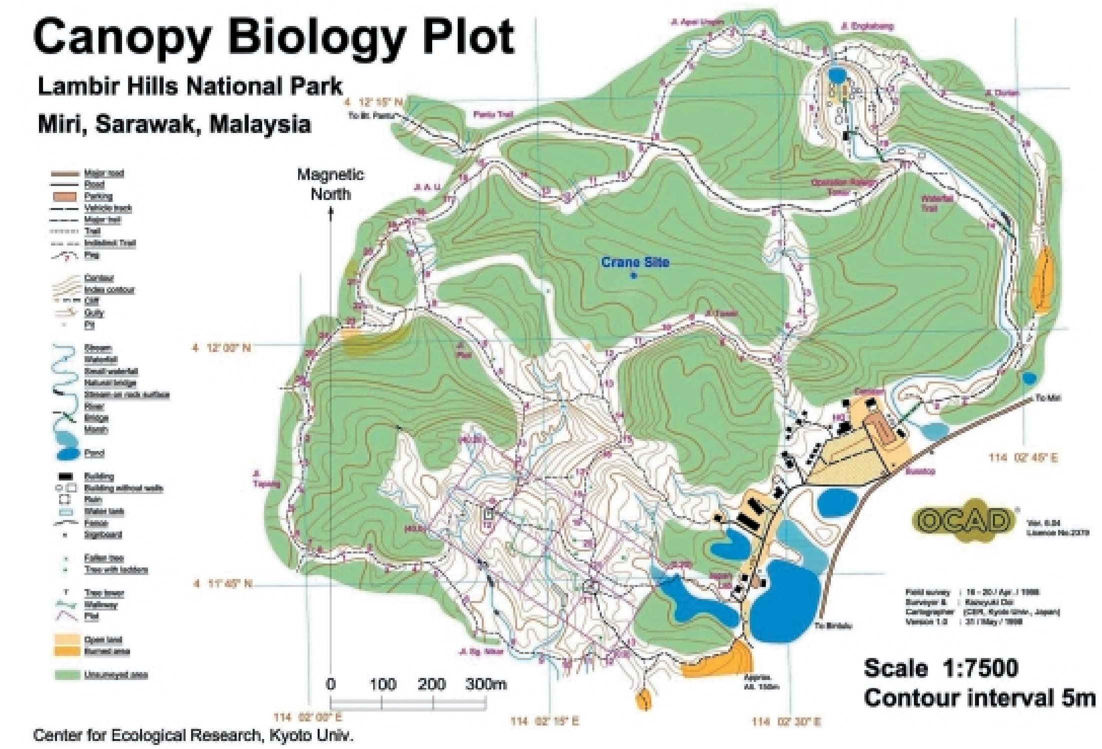

Fig. 76. Map of the main research sites in Lambir National Park. The 4ha plot around the canopy crane and the 8ha plot with canopy towers and walkways are indicated with the red square and rectangle, respectively.

of Sarawak and the JST. JST staff and other researchers manage the crane and its timetable. The conditions and the availability of the crane may be checked through the Internet. Collaborators from different disciplines are welcomed and any scientist wishing to perform research at Lambir Hills using our facilities should contact the present first author and submit a research proposal. After approval, the applicant will team up with an appropriate collaborator for the project.

Lambir Hills forest and crane

The forest of the National Park is an old-growth lowland dipterocarp forest, without any record of logging. Its topography is hilly and complex at the smaller scale; at the crane site it is rather flat, whilst it is rougher around the canopy walkway (Fig. 76). The soil is a mosaic of udult yellow-red ultisol and humult soil. In addition to Dipterocarpaceae, Euphorbiaceae, Myristicaceae, Burseraceae, Lauraceae and Myrtaceae are the major constituents of the forest and the National Park includes many local endemic plant species (about 35% of vascular plants) and those endemic to Borneo Island (about 75%). Whilst the forests receive about 2700mm of annual rainfall, weak and strong droughts occur occasionally, but without clear seasonality.

The canopy crane in Lambir is 80m tall (Figs 77 and 78) and includes three observation platforms (at 20, 40 and 60m above ground), and an elevator to reach these platforms and the control cabin. The crane may be operated from the control cabin or by remote control from the gondola. Beside the canopy crane, a 300 m-long canopy walkway 30-40m above the ground, and two tree towers (40 and 60m tall) can also be used for canopy studies nearby. Accommodation for researchers is available within the National Park, or in the city of Miri, about 40 minutes drive from the National Park. A small field laboratory, 15 minutes walk from the canopy crane, is also available for researchers, with some basic equipment, such as dryer, freezers, balance, incubator, telephone and internet access.

Two permanent plots were established around the canopy crane (4ha) and walkways (8ha), respectively (Fig. 76), and all trees above 10cm of diameter at breast height (dbh) in both plots were recorded and mapped. The highest trees around the canopy crane are about 50-55m tall (Fig. 79), whilst those around the canopy walkway are over 60m tall. The species richness is very high in the National Park, as more than 600 species of trees above 10cm of dbh were recorded in the 8ha plot. Moreover, a 52ha permanent plot located about 1km from the site includes about 1,200 species of trees above 1cm in diameter. To facilitate studies in a forest of such high diversity, a Tree Census Database has been developed, with characteristics of each tree including leaf images (Fig. 80). Such datasets are integrated with continental/global and regional scale data based on remotely sensed satellite images and other GIS datasets to build a multi-scale data system for a comprehensive understanding of nature and human impacts in the region (see research topics, below). The main research topics and findings using the canopy crane and other canopy access systems at Lambir Hills can be summarized as follows.

General flowering and plant-animal interaction

Plant-animal interactions, particularly pollination, seed dispersal and seed predation have been observed intensively at Lambir for more than ten years. In particular, interactions related to plant reproduction are complicated by general flowering, a phenomenon unique to dipterocarp forests in this region. During general flowering, which occurs once in several years, most dipterocarp species and plants of other families massively flower sequentially for several months, whilst flowers are rather scarce outside of general flowering (Sakai, 2002a). Ongoing monitoring of plant phenology for ten years covers large general flowerings which occurred in 1996 and small ones in 1997, 1998, and 2001 (Fig. 81). Responses of insect populations observed using light traps were different among species (Kato *et al.*, 2000; Itioka *et al.*, 2001). Giant honeybees migrate into forests as soon as the forests start flowering and their numbers increase dramatically, whilst some other insects adhere to regular emergence in a particular month of the year irrespective of general flowering.

A survey of pollination systems at the community level including 270 plant species showed that beetles and social bees were important pollinators in the forest. The roles of large and medium sized bees in the canopy as pollinators were rather minor compared with that in Neotropical forests (Momose *et al.*, 1998). Synchronized flowering of

Fig. 77. The end section of the Lambir Canopy Crane jib being lowered into position (photo Tohru Nakashizuka).

Fig. 78. Researchers in the gondola above the Lambir Hills forest (photo Tohru Nakashizuka).

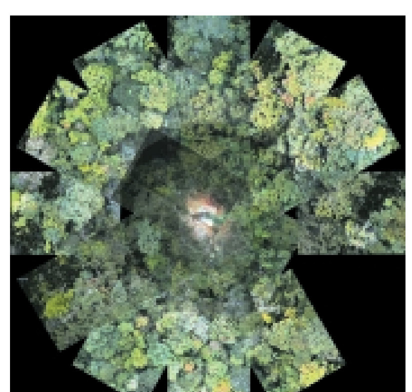

Fig. 79. Bird's eye view from the canopy crane (M. Yoshimura & M. Yamashita, unpublished data)

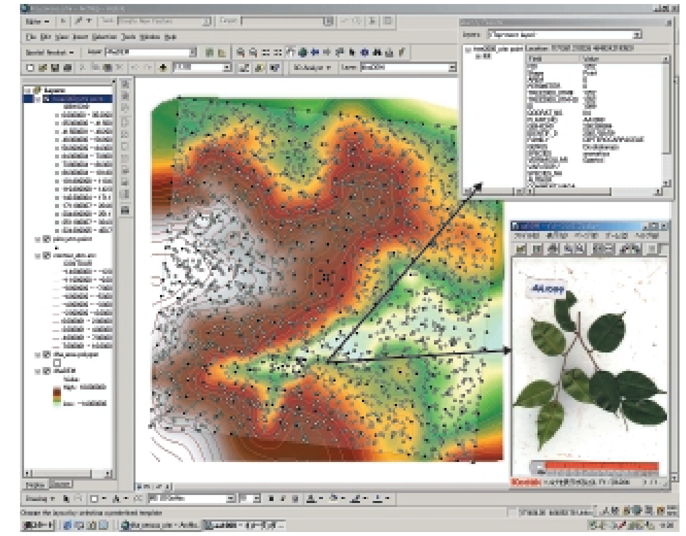

Fig. 80. The tree census database for the 4ha plot around the Lambir Canopy Crane. The colour of each point indicates the size of the tree. White points are small trees whilst dark blue points represent large trees. The leaf image of each tree is viewed by clicking on the points (M. Yamashita, unpublished data).

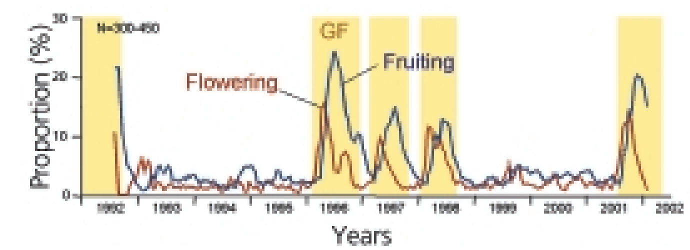

Fig. 81. Changes in the proportions of flowering and fruiting individuals (237 species, 428 individuals) observed from walkways and tree towers. General flowering (GF) periods are indicated with pale-yellow background. Modified from Sakai (2002a).

different species may promote pollen flow (Kenta *et al.*, 2002) and reduce seed or seedling mortality. Observation of seed predators in several general flowering events revealed that interactions between plants and insect seed predators (mostly Coleoptera and Lepidoptera) are quite variable. Some insect species are the dominant seed predator of a plant in a year but not in the next. Many problems remain in relation to plant-animal interactions in general flowering.

The understanding of the mechanisms of general flowering, which play key roles in the ecosystem, is essential for the conservation and sustainable use of the forests in the area. Environmental data collected at Lambir Hills show strong correlation between flowering and drought. Large-scale experiments to evaluate the effects of drought have been proposed. Conversely, how each plant responds to environmental cues may depend on its own resource condition. Which part of a huge dipterocarp tree functions as resource storage for reproduction? And how much of the resource is allocated to flowers, fruits and vegetative parts? Such questions also represent different topics of our study.

Defense against herbivory

Plants evolve various modes of anti-herbivore defenses to reduce and/or escape from damage by herbivores. Most plant species are armed with chemical or physical defenses against herbivores, and sometimes they adjust their life histories to seasonal variance in potential herbivory. In the tropics, where ants are constantly abundant, many plants have mutualisms with ants to protect themselves, even providing nest sites and sometimes nutrients for ants in addition to nectar. Such plant species, called 'ant-plants', derive benefit from symbiosis since the ants protect their nest plants from herbivores.

Ant-defense system is very effective but costly. Plants have to provide the partner ants with nutrients and/or energy sufficient for defensive activities instead of allocating them to growth, reproduction and non-ant defense tactics. Drs Itino, Itioka and others pursue such dilemma of a group of ant-plants, *Macaranga* (Euphorbiaceae). More than 16 such plant species occur in Lambir Hills National Park, and 10 species have mutualisms with particular ant species (*Crematogaster* spp.). In being inhabited by ants in their hollow stem, *Macaranga* resemble *Cecropia* in the Neotropics, but *Macaranga* differs in its high degree of specificity of ant species (Itino *et al.*, 2001). Volatiles from *Macaranga* saplings help ant queens to find the right hosts (Inui *et al.*, 2001). Is it important to find the right *Macaranga* host for ants? Field experiments, bioassays in the laboratory and chemical analysis all indicated that the intensity of ant defenses, the balance between ant versus non-ant defenses, and the anti-herbivore strategies differ between *Macaranga* species. Therefore, a 'faulty' association cannot provide enough defenses to survive (Itioka *et al.*, 2000; Nomura *et al.*, 2000). The variation in balance of ant and non-ant defenses among species-pairs is strongly associated with each other, and with variation in life-history strategies.

In recent years the researchers have been broadening their scope of study. Most plants have more than one way to protect themselves or to escape from herbivores. For example, the leafing phenology, the chemical and physical leaf characteristics, and the allocation of nutrition represent some of the key factors. These factors are also related with characteristics of plant life history, photosynthesis, reproduction, etc. Therefore, researchers monitor these factors on different plant species at the crane site. Only by studying these traits simultaneously may we understand the 'real' costs and trade-off of herbivory, and may answer the question 'why forests are green'.

Forest dynamics and carbon budget

One of the important and urgent questions to be answered is whether 'the lungs of the earth', the tropical forest, is important as a sink of carbon in terms of global carbon dynamics. It requires complicated procedures to obtain accurate estimates of the carbon budget of the tropical forests. The integration of the eco-physiological process of a leaf or a branch into individual tree and community level is the first step to estimate the carbon dynamics. The physiological activity of a leaf or a branch varies within a three-dimensional structure of the canopy due to physiological differences among leaves and microclimatic variation (Koike *et al.*, 2001; Kumagai *et al.*, 2001). Some leaves receive high levels of illumination whilst others are always shaded. Leaves in the treetop often suffer severe water stress. Thus, the integration of such small-scale eco-physiological observations into a whole tree system represents one of the challenges of this project, which relies on the canopy crane.

The carbon dynamics of the community level can be estimated by measuring eddy covariance or forest tree production. Due to the spatial and temporal heterogeneity of the forests, which originates from its regeneration process, estimations are not a simple task. Usually, the forest community consists of a mosaic of different regeneration stages. Some patches are in the phase immediately after the tree-fall, while others are growing very rapidly. The decomposition of fallen trees causes emission of carbon into the atmosphere, while growing young trees absorb carbon. The mature patches are thought to reach the local balance of carbon budget. Such heterogeneity detected by analyzing the three-dimensional structure and its dynamics of the forest should be combined with analyses of flux measurement. Global meteorological events such as El Niño-Southern Oscillation (ENSO) also affect the fluctuation in forest dynamics and hence the carbon dynamics. For example, tree mortality during the severe drought of 1998 was 4-6 times greater than that of usual years (Nakagawa *et al.*, 2000).

Remote sensing fundamentals and scaling-up of canopy processes and mechanisms

Remote sensing is a powerful technique to obtain periodically information on the Earth's surface on a large scale. In recent years remote sensing and its related technologies have been defined as geoinformatics. In particular, remote sensing now represents the tool for understanding the physical phenomena rather than for describing landscape dynamics. One of the most important problems is how to be able to scale up the processes and mechanisms occurring in the canopy.

The spectral properties that are caused by the incident solar radiation, surface structure and its measurement geometry are fundamental in remote sensing. Thus, it is crucial to evaluate the effects of all of these factors by combining the various field data with supporting geoinformatics. The Lambir Hills Canopy Crane has provided a platform for these studies. Drs. Yoshimura and Yamashita developed systems to identify the actual three-dimensional canopy structure, and have enabled its computerized reconstruction as a 'Cyber Tropical Forest'. The system enables us to simulate forest activities under different conditions, to formulate hypotheses and predictions, to compare them with the 'real forest', and to construct new models for various estimations taking into consideration complicated canopy structure and forest dynamics.

4.3.4. Surumoni Project, Venezuela

Hans Winkler & Christian Listabarth

Background

The Surumoni crane project was one of the first crane facilities established world-wide and has, thus far, remained the only one within the world's largest rain forest area, the Amazon basin. Now it becomes the first one that may claim 'misión cumplida', albeit involuntarily. In this chapter we will relate the project history from the provider's view and summarize the project from an input-output relationship. We continue with a focus on the science that has been and is being generated during and in the aftermath of the active five years period of this project. First we shall outline background data to present the crane site. Then, we review substantial and published work to point out the major findings in this project, being keen about the prospect that many more will emerge.

In 1993, the Austrian Academy of Sciences (AAS) responded to a joint effort of Austrian and German researchers, led by W. Morawetz, with the decision to prepare a facility for biologists to study the tropical forest canopy. Though this was most welcome in scientific terms, it was an onerous task, both administratively and financially.

A large-scale strategy was planned, including (i) the hosting of an European Science Foundation financed meeting on Canopy research with prominent US participation in Vienna (probably resulting in the origin of the international network that became the Global Canopy Programme in 1999, see Chapter 2); (ii) the sponsoring of a crane and establishment of a forest canopy observatory; (iii) the investigation of potential host countries, the selection of one and negotiation of the issue, and (iv) the implementation of the project on time (according to scientific funding applications and commitments made in these). How this became reality has been discussed elsewhere (Winkler & Listabarth, 2002).

Operative in November 1995, the crane was donated to the Venezuelan government, whilst all scientific, administrative, financial and logistic responsibilities remained with the AAS. One of the objectives of this cooperation was the prospect that during a five years period also the latter tasks would be transferred to the host, who would become an independent crane provider thereafter (not excluding the AAS commitment and willingness to continue its efforts, if needed).

Unfortunately, this did not work and our endeavours could not be sustained after that period, due to opportunities not seized and political incapability and incompetence. Even within the active period, the few tasks of the national authorities were never performed satisfactorily (e.g. to provide legal support (adequate research permits) and logistic facilities for project participants). Moreover, the Venezuelan counterparts also failed to take advantage of the guaranteed benefits and neglected their future role as research coordinators completely. Thus, active participation by Venezuelan scientists was less than 5% (although granted free access to the system for as much as 50% of its potential availability). Most regrettably, even after formal discussion not a single individual had ever appeared to receive hands-on training in system operation, maintenance and administration.

Once the cooperation ended formally in 2000, the situation degenerated completely since AAS personnel and scientists had to leave the site, while the Venezuelan government did not suggest an interim solution. Our various attempts to rescue the facility (offering budget and human resources) and to prevent the impending collapse of the eagerly built infrastructure failed on political grounds, because not even reliable working conditions were granted. Instead, and against all advice from Venezuelan scientists, the Ministry of Environment and Natural Resources declared the project a national issue. Whatever this is, we would have been happy to see this project continued. Unfortunately, there is not much indication that this will ever be the case, and the project appears dead for good.

What may be learned from this experience? A project such as this one needs active and effective national support, and political stability to be performed successfully. Further, it would have helped to receive influential institutional support through the national scientific community (although we acknowledge the efforts of our Venezuelan colleagues Aragua Cedeño, Klaus Jaffé and numerous others for their support) to overcome governmental bureaucracy and neglect. However, great opportunities may be lost even if good intention prevails, and both the scientific community and the host country have 'lost out' by the decease of the first and only Amazonian canopy crane facility.

After this rather unexpected and painful experience as a crane provider, we are now in a position to summarize the input-output relationship. In this respect, there is no reason to complain. Having invested slightly more than $1 million for the project implementation (equipment, its emplacement, local infrastructure building), and the operation, administration and maintenance of the observation system during the operative period of five years, and earned some $150,000 in revenues, this gives a net expense of *circa* $900,000 (excluding institutional personnel). Through this effort, the AAS facilitated unique working conditions for as much as 104 scientists and students, plus a couple of visitors, TV-teams and journalists. Due to three extremely productive teams (Konrad Lorenz-Institut für Vergleichende Verhaltensforschung, Universities of Bonn and Mannheim) and various contributions of outstanding students there is a great publication record that continues to grow (for a regularly updated account see http://www.oeaw.ac.at/klivv/surumoni/index.htm). Actually, there are 154 entries, including contributions in journals, books, abstract volumes, theses and articles in popular press. Considering full length papers only (journals, books and theses, n = 70), this appears to be as little as $12,850 per contribution, and any forthcoming paper will improve this figure. Given the technical durability of such an installation (10-15 years at least), and a growing scientific output as data accumulate with time, canopy studies could finally become no more expensive or even cheaper than, for example, littoral marine ecology field work. It is probable that this is the best argument to encourage institutions, potential donors, sponsors and funding agencies, who might be shocked when facing the initially high costs for establishing a canopy crane facility.

The principal research topics within the Surumoni project have included biodiversity studies, plant-animal interactions (ant-plants and frugivory), ecomorphology and communication of birds, and the energy and water budget.

Local settings

The Surumoni crane is located 15km west of the small village of La Esmeralda, near the mouth of the Río Surumoni, a blackwater tributary of the Orinoco River in Venezuela (Table 18). The site is part of the 87,000km^2 large Man and the Biosphere reserve Alto Orinoco - Casiquiare. This region forms a transitional zone between the Guayana-Highlands in the north and north east and the lowlands of the Río Negro - Casiquiare Basin in the south and south east that extend southward into the central Amazon Basin of

Brazil. The large and extensive Duida-Marahuaca massif, is located about 15km to the north of the crane site and reaches 2,358m in elevation at the south-western rim of the Cerro Duida and 2,800m at the highest point of the northern Cerro Marahuaca.

Table 18. Site and crane characteristics of the Surumoni Project.

Variable	Characteristics
Location	Near La Esmeralda, South Venezuela 3°10' N, 65°40' W
Altitude	105m
Mean annual air temperature	26°C
Mean annual rainfall	2700mm
Type of forest	Amazonian lowland tropical forest (terra firme)
Area of forest accessed by the crane	1.5ha
Canopy height	25m
Crane model	Liebherr EC50, mobile on a 120m rail-track
Height of tower / Length of jib	40m/40m
Maximum height reached by the gondola	*circa* 35m
Gondola type	a: Cylindrical, diameter 1m, for lowering into the canopy b: Rectangular, weight 260kg, for working on the canopy periphery
Number of persons carried by the gondola	a: 1 person b: 3 persons
In operation from - until	1995 - 2000
Main research topics	• Biodiversity • Plant-animal interactions • Ecomorphology and communication in birds • Energy and water budget
Remarks	The crane was operated from the gondola with a remote control; it is not in operation at present.
Web site	http://www.oeaw.ac.at/klivv/surumoni/
List of publications	http://www.oeaw.ac.at/klivv/surumoni/index.htm

When the canopy crane became operational in November 1995, this area was a virtually unknown region of the Central Amazonian landscape. Subsequently, this site has probably become the most intensively investigated within the Venezuelan South (except for San Carlos de Río Negro). The Amazonian lowlands are a mosaic of natural vegetation types such as lowland rainforests, swamp forests, and savannas, and evergreen riparian forests spread along the banks of the Río Orinoco. Several forest habitats structure this mosaic even more intricately at local scales (Fig. 82, Stauffer & Listabarth, 2000). Most of the crane-plot area is covered by *terra firme* forest, and neither soil conditions nor the composition of the vegetation suggest regular annual inundation. Only a small part in the very south of the plot is flooded annually. The presence of small pieces of charcoal found in the upper layer of the soil has suggested possible anthropogenic impact some 100 years ago. A more detailed description of this area including climate, hydrography, geomorphology, biogeography and vegetation can be found in Anhuf and Winkler (1999).

Despite sampling restrictions and thus an incomplete botanical inventory of the local area, we have a reasonable knowledge of the diversity and structural forest parameters of the crane site (unpublished data provided by H. Rainer, University of Vienna, and B. Otto, J. Wesenberg & P. Horchler, University of Leipzig; see also Appendix). So far, 63 species of non-vascular plants (mosses and liverworts) and 316 species of vascular plants (in 202 genera representing 76 families) have been recorded for the plot (Table 19). The 1.5ha oval plot below the crane contains 781 living trees (census October 1999) with a diameter at breast height ≥10cm. These belong to 141 species representing 95 genera and 35 families, of which 10 families represent 64% of all plot species (Table 20). Similarly, the ten most abundant tree species represent

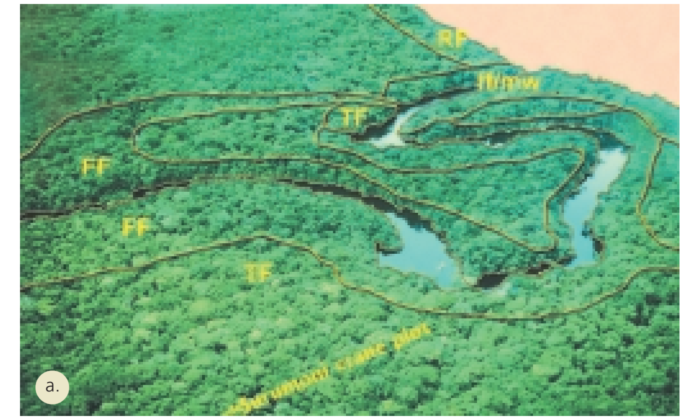

Fig. 82. (a) View of the Surumoni-Orinoco junction on a low-altitude flight. Note the mosaic distribution of habitats that can be distinguished clearly by inundation regime and water quality within an area of less than 1km². There are three major habitats, the *terra firme* forest (TF) where the crane was placed (bottom), the igapó-like flooded forest along the Surumoni (FF) and the riverine forest along the Orinoco (RF). Additionally, there are two transition zones between the flooded forest and its bordering habitats. The forest flooded by mixed waters (ff/mw), and the FF-TF transition (without signature) (photo Christian Listabarth). (b) The Surumoni Crane in similar view as Fig.82a (photo M. Heindl).

more than half of the tree individuals in the plot. An interesting feature of the species composition is the dominance of *Goupia glabra* (Celastraceae), a large pioneer tree frequent in late secondary forests. At the Surumoni, 90 individuals of this species form 30% of the crown cover (P. Horchler, unpubl. data). Almost equally abundant (but far less dominant) was *Oenocarpus bacaba* (Arecaceae). Median stem diameter is 15.3cm and the average stem basal area, calculated for the homogenous terra firme part of the crane plot, is 21.1m²/ha. Stem density for the same area is 546 living trees per ha, with an estimated number of 92 species per hectare. The forest reaches an average height of 19.0m. Emergent trees did not occur in the plot, but several were observed nearby.

Biodiversity

A project of the University of Graz dealt with the distribution and frequency of bark lichens. Each species appeared to have an optimum in one of the six forest strata distinguished and no lichen species occurred in all vertical zones. Species richness increased from the ground level to the canopy (Komposch & Hafellner, 2000).

W. Barthlott (University of Bonn) directed a project on the diversity and distribution of the community of vascular epiphytes. In 1996, the crane plot had a total of 778 individuals of epiphytic plants belonging to 53 species. Orchids and aroids were the most common taxa. The distribution of epiphytes within the plot was dependent on phorophyte distribution, was limited by the presence of suitable substrate and thus highly clumped, leaving 61% of the crane plot free of epiphytes (Engwald *et al.*, 2000, Nieder *et al.*, 2000). Epiphyte species were rather diverse with respect to their vertical distribution. Even within genera significant differences between species were found. Light conditions seemed to determine the frequency and distribution of particular species to a large extent. Due to the irregular canopy surface of the plot and varying light conditions, the vertical distribution of epiphytes was not strongly stratified (Nieder *et al.*, 2000). From 1996 to 2000 a high turnover of species and individuals and a significant increase in epiphyte abundance and epiphyte species richness (80 species in 2000) was observed (Schmit-Neuerburg, 2002).

Ants undoubtedly constitute a most important component in any rain forest ecosystem. An Austrian student screened the ant fauna of the study plot. Preliminary results obtained with tuna baits suggest that

Table 19. Botanical inventory and growth forms of determined species of the plot area. Those groups marked with an asterisk are likely to be assessed completely.

Taxon	Total	Terrestrial, erect plants	Trees * DBH>10cm	Vines	Epiphytes *	Hemi-epiphytes	Hemi-parasites * (mistletoes)	Stranglers
Hepatophyta	45	-	-	45	-	-	-	-
Bryophyta	18	-	-	-	18	-	-	-
Pteridophyta	17	6	-	-	10	1	-	-
Spermatophyta	299	196	141	52	27	14	8	2
Dicotyledoneae	244	181	137	47	4	2	8	2
Monocotyledoneae	55	15	4	5	23	12	-	-
Total of vascular plants	316	202	141	52	37	15	8	2

at heights between 10 and 35m 20-30 species dominate, mainly representing the subfamilies Myrmicinae, Formicinae, Dolichoderinae. Commonly, ants were not restricted to one stratum. Ants of the genus *Pseudomyrmex* are a possible exception as they were observed in the upper canopy only. The ant fauna at the ground level was much more diverse (T. Schmuck, unpubl. data). The latter trend was also observed in palms, reptiles and frogs.

Studies on the phytophagous canopy beetle fauna (838 species) revealed that no distinct beetle assemblages on individual host trees could be identified. Clearly, beetles were attracted to flowering trees or ones with extrafloral nectaries, on which they constituted temporary feeding guilds. The structure of these resource-driven assemblages differed not only in space and across host species (with broad overlap, though), but also in time within season and between day and night (Kirmse *et al.*, 2003).

Avian ecology, a study led by H. Winkler comprised a general survey of the avifauna and its ecomorphology and, among others, more specialized studies on vocal communication and frugivory. A total of 270 species of birds have been recorded at the crane site (Fig. 83), and about 50 more in the area between Surumoni and La Esmeralda. A gross analysis of the strata use by birds (n = 185 species) revealed that 42% of the species are confined to the canopy, 31% use the interior of the forest, and the remaining 27% can be found in either zone (Winkler & Preleuthner, 2001).

Plant animal interactions

A student from the University of Bonn observed the interactions of sugar-feeding ants with homopterans and their host trees, and with plants that produce extrafloral nectaries. Sixty-three percent of the trees studied hosted honeydew-consuming ants and the interaction appeared to be a widespread phenomenon at Surumoni. Although many ant species were recorded simultaneously on the same tree, usually only the ants of one colony monopolised all the homopterans of a single tree. In but a few such associations a strong preference of ants for a specific host was found. Extrafloral nectaries were exploited by all ant species alike (Blüthgen *et al.*, 2000).

Ant gardens are a conspicuous feature of the Surumoni site. They develop from an arboreal ant nest around the roots of one or more epiphytes. Ant gardens were mapped, and the plant involved and ant species identified. The gardens are most abundant in the sunniest sectors of the crane plot. In these gardens, epiphytes of five families were observed with *Anthurium gracile* (Araceae) as the most common species. The gardens were used by several species of ants representing 9 genera. Detailed analyses of the relationships between ants and plants revealed that the plants benefit from nitrogen fixing cyanobacteria that are dispersed by the ants together with the seeds. Both the ant and the plant benefit from this relationship (Cedeño *et al.*, 1999; Blüthgen *et al.*, 2001). Additionally, ant gardens were shown to be ephemeral systems. From 1996 to 2000, almost half of the epiphyte individuals disappeared and almost none of the ant gardens recorded in 2000 was occupied by ants (Schmit-Neuerburg, 2002).

In a most interesting cooperation being initiated in the crane gondola and between two strongly-motivated students who actively demonstrated how synergy between teams may work, Blüthgen and Wesenberg (2001) experimentally showed that the drilling of holes into juvenile twigs of *Vochysia vismiaefolia* may indeed induce the formation of domatia. An undescribed species of *Pseudomyrmex* produced and inhabited these structures. Their results challenge extant hypotheses about the evolutionary origin of ant-plant

Table 20. The ten most diverse tree families of the Surumoni plot (n=141 spp.).

Family	No. Species	%
Leguminosae	20	14.2
Lauraceae	12	8.5
Chrysobalanaceae	10	7.1
Euphorbiaceae	9	6.4
Annonaceae	8	5.7
Burseraceae	7	5.0
Sapotaceae	7	5.0
Apocynaceae	6	4.3
Lecythidaceae	6	4.3
Moraceae	5	3.5

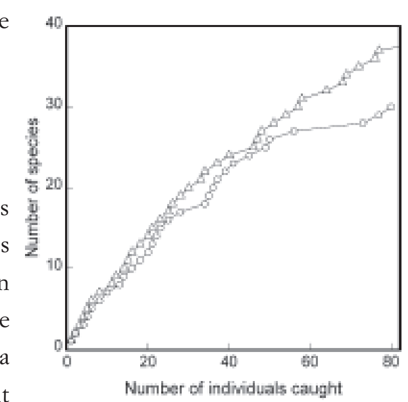

Fig. 83. Species incidence curves for birds caught in mist-nets placed in the understorey (circles) and the canopy (triangles). The understorey curve agrees well with those found at other Neotropical sites. No comparable data for the canopy exist.

Fig. 84. Conspicuous fruits of palm trees from three different strata of the forest (a) *O. bacaba*, canopy; (b) *I. setigera*, subcanopy; (c) *B. hirta*, understorey: Note that fruits do not only contrast against the (mostly dark) background of the forest interior but that plants increase contrasts themselves (photos C. Listabarth).

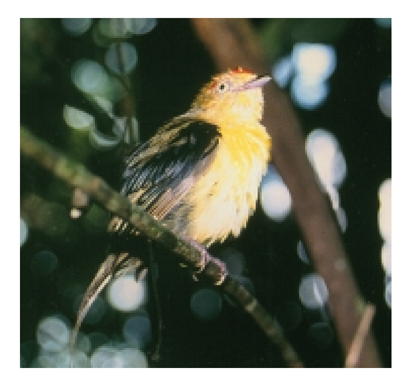

Fig. 85. Males of Wire-tailed Manakins (*Teleonema filicauda*) appear especially conspicuously coloured at their display sites (photo K. Reckardt).

associations.

A study lead by K. Jaffé dealt with the largely disputed role of ants as flower visitors. In a comparison of ant avoidance mechanisms between flowering species of the savannah and the forest canopy habitats, Jaffé *et al.* (2003) showed that flowers of the savannah were much more likely to repel nectar-robbing ants than those of the forest canopy. They hypothesise that it is probable that flowers in the canopy have probably adapted to tolerate ants rather than to repel them, because ants might benefit plants and their flowers by providing protection against herbivores.

Frugivorous and omnivorous birds dominated the canopy avifauna. Fruit standing crop varied between 9.8kg/ha and 60.4kg/ha and was highest in the subcanopy and in the canopy (Schaefer *et al.*, 2002). The crane provided ideal conditions for studying specific questions of plant - frugivore interactions. Observations on fruiting trees were focused on the frugivore assemblage and their foraging behaviour. Trees could easily be assigned to either specialists or generalists with respect to dispersal system. However, birds (17 species studied) were more difficult to classify. The degree of frugivory, for instance, was not correlated with specialisation for particular fruits (Ertan, 1999, Walther, 2000). Fruit choice was dependent on the abundance of alternative fruits, fruit accessibility, and secondary metabolite content (Schaefer *et al.*, 2003). Fruit colours rendered fruits conspicuous against the background in all levels of the forest (Fig. 84).

Ecomorphology and communication in birds

Work on the avifauna began with extensive observations on foraging behaviour and habitat use. In addition birds were measured in collections and in the field for ecomorphological analyses. In morphological terms, canopy birds do not form a well-defined group. Insectivores, omnivores, and frugivores are also rather indistinct. Morphological differences were mainly associated with mode of locomotion. Due to the high diversity of species, comparative studies of ecomorphological relationships concerning the evolution of certain morphological features and their ecological significance proved to be very fruitful (Winkler & Preleuthner, 1999).

The crane and the rich avifauna were ideal for the study of vocal communication, too. Measurements from two Viennese research groups provided much insight into the acoustic properties of the forest, conditions for sound propagation, and related adaptations in the song of some birds. The canopy is conducive to acoustic communication in comparison with conditions that prevail closer to the ground. The factors that most influence the evolution of bird song are reverberation and ground attenuation (Nemeth *et al.,* 2001). Optical communication of birds was affected by the light environment. Spectral composition of ambient light varies gradually from the understorey to the canopy, and manakins (Pipridae) displayed at that position along the vertical gradient, where ambient light increased the contrast of their colour signals against the background (Heindl & Winkler, 2003; Fig. 85).

Energy and water budget

D. Anhuf and collaborators of the University of Mannheim established one of the most complete sensor networks in a small mini-watershed at the crane site and developed an elevation model for the crane site (Anhuf *et al.*, 1999).

During daytime solar radiation on the canopy is converted into fluxes of sensible and latent heat. During the night, heat is lost through radiation, and sensible as well as latent heat, via condensation, contribute to the energy budget of the canopy. Some heat also flows from the ground layer. Accordingly, temperature fluctuates by almost 10°C in the upper canopy and only slightly near the ground (Anhuf & Rollenbeck, 2001; Szarzynski & Anhuf, 2001).

The canopy intercepted about 18% of the annual precipitation. Interception varied greatly between the rainy and the dry season, attaining values of 5% and 56%, respectively. Stem flow contributed only 2% to the water that reaches the ground. About 64% of the precipitation went into runoff and interflow, 11% was transpired, leaving 7% contributing to the ground water (Fig. 86). Remarkably, the much lower portion of transpiration loss measured and extrapolated in this study sheds new light on extant climatic models (Anhuf *et al.*, 1999, and unpubl. data).

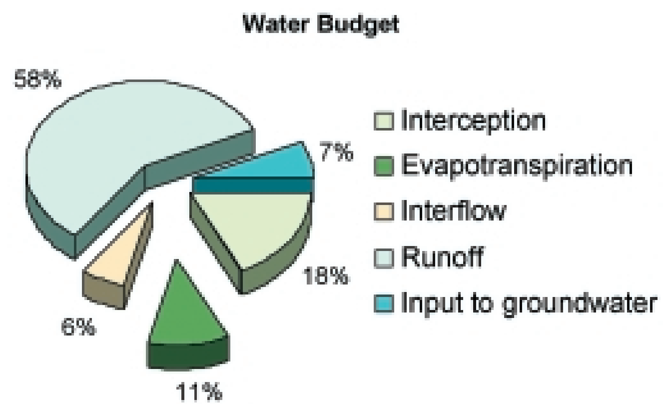

Fig. 86. Water budget from the Surumoni watershed.

Appendix: Vegetation characteristics of the Surumoni site

Wilfried Morawetz, Jens Wesenberg & Peter J. Horchler

Forest structure and species composition

An interdisciplinary approach is crucial in order to obtain a sound knowledge of interactions in the canopy (Morawetz, 1998; see also Stork *et al.*, 1997a). Forest structure and plant species inventory, detailed here for the Surumoni site, represent the foundations for such investigations.

Details about the settings and the infrastructure of the Surumoni site may be found in Morawetz (1998), Anhuf and Winkler (1999), Winkler & Listabarth (2002) and in the preceding section of this chapter. Most of the crane plot area is covered by a moist evergreen medium tall lowland rain forest, which, overall, is rarely flooded by the black Surumoni and/or white Orinoco water. Nevertheless, a small part of the plot (17%), located in the southern area, is flooded for at least nine days every year (R. Rollenbeck, pers. comm.).

A relevé of a typical vegetation profile, developed by A. Liebig (Leipzig), is shown in Figure 87.

Fig. 87. Vegetation profile in the Surumoni canopy crane plot. All larger palms are *Oenocarpus bacaba*, the low understorey palms are *Geonoma deversa*. The larger trees are Gg: *Goupia glabra* (Celastraceae), Cu: *Couma utilis* (Apocynaceae), Dg: *Dialium guianense* (Caesalpiniaceae), Em: *Eschweilera micrantha* (Lecythidaceae), Lo: *Licania octandra* (Chrysobalanaceae), Ls: *Licania subarachnophylla* (Chrysobalanaceae), Ms: *Mouriri sideroxylon* (Melastomataceae), Rg: *Richeria grandis* (Euphorbiaceae), Tu: *Tovomita umbellata* (Clusiaceae), Oa: *Ocotea aff. amazonica* (Lauraceae), Rt: *Ruizterania trichanthera* (Vochysiaceae).

The 1.5ha oval plot below the crane (Fig. 88) contains 781 living trees with a dbh≥ 10cm (data of October 1999). These belong to 141 species representing 94 genera and 35 families. Average stem diameter is 19.5cm (median 15.3cm) and the average stem basal area calculated for the homogenous, rarely flooded, upper part of the crane plot is 21.1m^2/ha. Stem density for the same area is 546 living trees per hectare. The number of tree species per hectare calculated for the same area would be 92. The forest reaches an average height of 19.0m (median 19.5m, SD 5.2m) without emergent trees being present. The distribution of stem diameters to dbh classes shows the 'classical' inverse exponential shape, typical for many natural forests. The distribution of the trees' growth height to size classes shows almost a normal curve, with a peak around 20m.

An interesting feature of the species composition is the dominance of *Goupia glabra* (Celastraceae), a large pioneer tree frequent in late secondary forests. Its Importance Value Index amounts to 48.4 (IVI, i.e. the sum of the relative abundance of species, the relative frequency in all 10x10m grid cells of the crane plot and the relative basal area; Curtis & McIntosh, 1951). The dominance of this species extends further westward of the crane plot, where it is even more dominant and forms denser populations. Frequent records of young charcoal (80-180 years ago) in areas of dense *Goupia glabra* stands lead to the assumption that an extensive fire event triggered the establishment and long term dominance of this species. In the crane plot, 90 individuals of this species form about 30% of the crown cover.

Other common tree species are *Oenocarpus bacaba* (Arecaceae), *Licania apetala* (Chrysobalanaceae), *Dialium guianense* (Caesalpiniaceae), *Ocotea aff. amazonica* (Lauraceae), *Podocalyx loranthoides* (Euphorbiaceae), *Protium spruceanum* (Burseraceae) and *Ruizterania trichanthera* (Vochysiaceae). Figure 89 indicates the most important tree species in the canopy crane plot.

A representation of the distribution of stem diameters of the 10 most important tree families in the crane plot is illustrated in Figure 88. Note in red *Goupia glabra* and also the high amount of dead upright trees.

Palms are common but only 9 species are represented in the plot and most of them grow in the understorey, such as *Bactris hirta*, *Iriatella setigera* and *Geonoma deversa*, together with Melastomataceae, Marantaceae and Rubiaceae. *Oenocarpus bacaba* and *Euterpe precatoria* are typical canopy palms.

Phenology

A study of the flowering phenology of canopy trees was performed by Jens Wesenberg (Leipzig). The flowering behaviour of 105 individuals belonging to 54 species was monitored monthly during a total period of 24 months. During this period, a high percentage of the trees surveyed (*ca.* 35%) showed at least temporally non-annual reproductive patterns. Twenty-seven percent of all trees showed a single flowering event per year, whilst 25% showed several flowering periods per year. Twelve percent of the trees flowered nearly continuously. One tree never flowered during the observation period.

The community flowering pattern (Fig. 90) shows a bimodal distribution with a first peak at the end of the dry season / beginning of the rainy season and a second peak in the transition period between the rainy and

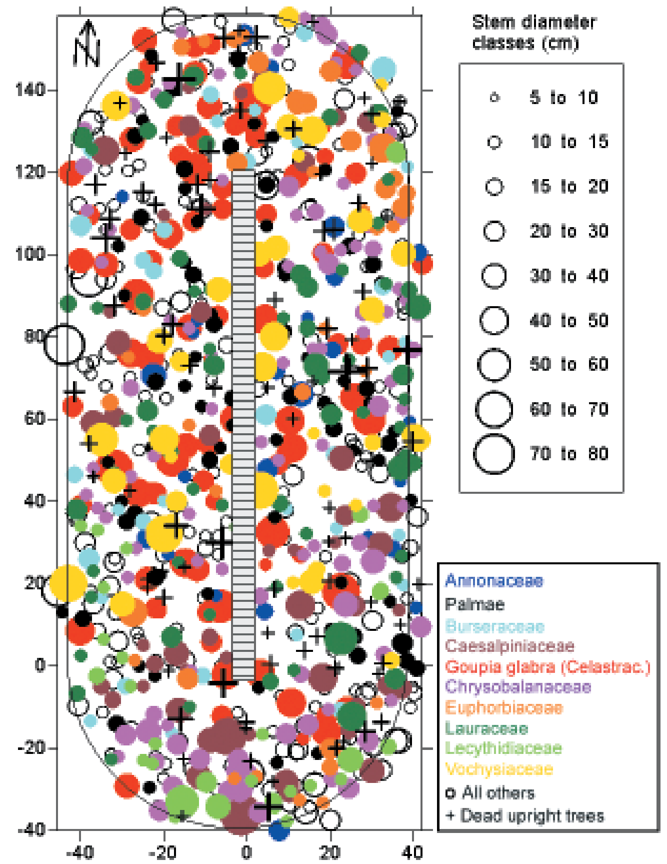

Fig. 88. Map of tree stems (≥ 10cm dbh) of the 10 most important families in the canopy crane plot (circle size exaggerated).

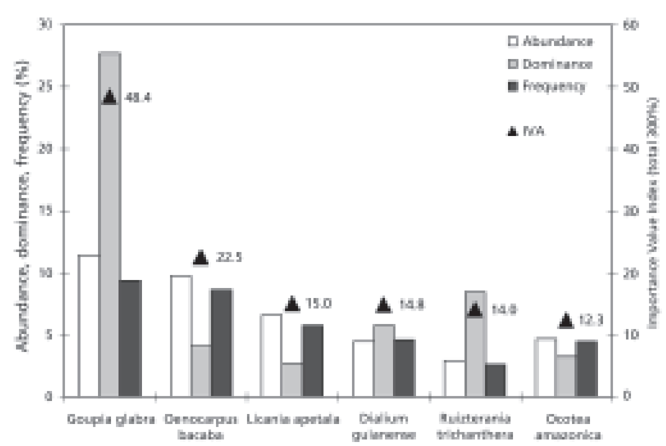

Fig. 89. The most important tree species ranked according to their importance. IVI = Importance Value Index.

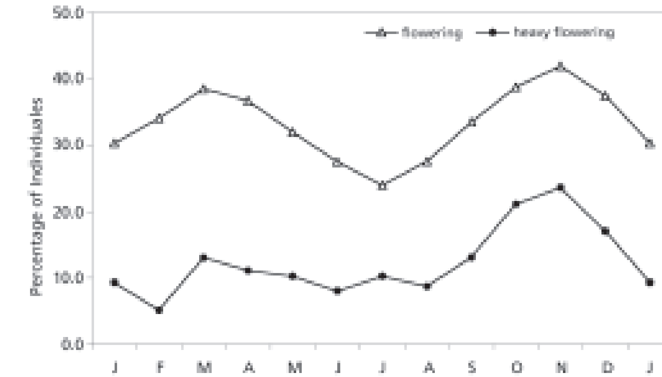

Fig. 90. Community flowering pattern resulting from the observation period June 1997 - November 1999.

Fig. 91. A rust fungus (*Aecidium cf. huallagense* P. Henn.) on leaves of *Guatteria schomburgkiana* (Annonaceae) from the middle canopy of the Surumoni plot. Rusts are scarce representatives of the Amazonian rainforest fungi.

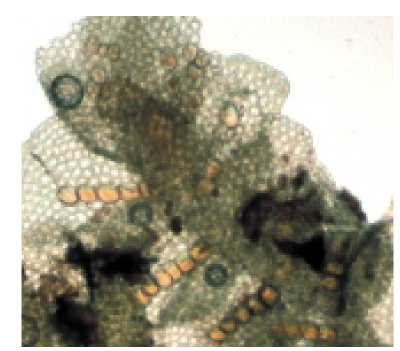

Fig. 92. A so far undescribed liverwort of the genus *Vitalianthus* from the canopy of the Surumoni crane site (photograph with microscope). The leaves have characteristic brownish golden ocelli (bark particles are blackish).

dry seasons. If only the intensively flowering individuals are considered, the first peak appears much weaker because many trees flowering during this time produced only low quantities of flowers. Bud formation preceding the flowering peaks coincided with periods of high radiation intensities. The inter-annual variance of Photosynthetically Active Radiation (PAR) is apparently lower during the bud formation preceding the peak of heavy flowering.

Fungi

P. Otto (Leipzig) studied wood-inhabiting and leaf-colonising fungi (Ascomycetes) in different strata of the canopy (Fig. 91). So far, only the determination of specimens and the data analysis for the foliicolous fungi have progressed to a larger extent. Screening results for more than 1,000 leaves of 30 plant families (leaves collected in the field as well as from herbarium specimens) revealed a total of 24 genera (14 families) of epiphyllous Ascomycetes. Some 19 taxa (13 genera) of this fungal group could even be detected on 100 leaves of the common tree species *Dialium guianense*.

These results indicate that (1) the canopy of this Amazonian rain forest is a suitable habitat for leaf-colonizing fungi; (2) there are remarkable differences of fungal diversity and frequency between host plant families; (3) in the canopy many epiphyllous fungi show preferences to particular leaf parts (e.g., margin, median nerve); and (4) there is a distinct decrease of these fungi from the understorey towards the tree top because of changing climatic conditions.

Mosses and liverworts

B. Otto (Leipzig) in cooperation with Jan-Peter Frahm (Bonn) investigated the bryophytes of the canopy. In the crane site altogether 45 liverworts (Fig. 92; including 36 species of Lejeuneaceae) and 18 mosses (including 5 species each in Calymperaceae and Sematophyllaceae) were observed, most of them on leaves. Only few species occurred in the canopy on bark, twigs and leaves. Evidently the unfavourable climate at times (e.g., mid-day maximum temperature of 37°C and minimum relative air humidity of 36%) is responsible for the low species diversity observed there. In the upper canopy, epiphyllous bryophytes are absent, the species growing there being exclusively corticolous. Typical genera of this stratum are for example *Acrolejeunea*, *Microlejeunea* and *Caudalejeunea*. It is noteworthy that an undescribed species of *Vitalianthus* was collected in the middle and upper canopy.

Mistletoes

A project on mistletoe ecology was performed by P. Seltmann (Leipzig), comparing the savanna of La Esmeralda and the Surumoni crane plot. The objectives of this study were to gather information on host tree spectra and infestation rates. Eight mistletoe species were observed in the crane plot, 3 in the savanna. In the forest 21% of all investigated trees and shrubs were infested, but only 8% in the savannah. Two mistletoe species with epicortical roots (forest: *Oryctanthus alveolatus*; savannah: *Phthirusa stelis*) were the most successful mistletoe species. The data of host spectra in the savanna suggest that, in contrast to the forest, *Phthirusa stelis* and *Oryctanthus sp.* evolved local preferences to one or two abundant host species. This suggests that genetically different parasite races may occur at the research sites.

Lianas

In part of the crane plot (0.52ha), K. Schulte (Frankfurt) performed a study on the structure and spatial distribution of the liana community. Some 1167 liana stems belonging to 47 identified species and 10 (sterile) morphospecies were recorded. The majority of stems had small diameters (76.5% with dbh <1cm), reaching heights less than 10m (85.9%). Ecological types included stem-twiners (55.4%), leaf climbers (24.4%) or branch climbers (17.3%). The most important families were Dilleniaceae (33%), Fabaceae (16%) and Caesalpiniaceae (13%). While the majority of canopy trees were covered only to a small extent by lianas, crown coverage by lianas was greater near the riverside. Within the canopy, 3 liana species (*Pinzona coriacea*, *Bauhinia rutilans*, *Machaerium madeirense*) were dominant. Liana crowns were situated to a large extend in the outer zone of canopy tree crowns (74.9%), followed by the inner zone (16.2%) and, interestingly, only 8.4% in the middle zone (division of growing zones according to Johansson, 1974; Fig. 93).

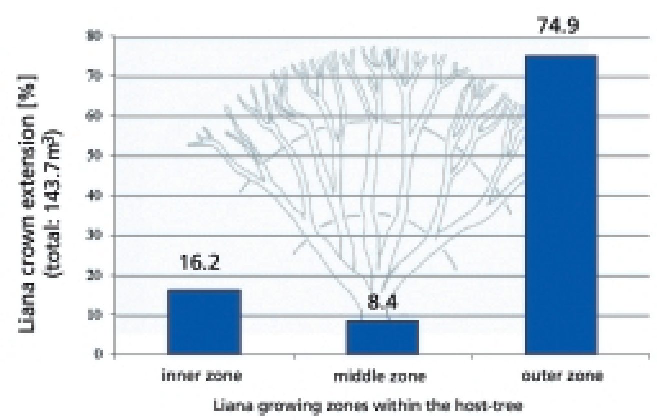

Fig. 93. Liana crown extension within the different zones of the host-tree.

4.3.5. Tropical Canopy Biology Program, Republic of Panama

S. Joseph Wright, Vibeke Horlyck, Yves Basset, Héctor Barrios, Ariadna Bethancourt, Stephanie A. Bohlman, Gregory S. Gilbert, Guillermo Goldstein, Eric A. Graham, Kaoru Kitajima, Manuel T. Lerdau, Frederick C. Meinzer, Frode Ødegaard, Don R. Reynolds , David W. Roubik, Shoko Sakai, Mirna Samaniego, Jed P. Sparks, Sunshine Van Bael, Klaus Winter & Gerhard Zotz

The first canopy crane was erected in a seasonally dry tropical forest in Panama in 1990, and a second canopy crane was erected in an aseasonal, ever-wet tropical forest just 80 km distant in 1997. Research conducted from these two canopy cranes under the auspices of the Smithsonian Tropical Research Institute had generated more than 130 scientific publications by 2003. A few highlights from this research are presented here. We have chosen to emphasize studies that addressed global biodiversity, global carbon cycles and climate change, and the movement of trace gases between forests and the atmosphere. Additional advances in the basic biology of canopy dwelling organisms are presented first to set the stage for biodiversity, carbon and atmospheric studies.

Institutional background

S. Joseph Wright, Vibeke Horlyck & Yves Basset

The late Alan P. Smith, a research scientist at the Smithsonian Tropical Research Institute (STRI), and STRI engineer Fernando Pascal first developed the idea of using construction cranes to access the forest canopy (Parker *et al.*, 1992; Anonymous, 1993; Illueca & Smith, 1993; Smith *et al.*, 1993; Allen, 1996). In 1990, Smith rented a construction tower crane for two years. A larger crane was permanently installed in 1992 in the Parque Natural Metropolitano (PNM), near Panama City on the Pacific coast of the Isthmus. A second crane was installed in 1997 in the San Lorenzo Protected (SLP) Area on the Caribbean coast. These two canopy access facilities were funded by the Smithsonian Institution and its National Board of Associates and by the governments of Belgium, Denmark, Finland, Germany and Norway through the clearinghouse mechanism of the United Nations Environment Programme.

STRI manages the canopy cranes, which represent the core of the Tropical Canopy Biology Program. STRI is a unit of the Smithsonian Institution based entirely in Panama, is dedicated to research in tropical marine and terrestrial environments, maintains its own staff of 28 research scientists, and hosts 300 visiting scientists each year, facilitating their work and providing laboratories, housing and library facilities. Visiting researchers are welcome to use the cranes within the Tropical Canopy Biology Program and fees for longer research projects (Tables 21 and 22) are negotiable. In addition, STRI provides a wide range of fellowships that may facilitate canopy research in Panama. These are open to all nationalities and all investigators from pre-doctoral students to full professors (see details at www.stri.org).

The two canopy cranes are 80 km distant from each other and are located in a semi-deciduous Pacific coastal forest (Parque Natural Metropolitano) and a wet evergreen Caribbean coastal forest (San Lorenzo). Since there is a steep rainfall gradient from the Pacific to Caribbean coast in Panama, this provides an ideal opportunity to compare the influence of rainfall on different forest processes. Annual rainfall averages 3,400 mm at San Lorenzo and just 1,740 mm at the Parque Natural Metropolitano. Consequently, there is a near complete change in plant species composition between the two sites.

The crane in the Parque Natural Metropolitano (PNM, Fig. 94, Table 21; Parker *et al.*, 1992; Smith *et al.*, 1993) yields access to 0.85 hectares of forest, characterized as a tropical semi-deciduous dry forest with a

Fig. 94. The Parque Natural Metropolitano Crane (photo Marcos Guerra).

dry season extending from December to April. The crane stands in the center of a 1 hectare plot where all 316 trees with a bole size of 10 cm in dbh or greater have been measured, mapped and identified. Trees in this plot are 30-40 meters tall, and the summed basal area of all stems larger than 10 cm in dbh is 26 m² per hectare. The dominant tree species is *Anacardium excelsum* (Anacardiaceae), however, more than 60 species of trees and lianas can be reached within the crane perimeter.

The 265-ha Parque Natural Metropolitano is one of the few remaining dry coastal Pacific forests in Central and South America. This forest has been protected since the construction of the Panama Canal beginning in 1903. A total of 284 species of trees, 45 species of mammals and 254 species of nesting birds have been recorded in the Parque Natural Metropolitano. BirdLife International and the Panama Audubon Society have declared this forest to be an area of global importance for birds, because of its value for migratory raptors. It also protects several nationally threatened birds, including the Sepia-capped Flycatcher (*Leptopogon amaurocephalus*). In addition, several species listed on the Cites Appendix I are also present, including Geoffroy's tamarin (*Saguinus geoffroyi*), jaguarundi (*Herpailurus yaguarondi*), margay (*Leopardus wiedii*) and peregrine falcon (*Falco peregrinus*).

The crane in the San Lorenzo Protected Area (SL, Fig. 95, Table 22) provides access to 0.92 hectares of tropical wet evergreen forest, which includes more than 240 species of trees and lianas. The crane stands in a six-hectare plot where all 22,400 trees with a bole size of 1 cm in dbh or greater have been identified,

Table 21. Site and crane characteristics of the Parque Natural Metropolitano Canopy Crane.

Variable	Characteristics
Location	Parque Natural Metropolitano, near Panama City, Pacific coast, Panama 8°59'N, 79°33'W
Altitude	30m
Mean annual air temperature	1865mm
Mean annual rainfall	26.3°C
Type of forest	Tropical dry semi-deciduous forest
Area of forest accessed by the crane	0.85ha
Canopy height	30-40m
Crane model	Potain F15-15C, fixed
Height of tower / Length of jib	42m/52m
Maximum height reached by the gondola	39.5m
Gondola type	a: squared, 0.64x0.64x2.23m b: squared, 1.22x1.22x2.23m c: squared, 1.23x1.52x2.39m
Number of persons carried by the gondola	a: 1 b: 4 c: 6
In operation since	1990
Main research topics	• Structure and dynamics of the upper canopy • Plant growth and phenology • Biodiversity (fungi, epiphytes, insects) • Biotic interaction (pollination, herbivory) • Plant ecophysiology (carbon assimilation, water use, etc.) • Plant physiological responses to a changing environment (elevated CO2, isoprene emission, plant uptake of reactive nitrogen, etc.)
Remarks	Comparative studies possible with the San Lorenzo crane
Management	Smithsonian Tropical Research Institute
Contact	Dr S. Joseph Wright, STRI, wrightj@tivoli.si.edu
Web site	http://canopy.stri.si.edu/ http://www.stri.org/tesp/PNM.htm
List of publications	http://canopy.stri.si.edu/publications.html
Fees for researchers	USD 26 per hour

measured and mapped. Structurally, the forest can be characterized as including 3338 stems per hectare (> 1 cm dbh) and a total basal area of almost 32 m² per hectare with the tallest trees being 45 m tall. This forest has escaped anthropogenic disturbance for more than 150 years and supports a high diversity of flora and fauna. At the crane site, Geoffroy's tamarin and the Howler monkey (*Alouatta palliata*), both listed in the CITES Appendix I, are readily observed. Further, other mammal species of interest present in the area include jaguar (*Panthera onca*), ocelot (*Leopardus pardalis*), southern river otter (*Lontra longicaudis)* and jaguarundi.

The canopy cranes in Panama have facilitated canopy research for 13 years. During this period, a wide range of research topics have been investigated by various research teams of international origin, including several Panamanian scientists. Wright and Colley (1994, 1996) outlined many of the research projects then on-going at the PNM crane. Here, with the help of many colleagues, we summarize just those studies that refined our understanding of the distribution of biodiversity, of global carbon cycles and of the movement of trace gases between forests and the atmosphere. Additional advances in the basic biology of canopy dwelling organisms are presented first to set the stage for biodiversity, carbon and atmospheric studies.

Fig. 95. The San Lorenzo Crane (photo Marcos Guerra).

Biological Background

All plants face a fundamental tradeoff between the uptake of carbon dioxide during photosynthesis and the concomitant loss of water vapour through transpiration. Gases move into and out of leaves passively through small pores in the leaf surface called stomates. Plants control the opening and closing of stomates; however, stomates must be open for carbon dioxide uptake from the atmosphere. The very low concentration of carbon dioxide in the atmosphere and the very high concentration of water vapour internal to leaves insure that several hundred molecules of water vapour are lost for every molecule of carbon dioxide that enters a stomatal pore. Leaves desiccate and are damaged when roots and xylem are unable to replenish the water vapour lost to transpiration. This is a real danger when rainfall and water availability are seasonal or whenever the evaporative demand of the atmosphere is excessive (typical near mid-day on sunny days for the uppermost canopy leaves). Thus, water availability controls carbon uptake in tropical forests, which in turn sets the stage for biodiversity, carbon flux, and forest-atmosphere gas exchange.

Water movement in tropical trees: physiological integration from leaf to canopy
Frederick C. Meinzer & Guillermo Goldstein

Because of their large size and logistical difficulties in gaining access to their crowns, the physiology of trees has traditionally been studied over a narrow range of scale, usually limited to individual leaves or branches. However, because trees are large, integrated organisms rather than mere collections of leaves, the entire individual is often the appropriate scale for characterizing physiological behavior that determines their utilization of water. The availability of the STRI canopy cranes over the last decade has presented exciting opportunities for studying large trees as whole, integrated organisms. This approach has led to considerable progress in understanding how the fundamental process of transpiration is regulated and integrated from the leaf to the whole tree and has highlighted the often dominant role that tree size, architecture and allometry play in governing physiological behavior. Taken together, our findings have pointed to substantial functional convergence in regulation of water use among taxonomically, phylogenetically and architecturally diverse tree species (Meinzer, 2003).

Among co-occurring Panamanian canopy tree species, tree size, rather than species, is the major determinant of total daily water utilization per individual (Meinzer *et al.*, 2001; James *et al.*, 2002; Meinzer, 2003). On a leaf area basis, tree hydraulic architecture was found to be the major determinant of differences in stomatal regulation of transpiration among species. When stomatal conductance of four co-occurring species was normalized by the branch leaf area/sapwood area ratio, an index of potential transpirational demand in relation to water transport capacity, contrasting stomatal responses to humidity coalesced into a single relationship between conductance and evaporative demand (Meinzer *et al.*, 1997). Consistent with this finding, a subsequent study revealed a common relationship between stomatal conductance and the leaf area-specific total hydraulic conductance of the soil/leaf pathway among five co-occurring species

Table 22. Site and crane characteristics of the San Lorenzo Canopy Crane.

Variable	Characteristics
Location	San Lorenzo Protected Area, near Colon, Caribbean coast, Panama 9°17'N, 79°58'W
Altitude	130m
Mean annual air temperature	3152mm
Mean annual rainfall	25.8°C
Type of forest	Tropical wet evergreen forest
Area of forest accessed by the crane	0.9ha
Canopy height	35-45m
Crane model	Kroell K-70, fixed
Height of tower / Length of jib	52m/54m
Maximum height reached by the gondola	49.5m
Gondola type	a: cylindrical, diameter 0.53m, height 2.35m b: squared, 1.22x1.22x2.23m
Number of persons carried by the gondola	a: 1 b: 4
In operation since	1997
Main research topics	• Structure and dynamics of the upper canopy • Plant growth and phenology • Biodiversity (fungi, epiphytes, insects) • Biotic interaction (pollination, herbivory) • Plant ecophysiology (carbon assimilation, water use, etc.) • Plant physiological responses to a changing environment (elevated CO_2, isoprene emission, plant uptake of reactive nitrogen, etc.)
Remarks	Comparative studies possible with the Parque Natural Metropolitano crane
Management	Smithsonian Tropical Research Institute
Contact	Dr S. Joseph Wright, STRI, wrightj@tivoli.si.edu
Web site	http://canopy.stri.si.edu/ http://www.stri.org/tesp/fts.htm
List of publications	http://canopy.stri.si.edu/publications.html
Fees for researchers	USD 200 per day

(Andrade *et al.*, 1998). Moreover, divergent leaf area-based transpiration rates converged when they were normalized by the branch leaf area/sapwood area ratio. In yet another study conducted at the PNM crane, a common relationship between sapwood specific hydraulic conductivity and rates of water movement through sapwood was observed (James *et al.*, 2003).

Utilization of water stored in stems and other organs was found to lower the effective resistance of the hydraulic pathway by transiently uncoupling canopy transpiration from water absorption by roots (Andrade *et al.*, 1998; Goldstein *et al.*, 1998). Total internal water storage capacity increased sharply with tree size and trees with greater storage capacity maintained maximum rates of transpiration for a substantially longer fraction of the day than trees with smaller water storage capacity (Goldstein *et al.*, 1998). Reliance on stored water to temporarily replace transpirational losses thus appears to be an important homeostatic mechanism for maintaining photosynthetic gas exchange as hydraulic path length and potential resistance increases with tree size and canopy height. In a more recent study, several whole-tree water transport properties, including minimum branch water potential, hydraulic conductance on a sapwood area basis, and movement of a tracer injected into the sapwood were found to show species-independent scaling with sapwood capacitance, a measure of intrinsic sapwood water storage capacity (Meinzer *et al.*, 2003).

Differences in water movement among tree species consistently disappear when re-expressed in terms of tree size or tree sapwood area. This functional convergence promises to simplify hydrological models of tropical forests. Water loss by the hundreds to thousands of tree species that often co-exist in a single tropical forest can be captured by a single relationship with tree size or sapwood area.

Carbon uptake: the canopy microclimate and plant growth

Kaoru Kitajima

Light availability is the major determinant of photosynthetic productivity in the canopy. Many factors, such as leaf optical properties, arrangement and density of leaves in canopy branches, patterns of leaf production and self-shading affect the amount of light reaching lower layers of the forest. Light at the canopy surface can exceed the solar constant due to reflectance by banks of clouds. As much as 99% of the light received by the uppermost canopy surface can be absorbed or reflected over just the first 5 m of the upper canopy (Mulkey *et al.*, 1996a). Liana leaves often represent 20-40% of the canopy leaf surface (Avalos & Mulkey, 1999), and significantly modify light heterogeneity. Although the leaf optical properties of lianas and trees differ little (Avalos *et al.*, 1999), large differences in branch architecture and seasonal leaf production affect competitive interactions for light between trees and lianas.

When water supply becomes limited, stomatal conductance (the degree of stomatal openness) and photosynthetic rates go down. Consequently, hydraulic characteristics, leaf arrangements, boundary layer characteristics and stomatal behavior affect both transpiration rates (see section on water use, above) and photosynthetic productivity on both daily and seasonal time scales (Hogan *et al.*, 1995; Zotz & Winter, 1996). Intrinsic water use efficiency, the ratio of photosynthetic rates to stomatal conductance, is often estimated from ratios of stable carbon isotopes, but Terwillliger *et al.* (2001) found that leaf age can significantly bias this relationship.

Leaf photosynthetic productivity of canopy leaves, measured as in-situ rates of CO_2 uptake, varies greatly among species, and among seasons within a species. Zotz *et al.* (1995) used the PNM crane to measure CO_2 uptake rates for the tree *Ficus insipida*, which proved to have the highest rates of photosynthesis yet known, both in terms of maximum values under the full sun light (A_{max}) and total daily net values, yet observed for a wild plant. Along with their previous data from other canopy epiphytes and trees, they have also demonstrated that A_{max} predicts daily net photosynthetic production by individual leaves. Differences in A_{max} among tree species are strongly linked to their life history traits, such as successional status and leaf longevity. Mulkey *et al.* (1995) showed that a general negative relationship exists between photosynthetic capacity and mean leaf longevity. Further, age-related declines in A_{max} are also related to leaf longevity in a manner predicted by a cost-benefit theory of leaf longevity (Kitajima *et al.*, 1997a, 2002).

Seasonal changes in light and water availability significantly alter canopy photosynthetic productivity. During the rainy season, water is generally not limiting, although photosynthetic rates are often depressed in the afternoon due to stomatal closure after trees lose large amounts of water in the morning (Zotz *et al.,* 1995). However, lower light availability caused by heavy cloud cover appears to be a greater constraint on canopy photosynthetic productivity during the rainy season (Graham *et al.*, 2003). In contrast, the dry season is a time with high light availability and low water availability. Many tree species at PNM exhibit seasonal leaf phenotypes in a manner adaptive to these contrasting seasonal patterns of water and light availability (Kitajima *et al.*, 1997a). Leaves produced in the early rainy season have lower A_{max} than leaves produced immediately before the dry season. Early-wet season leaves have low photosynthetic rates, which are appropriate to the lower light availability encountered during the cloudy wet season. Pre-dry season leaves experience much greater light availability, and exploit the window of opportunity in the early dry season for high productivity when light is more abundant due to less cloud cover before soils become progressively dry. An experimental study by Graham *et al.* (2003) clearly demonstrated that cloud cover depresses photosynthetic productivity during the rainy season (see below). In this study, light was augmented with high intensity lamps during the rainy season to approximate light intensity expected under clear skies during the dry season. In response to this high light treatment, *Luehea seemannii* produced leaves with high A_{max} similar to the dry season phenotype, and increased vegetative growth and reproduction.

Plant phenology and leaf area seasonality

S. Joseph Wright & Mirna Samaniego

Phenology, or the seasonal timing of growth and reproduction, remains one of the most effective mechanisms available to plants to cope with the seasonally contrasting availability of light and water that characterizes many tropical forests. The timing of leaf production by tropical trees and lianas can be predicted with great confidence from seasonal patterns of rainfall and solar irradiance and mechanisms of drought resistance. If water is readily available, most tropical tree species will produce leaves and reproduce in the season of greatest irradiance. This situation characterizes evergreen rain forests and also the rare seasonal forest where the dry season is consistently cloudy so that peak irradiance occurs in the wet season. In most seasonal forests, however, the dry season is less cloudy than the wet season and peak irradiance occurs in the dry season. Under these circumstances, disproportionately large numbers of species with adaptations such as deep roots that maintain dry-season water uptake still produce leaves and reproduce in the drier, sunnier season, whereas growth by species that lack these adaptations is largely limited to the wetter, cloudier season (Wright, 1996).

Canopy leaf area is generally assumed to be maximal throughout the rainy season in tropical forests. The PNM crane made possible the first quantitative counts of seasonal changes in leaf number for a tropical forest canopy. Counts were performed for 100 randomly chosen branches from the uppermost canopies of the seven abundant tree and liana species. Leaf area seasonality was much more complex than anticipated. Each species examined had a unique seasonal pattern of canopy leaf numbers, and leaf numbers varied two-fold during the eight-month wet season for each species. This unexpected seasonality alters individual allocation strategies, interactions between species, and forest carbon fixation. Species with similar seasonal leaf dynamics will have a greater impact on one another than will species with dissimilar seasonal leaf dynamics. To the extent that this reduces growth and increases the risk of mortality, ecological associations may arise between species pairs with dissimilar seasonal leaf dynamics. Seasonal leaf dynamics will also affect annual carbon gain and water vapour loss at the level of forest stands. Current models of forest carbon gain assume that the photosynthetic capacity of tropical deciduous forests increases seasonally with actual evapotranspiration. To the extent that seasonal changes in leaf numbers alter forest-level carbon gain, these models are wrong. Accurate models of the contribution of tropical forest to global carbon balances will incorporate accurate estimates of leaf area seasonality.

Biodiversity

Forest epiphytes

Gerhard Zotz

The study of vascular epiphytes or air-plants, which root in the crowns of host trees and not in the soil, is still in its infancy due to the difficulty posed by access to the canopy of tall forests. An inventory of the epiphyte flora of the San Lorenzo crane site was recently completed (Zotz & Büche, 2000; Zotz & Vollrath, 2003). While identifying all species within the crane perimeter, we conducted a comprehensive, quantitative census within an area of approximately 0.4 ha. There, we observed more than 12,000 individual epiphytes belonging to more than 100 species. For each individual epiphyte we noted host tree species, plant size, attachment height, and other variables such as substrate (branch) diameter or inclination. Besides being one of the most complete censuses ever conducted with vascular epiphytes of a tropical forest, this data set is now used as the basis for the long-term monitoring of epiphyte community dynamics. Going beyond this descriptive approach, we have also undertaken transplantation experiments to conduct controlled physiological studies and to understand the mechanisms underlying differences in the vertical distribution of epiphyte species.

Canopy fungi

Don R. Reynolds, Gregory S. Gilbert & Ariadna Bethancourt

The canopy is a distinctive habitat for a large number of algae, bryophytes, fungi, and bacteria. Our work focuses on a guild of ascomycete fungi found only on the surface of living leaves. These epifoliar, or leaf-surface, fungi (Fig. 96) complete their life cycles on the leaf surface without causing apparent damage to the plant host. They obtain their nutrition either as saprobes that consume detritus on the leaf surface, as honeydew specialists that depend on the waste products of piercing and sucking insects, or as apparently innocuous symbionts that use specialized hyphae adapted to absorb nutrients directly from the plant. In turn, they can be important nutritional sources for other microbes and for a wide diversity of arthropods.

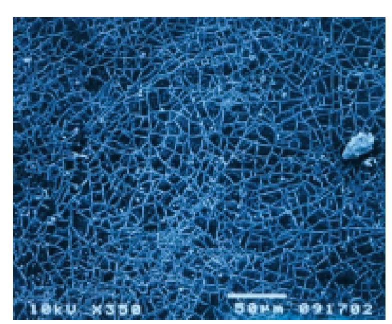

Fig. 96. Electron micrograph of the dense mycelial growth of the epifoliar fungus *Scolecopeltidium mayteni* on the leaf surface of *Trichilia tuberculata*.

All the leaf-surface fungi share common attributes suited to growth in the harsh conditions of the leaf surface in the forest canopy. These include dark pigmentation that protects against UV irradiation, growth

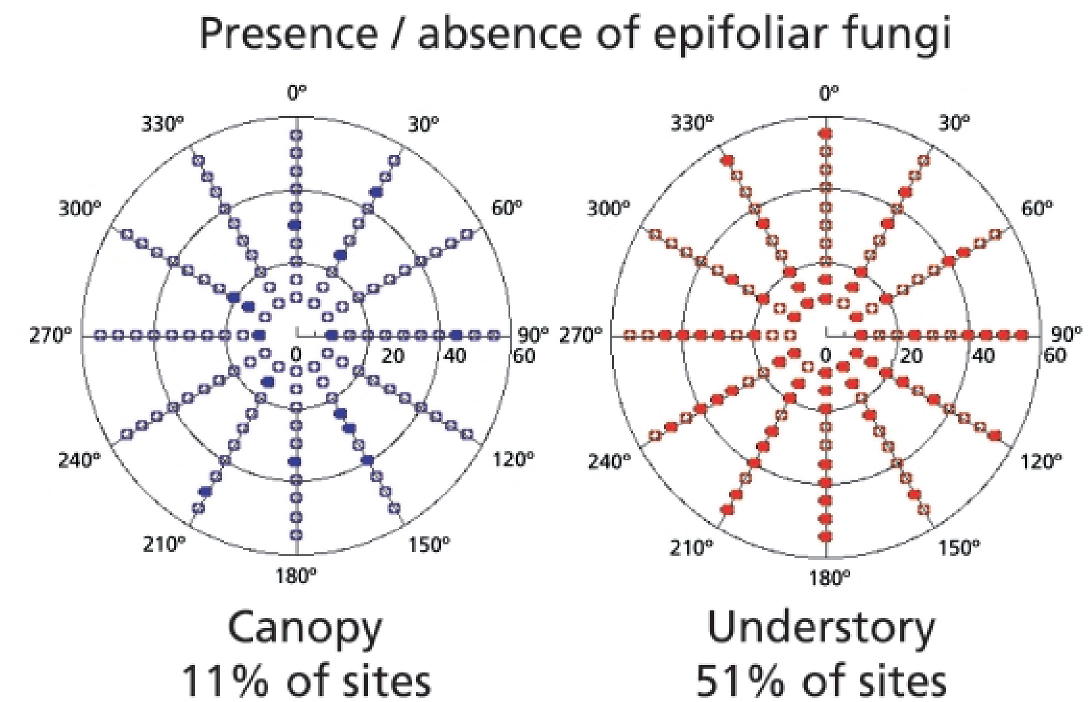

Fig. 97. Epifoliar fungi are much more abundant in the forest understorey than in the exposed canopy in Cape Tribulation, Australia. Filled circles represent sites in 55-m radial transects where leaf-surface fungi were found; open circles indicate that plants were free of such fungi.

and development patterns intimately linked with leaf surface features, and spore dispersal strategies that permit dispersal through flow of water through the canopy. Temperature, moisture, and irradiation extremes in the canopy are likely to be important factors limiting their distribution. In particular, the abundance of epifoliar fungi in the dark understorey increases with increasing light availability, but declines sharply in parts of the canopy exposed to full sun (Fig. 97).

Our research aims to evaluate how host specificity and microclimatic preferences drive the abundance, distribution, and diversity of leaf-surface fungi in tropical forests. Using systematic three-dimensional sampling strategies, careful taxonomic work, and detailed measurement of variation in moisture, light, and temperature in the canopy and understorey environments, we are disentangling the effects of host distribution and environmental constraints on the growth of leaf-surface fungi. A rigorous comparison of diversity and distribution patterns across canopy sites in Panama and Australia is providing new insights into the biogeography of these fascinating fungi and the factors that lead to habitat specialization.

While the fungal guild studied above may be harmless for their hosts, other fungi as well as protists, bacteria, viruses and nematodes may cause plant diseases. Adult trees may serve as reservoirs for pathogens and may spread disease to undestorey juveniles. Gilbert (1995) investigated the incidence of foliar diseases of sun leaves and shade leaves of five tree species at PNM. He found that foliar plant diseases were common (more than 75% of leaves in *Luehea*) and that diseases present in the canopy also affect leaves in the shade below. This indeed suggests a potentially important link between diseases of adult trees in the canopy and juveniles in the understorey. Thus, long-term studies to evaluate the role of disease in the canopy and the extent of the canopy-understorey connection appear to be crucial for understanding basic forest dynamics.

Insect diversity and host specificity

Frode Ødegaard

A study of host specificity of two beetle families, the leaf beetles and weevils, associated with 24 tree species and 26 liana species was carried out in the canopy at the dry forest crane site. After 700 hours spent in the crane gondola during one year, a total of 35,479 beetle individuals belonging to 1,167 species were collected (Ødegaard, 2003). Out of this material 2,561 host observations of 697 beetle species were recorded as feeding observations or inferred from probability-based methods (Fig. 98). Lianas appear to be very important growth forms of plants for the maintenance of species richness at this site (Ødegaard, 2000a). Lianas and trees were hosts for a similar number of phytophagous beetle species, but the beetles associated with lianas were more host-specific than those associated with trees. For instance, a large group of virtually unknown weevils survive by scraping the tendrils of lianas that weave through the canopy. These are important findings in the context of estimating global species richness of arthropods, because previously trees have been regarded as the only hosts of importance in tropical forests.

The average host specificity for the phytophagous beetles in this forest in Panama is estimated to range from 7-10% if the forest consists of between 300 and 550 species of trees and lianas, i.e. fewer than one out of ten species are on average monophagous in the beetle community. The species richness of phytophagous beetles in the same forest is estimated to contain 1,600-2,000 species (Ødegaard *et al.*, 2000). These results were used to revise host specificity-based estimates of global arthropod species richness. It is concluded that the higher estimates of 30-100 million species of tropical arthropods are not tenable. By way of comparison, the revised estimate gives approximately 5 million species, which resembles the results of other independent estimation methods. However, uncertainty is still too high for promoting a confident conclusion on the number of species existing on the planet (Ødegaard, 2000b).

A comparative study of 52 plant species from the San Lorenzo crane site yielded about 40% more beetle species than in the dry forest. The beetle fauna at this site was even more host specific than in PNM. Lianas did not dominate in the wet forest but their beetle faunas were more specific than on trees, confirming the results from the dry forest. The species composition in PNM and SL was rather distinct as only 12% of the total number of species was common to both sites (F. Ødegaard, unpubl. data).

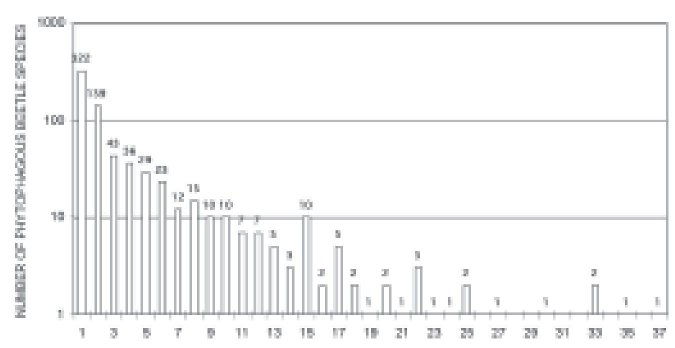

Fig. 98. Distribution of diet richness of 697 phytophagous beetle species associated with 50 plant species in a tropical dry forest in Panama. The number of beetle species utilizing 1, 2, 3,..., 50 host plants is shown. Monophagous species dominate (322 sp.) while the most generalized species feeds on 37 of the 50 plant species.

Milton García (University Santa Maria La Antigua and STRI, Panama) has also studied the beetle fauna of the tree *Luehea seemannii* (Tilliaceae) with the crane at PNM. This tree species is famous for being the primary focus of Terry Erwin's canopy fogging in Panama, which led to a controversial estimate of 30 million insect species on Earth (Erwin & Scott, 1980; Erwin, 1983). García's study, which could be performed *in situ* in the canopy with the crane as opposed to Erwin's foggings carried out from ground level, highlighted that only a fraction of beetle species collected on this tree was effectively able to feed on its foliage. Most beetle species had no specific relationships with *Luehea seemannii* and could be considered as transient (García, 1999).

Vertical stratification of insects

Yves Basset & Héctor Barrios

David Roubik studied the vertical stratification of euglossine bees by placing baited traps at different heights with the PNM crane. Few faunal differences were observed between the upper canopy and the understorey. However, two nocturnal bee species consistently foraged within the upper canopy and larger euglossine bees showed a tendency to forage high. These observations were directly related to their capacity to reduce heat loss during flight as compared to smaller bees (Roubik, 1993). Roubik also showed that many bee species learn which layer of the forest is most rewarding with respect to flowers and keep returning to this layer. For some bee species this stratum fidelity changes seasonally. Thus these bees forage in the canopy during the dry season when trees and lianas flower profusely and in the understorey during the rainy season when shrubs and treelets reproduce.

In contrast, patterns of vertical stratification for insect herbivores (leaf-chewers and sap-suckers) appear to be more evident. Three studies compared the herbivore fauna feeding on seedlings/saplings in the understorey and conspecific mature trees in the canopy. Two studies were performed at PNM and one at SL, and they all converge to the same conclusions. The study in SL targeted herbivores associated with 25 saplings and 3 conspecific mature trees of *Pourouma bicolor* (Cecropiaceae). A similar area of foliage (ca 370 m^2) was surveyed from both saplings and trees but samples obtained from the latter included three times as much young foliage than the former. Arthropods, including herbivores and leaf-chewing insects with a proven ability to feed on the foliage of *P. bicolor* were 1.6, 2.5 and 2.9 times more abundant on the foliage of trees than on that of saplings, respectively. The species richness of herbivores and proven chewers were 1.5 (n = 145 species) and 3.5 (n = 21) times as high on trees than on saplings, respectively. Many herbivore species preferred or were restricted to one or other of the host stages. Host stage and young foliage area in the samples explained 52 % of the variance in the spatial distribution of herbivore species (Basset, 2001b).

Two similar studies were performed at PNM on *Luehea seemannii* and *Castilla elastica* (Moraceae). For the latter, 2,000 understorey saplings and 12 canopy trees were surveyed. Sample sizes in the canopy and understorey were equal; amounting, in both cases, to 364 m^2 of leaf area surveyed. Arthropod abundance was significantly higher in the canopy than in the understorey. A total of 120 morphospecies of insect herbivores were collected from both matures trees and saplings. For a similar leaf area sampled, insect herbivores were 19 times more abundant and 1.6 times more species-rich on the foliage of mature trees than on that of saplings. Herbivore species found on both saplings and trees comprised only one leaf-chewing species (Chrysomelidae) and 16 sap-sucking species (mostly Tingidae, Cicadellidae and Membracidae; Barrios, 2003).

Insect herbivory in rain forests is usually restricted to young, more palatable leaves, production and palatability of which can be drastically affected by light regime, thus affecting insect foraging patterns. This limitation may be particularly important for leaf-mining and gall-making insects. Hence, it is expected that both insect abundance and diversity differ between forest layers. Abundance and diversity of leaf-mining and gall-making insects was compared at the PNM and SL crane sites. Every 15 days during two consecutive years, 258 host plants were sampled at both the understorey and canopy levels at both sites. At both sites, the canopy fauna is more diverse (145 out of 258 species) than the understorey fauna. Only two out of 137 species of leaf-miners (1.5%) and one out of 109 gall makers (0.9%) are common to both levels, which confirms the high specificity of insect populations to specific vertical strata within the forest (Medianero *et al.*, in press).

Adult chrysomelids (leaf beetles) were surveyed with similar sampling effort by beating and flight-interception traps (FIT) in the canopy and understorey of the PNM and SL sites. Beating and FIT data yielded similar results and included 5412 individuals representing 269 species. At both sites, chrysomelids were significantly more species-rich in the canopy than in the understorey. The proportion of species shared between the two study sites was 20%, whereas 11% and 27% of species were shared between the canopy and understorey of the wet and dry sites, respectively. Thus, stratification was more marked at the wet site than at the dry site. This result may relate to differences in forest physiognomy (a tall and closed canopy at the wet site) and to the high interconnectivity via lianas between the understorey and canopy at the dry site (E. Charles & Y. Basset, unpubl. data).

Eventually another project contrasted the vertical distribution and the plant use at San Lorenzo of two different guilds of herbivores: leaf-chewing Curculionoidea (weevils) and sap-sucking Membracoidea (treehoppers). The data are largely congruent with the other studies mentioned above but point out that taxa with different life-histories may be distributed differently along the vertical profile of the rainforest. In this study sun-loving treehoppers were principally collected in forest gaps in the understorey and the proportion of the fauna shared with the canopy was higher than that for weevils (Y. Basset & H. Barrios, unpublished data).

These various studies suggest that the higher availability of food resources, such as young foliage, in the canopy than in the understorey, perhaps combined with other factors such as resource quality and enemy-free space, may generate complex gradients of abundance and species richness of insect herbivores in wet closed tropical forests.

Biotic interactions

Herbivory and seed predation

S. Joseph Wright & Mirna Samaniego

Insects, vertebrates and pathogens that consume leaf tissue have a tremendous impact on vegetation. Due to the inaccessibility of the upper forest strata, levels of herbivory in the canopy of tropical forests where more than 90% of forest leaves are concentrated are virtually unknown. A survey of canopy herbivory levels was initiated from the PNM crane beginning in November 1992. Levels of herbivory were unexpectedly low. The mean proportion of leaf area consumed by herbivores averaged just 8.3% over the lifetime of the leaves of the nine most common canopy tree and liana species. The canopy herbivory levels observed here average 67% lower than understorey herbivory levels observed in nearby forests on Barro Colorado Island and elsewhere in the tropics. Future work will explore the reasons for low herbivory levels in the canopy. Hypotheses to explain low canopy herbivory include high levels of plant defenses, high levels of predation on herbivorous insects, and/or an adverse impact of the canopy environment (i.e., low humidity and high temperatures) on herbivorous insects. Predator exclosure experiments and shading experiments to ameliorate the canopy environment have been initiated to test the latter two hypotheses. Plant defenses against herbivores include a wide variety of secondary compounds that are toxic to herbivores but potentially useful to humans. Examples include caffeine, strychnine, pyrethrin, cocaine and morphine. Canopy leaves with low levels of herbivory will be screened for active secondary compounds. The observed canopy herbivory levels will also be incorporated into carbon acquisition models. These models will scale from leaf-level processes to their canopy-level consequences. Herbivory was initially expected to be a critically important phenomenon in these models, however, the low observed rates of herbivory now suggest otherwise.

A different study aimed at (i) identifying the consumers of reproductive structures of canopy trees, lianas and epiphytes at PNM; (ii) assessing the percentage of each crop that is attacked; and (iii) determining the degree of specialization of insects on single host plant species. The fates of reproductive structures of *Anacardium excelsum*, which is an important timber species throughout its range, are illustrative. Sixty per cent of the flower buds are lost to the larvae of an unidentified species of Lepidoptera (butterfly or moth). Flowers potentially have both male and female functions. However, 89% of the flowers are female sterile due to predation by an unidentified thrip and by the Lepidoptera larvae mentioned previously. Fifty-four per cent of pollen is also killed by thrips and/or environmental conditions such as drought. Eighty-five per cent of the ovules that are fertilized are attacked and killed by the invasive, air-borne fungus *Fulvia fulva* (Cooke) Ciferri. Thirty-three per cent of the fertilized ovules are also killed by the larvae of an unidentified species of scarab beetle and by the larvae of a second unidentified Lepidoptera. These larvae are in turn parasitized by an unidentified species of wasp. In sum, the larvae of two species of Lepidoptera and one species of beetle, adults of one species of thrip and one species of fungus collectively kill 99.6% of the flower buds initiated by *Anacardium excelsum*.

Multi-trophic interactions in tropical forest canopies

Sunshine Van Bael

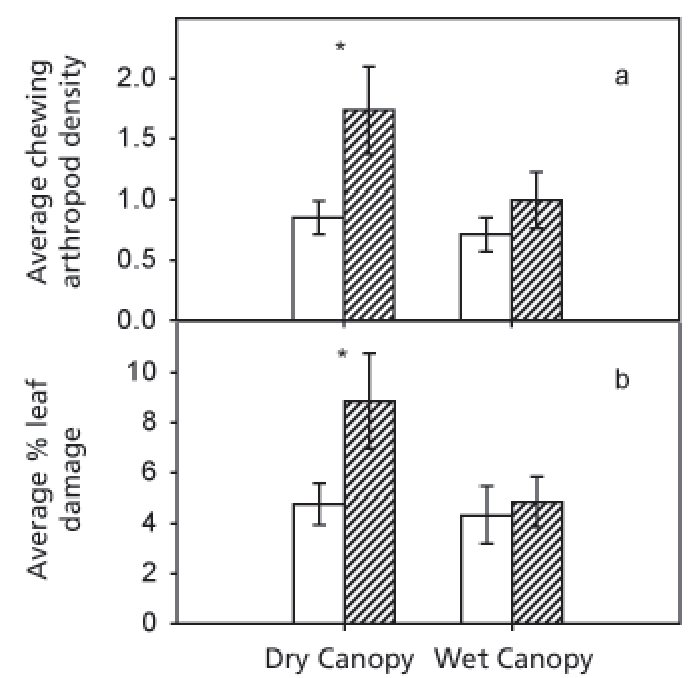

Fig. 99. Average chewing arthropod density and leaf damage for canopy branches, where foliage was inaccessible to birds (hatched bars) and where birds foraged (open bars). a) Chewing arthropod density (no./m^2 leaf area) averaged over the wet season (May-Dec.); b) % leaf damage at the end of the wet season (Dec.-Jan.). Error bars indicate one standard error. * $p<0.05$.

For decades, ecologists have debated the circumstances under which a predator limits its prey's consumption of organisms in lower trophic levels - a set of species interactions referred to as a predator-driven trophic cascade. Experimental tests have shown that insectivorous birds limit arthropod abundances and decrease damage to plants, but the few previous tests have been conducted in relatively low diversity settings such as temperate forests (Atlegrim, 1989; Marquis & Whelan, 1994) or agricultural systems (Greenberg *et al.*, 2000). To address whether trophic cascades occur in diverse, tropical forest canopies, I used canopy access to experimentally exclude birds and bats from canopy branches. I then compared arthropod densities and damage on foliage that was accessible to predators and inaccessible to predators. With the availability of two cranes in Panama, I was able to examine the effects of vertebrate predation across two Neotropical forests that differ in rainfall and species richness. Indeed, the results differed from site to site. At the less diverse, dry forest site, arthropod densities were significantly higher and leaf damage increased by 85% on foliage that was inaccessible to vertebrate predators (Fig. 99). In contrast, few effects of a vertebrate-driven trophic cascade were observed in the canopy of the diverse, wet forest. In general, foliage defense via vertebrate predators was greater for fast-growing, sun-loving tree species than for slow-growing, shade-tolerant tree species. These results have conservation implications as projected trends in habitat loss predict the decline and local extirpation of many bird species. With decreased defense from vertebrates, tree crowns will suffer increased damage levels, which may act as a persistent drain on the photosynthetic ability, growth (Marquis & Whelan, 1994), and eventually the fitness of canopy trees.

Pollinators in tropical canopies

Shoko Sakai & David W. Roubik

Formerly, biologists believed that most plants in tropical forests, which typically display high species richness and low population density of each species, reproduced through self-fertilization. In fact, the prevalence and the importance of outcrossing have been only recognized recently, even in tropical forests. In most tropical plants, outcrossing is achieved by animal pollen vectors, such as bees, beetles, birds, and bats, which visit flowers for their foods (pollen, nectar) or other resources such as resin, a material used by some bees to make their nests. Since such plant-pollinator interactions are thought to contribute to the increase and maintenance of biodiversity, information on pollination biology is essential for forest conservation.

However, studies on pollination biology in tropical forest canopies are limited because of difficulty of access. Studies using canopy cranes have discovered interesting pollination mutualisms, in which plants provide brood sites for their pollinators. *Castilla elastica* (Moraceae) at PNM is pollinated principally by thrips. The thrips reproduce and increase rapidly on the plants, and are dispersed by wind from canopy branches (Sakai, 2001). *Aristolochia* spp. (Aristolochiaceae) at the same site have similar mutualistic relationships with dipteran pollinators (Sakai, 2002b). On the other hand, many other plant species have less specialised relationships with their pollinators, resulting in a complicated network of interactions. Certain canopy studies focus on factors affecting this network and their outcomes for the genetics and species diversity of plants.

Recently, stability and specificity of relationships between plants and pollinators, and close adaptation of plants to particular pollinators, has been called into question (e.g. Johnson & Steiner, 2000). Ecological relationships seem rather specialised and stable among understorey plants of tropical forests (e.g. Kress & Beach, 1994; Kato, 1996; Sakai *et al.*, 1999). On the other hand, the relationships are looser in upper layers. Roubik *et al.* (2003) studied ecological certainty using forest canopy observations of insects visiting flowers, and collections of thrips in flowers fallen on the ground, at four lowland sites in central Panamanian forests, including Parque Natural Metropolitano and Parque Nacional Soberania. Thrips and bees were the principal flower visitors and potential pollinators for 30 plant species monitored for two or three sequential flowering seasons. Thrips in general shifted greatly in abundance from year to year for half the plant species, but were (as a group) consistently associated with host plants. For example, *Frankliniella parvula* (Thripidae) remained the dominant species on *Gustavia superba* (Lecythidaceae). For bees and other visitors, the observed species remained as dominant flower visitors for two or three seasons in half of the study plants. In contrast, many plants possessed loose pollination niches and the naturalised African honeybees had a prominent role in their visitation. Specialised flowers pollinated by large bees, however, had the least variable pollinator species and the largest variance among individual species, that is, the highest individual bee species dominance. The study concluded that loose niches were a quantitative and common phenomenon, and they often involved generalist plant-pollinator relationships.

Biotic responses to a changing environment

Elevated CO_2

Klaus Winter

Mature trees represent most of forest carbon. Understanding how these mature trees respond to elevated CO_2 with respect to their rate of photosynthetic carbon gain is therefore important. Nonetheless, few studies have attempted to investigate the effects of elevated CO_2 in mature forest stands because of the difficulties involved in exposing whole trees to such concentrations and also accessing the canopy. Hence, the effects of atmospheric CO_2 enrichment on mature trees in their natural environment are largely unknown. Körner and Würth (1996) experimented with a new and inexpensive technique which can be used *in situ* to address some key physiological questions related to the CO_2 problem. Small, light-weight cups mounted on the lower side of rigid leaves at the top of tall trees at PNM were supplied with CO_2-enriched air derived from a low-technology air mixing device utilizing forest floor CO_2.

The accumulation of non-structural leaf carbohydrates is one of the most consistent plant responses to elevated CO_2. It has been found in both fast-and slow-growing plants and is largely independent of the duration of exposure. Changes in leaf quality are thus to be expected, irrespective of other plant responses to atmospheric CO_2 enrichment. However, there is no experimental evidence from tropical forests, the biome with the largest biomass carbon pool. We reported *in situ* responses of mature tropical trees to a doubling of CO_2. Individually CO_2-enriched leaves on 25 to 35m tall forest trees living at 26-35°C can be assumed to experience little sink limitation, and so, may be expected to exhibit no or very little carbohydrate accumulation. We tested this hypothesis using the leaf cup method on leaves accessible via the PNM crane. We also investigated the influence of the leaf-specific light regime, another possible environmental determinant of leaf carbon gain and mobile leaf carbohydrates. Total non-structural carbohydrates (TNC) reached a new steady state concentration after less than 4 days of exposure to twice ambient CO_2 concentration. Against expectation, all four tree species investigated (*Anacardium excelsum*, *Cecropia longipes*, *C. peltata*, *Ficus insipida*) accumulated significant amounts of TNC (+ 41 to + 61%) under elevated CO_2. The effect was stronger at the end of the daylight period (except for *Ficus*), but was still significant in all four species at the end of the dark period. In contrast, neither artificial nor natural shading affected leaf TNC. Taken together, these observations suggest that TNC accumulation reflects a tissue response specific to elevated CO_2, presumably unrelated to sink limitations. Thus, leaves of tropical forests seem not to be an exception, and will most likely contain more non-structural carbohydrates in a CO_2- rich world (Würth *et al.*, 1998).

Further, small open-top chambers were used to enclose branchlets that were at a height of between 20 and 25 m in the canopy of the tree species *Luehea seemannii* at PNM. Elevated concentrations of CO_2 increased the rate of photosynthetic carbon fixation and decreased stomatal conductance of leaves, but did not influence the growth of leaf area per chamber, the production of flower buds and fruit nor the concentration of non- structural carbohydrates within leaves. The production of flower buds was highly correlated with the leaf area produced in the second flush of leaves, indicating that the branchlets of mature trees of *Luehea seemannii* are autonomous to a considerable extent. Elevated levels of CO_2 did increase the concentration of nonstructural carbohydrates in woody stem tissue. Elevated CO_2 concentration also increased the ratio of leaf area to total biomass of branchlets, and tended to reduce individual fruit weight. These data suggest that the biomass allocation patterns of mature trees may change under future elevated levels of CO_2. Although there were no effects on growth during the experiment, the possibility of increased growth in the season following CO_2 enrichment due to increased carbohydrate concentrations in woody tissue cannot be excluded (Lovelock *et al.*, 1999).

Cloud cover limits photosynthesis and growth of a rainforest canopy tree

Eric A. Graham

Global dimming refers to an observed reduction of 2.7% of solar radiation reaching the Earth's surface recorded each decade since the 1950s (Stanhill & Cohen, 2001). Heavy tropical cloud cover can also reduce radiation reaching fully exposed canopy leaves by 90% or more and limit their carbon uptake through photosynthesis (Mulkey *et al.*, 1996a). The implications for global carbon uptake are significant if carbon uptake by tropical trees is limited by year-to-year variation and decadal scale changes in cloud cover and irradiance. As an experimental test of light limitation by cloud cover during tropical rainy seasons and by the unusually heavy cloud cover associated with the 1998-99 La Niña event, we installed high-intensity lamps above the PNM forest canopy during 1998-2000 (Graham *et al.*, 2003). We supplemented light levels artificially whenever cloud cover reduced photosynthetic photon flux density (which refers to those wavelengths of light involved in photosynthesis or 400-700 nm, PPFD) for two replicate adult *Luehea seemannii*. Supplemental illumination only compensated partially for natural reductions in PPFD. We studied the response to augmented light of leaf-level photosynthesis, branch-level sap flow, leaf- and branch-level carbohydrate storage, branch extension growth, and fruit production.

During a representative cloudy day, photosynthesis increased with augmented light from the lamps for randomly chosen leaves (Fig. 100). Daily net carbon gain increased by an average of 18.4% (from 270.6 to 320.4 mmol m^{-2} d^{-1}) for exposed canopy leaves during the La Niña event. In addition, fully sun-exposed canopy leaves acclimated to the augmented illumination through an increase in photosynthetic potential. Branch extension growth, the number of new nodes, and the number of reproductive buds were all greatest on illuminated branches, intermediate for non-illuminated branches on illuminated trees, and least for control trees. The observed acclimation of photosynthetic potentials suggests that this widespread tropical tree species responds physiologically to seasonal and interannual variation of solar irradiance. Year-to-year climate variability may thus influence net CO_2 uptake and growth through variation in solar irradiance caused by clouds and atmospheric particulates (Roderick *et al.*, 2001) coupled with the photosynthetic flexibility of tropical canopy species.

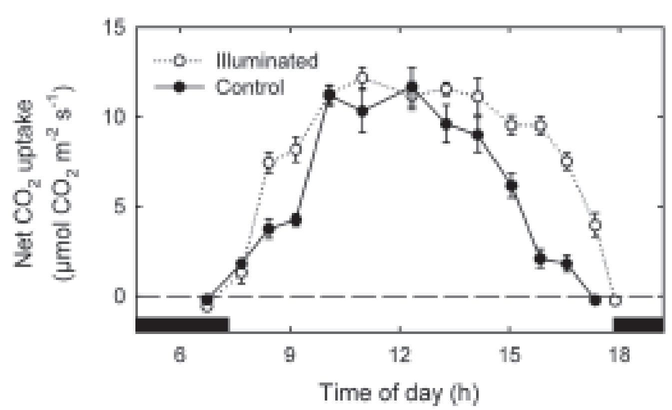

Fig. 100. Instantaneous net CO_2 uptake for illuminated leaves (open symbols) and non-illuminated leaves on experimental plus control trees (closed symbols). Data are means ± SE (n=10 leaves per treatment). Dark bars indicate when lamps were extinguished (modified from Graham *et al.*, 2003).

Isoprene emission

Manuel T. Lerdau

Isoprene, a 5-carbon compound produced by plants during the daytime, is the single most abundant reactive hydrocarbon in the lower atmosphere (Lerdau *et al.*, 1997). Unlike the reactive oxides of nitrogen, which are produced primarily through fossil fuel combustion and soil microbial activity, isoprene is produced only by plants and is a primary way in which biological processes influence the chemistry of the lower atmosphere. Isoprene may react with these oxides of nitrogen to produce ozone in the lower atmosphere, where ozone is an important pollutant. Isoprene may, alternatively, react with other oxidizing

chemicals in the atmosphere to remove ozone. In addition, the oxidation of isoprene in the atmosphere can increase the atmospheric lifetime (and hence strength as a greenhouse gas) of methane. Finally, isoprene emission from forests can equal the net storage of carbon by those forests and thus determine whether or not forests act as net sources or sinks of carbon.

Global models of isoprene emissions are needed in order to understand both atmospheric chemistry and carbon storage in ecosystems. To date these models have been based on studies of plants in temperate zones. It has been known for over twenty years, however, that tropical forests are the source of over 70% of the world's isoprene. Starting in 1995 researchers from the State University of New York at Stony Brook and the International Institute of Tropical Forestry in Puerto Rico have been studying isoprene emission at both the SL and PNM cranes. These studies have focused on both identifying and quantifying the crucial controls over isoprene emissions and on using these controls in improved global-scale models of emissions (Lerdau & Throop, 1999).

From detailed studies of the impacts of light and temperature upon emissions, we have demonstrated that the algorithms describing emission controls for temperate plants are not appropriate for tropical ones (Keller & Lerdau, 1999). Specifically, whereas temperate plants show isoprene emissions that saturate at approximately one half of full sun intensity, isoprene emission from tropical trees does not show light saturation. In addition, isoprene emission from tropical trees saturates at a higher temperature than does emission from temperate trees. These results mean that previous models of isoprene emissions from tropical forests may have underestimated emissions by 20%-50%. In other words, tropical forests play a much larger role in global atmospheric chemistry than previously supposed, especially in controlling the dynamics of ozone and methane in the lower atmosphere.

Studies of the physiological relationship between isoprene emission and photosynthesis have demonstrated that the enzymatic capacity of both processes are well correlated (Lerdau & Throop, 2000). This correlation allows one to predict isoprene emission based on photosynthetic capacity. Connecting photosynthetic capacity to isoprene emission allows one to apply satellite techniques developed for photosynthetic capacity estimations to predictions of isoprene emissions across large spatial scales. These satellite approaches are currently being used to develop and test new global models of emissions. These emissions models can, in turn, be used to predict the influence of tropical regions on atmospheric chemistry and climate and how that influence might change in response to climatic and land-use changes.

Plant uptake of reactive nitrogen

Jed P. Sparks

Gaseous nitrogen oxides (principally NO, NO_2, HNO_3 and organic nitrates) in the lower atmosphere primarily result from microbial production of NO in the soil and from anthropogenic biomass and fossil fuel combustion. These compounds are important participants in atmospheric chemistry and their concentration in the atmosphere controls the production of tropospheric ozone (O_3). Ozone is usually associated with the beneficial role it plays high in the atmosphere (the stratosphere) blocking ultraviolet radiation from the sun. However, low in the atmosphere (the troposphere) ozone is a highly reactive molecule that reacts with, and damages, the biological membranes found in both plants and animals. Additionally, chemical reactions involving nitrogen oxides in the atmosphere also lead to the acidification of precipitation and deposition of harmful nitrogen compounds to natural ecosystems worldwide.

Preliminary measurements have suggested that up to 60% of the soil emitted reactive nitrogen is assimilated by the overlying canopy. Current atmospheric models, however, tend to ignore the role of plant canopies, and instead focus on soil emission rates of reactive nitrogen as the primary biogenic input to tropospheric chemistry. We have studied intensely the factors influencing the capacity of leaves to assimilate reactive nitrogen at SL in the Republic of Panama (Sparks *et al.*, 2001). To date, we have demonstrated interspecific differences in the leaf level uptake rates of NO_2 (Fig. 101) and found these rates were sensitive to stomatal conductance (i.e., how open or closed the leaf stomata are to the atmosphere), the amount of photosynthetic enzymes in the leaf, and the concentration of NO_2 in the atmosphere. Interestingly, leaves appear to have the ability to both take up and emit reactive nitrogen from the leaves depending on the concentration of NO_2 in the surrounding atmosphere (Table 23). The ambient concentration outside the leaf above which uptake will occur is referred to as the compensation for NO_2. When scaled to the entire canopy, soil NO_2 emission rates to the atmosphere were estimated to be increased **or** decreased by ~19% by the overlying canopy depending on the ambient NO_2 concentrations. These promising results have led to expanded studies of leaf assimilation of NO_2 and other reactive nitrogen compounds in both tropical and temperate forest ecosystems. In the future as humans increase the level of reactive nitrogen in the atmosphere through pollution and biomass burning, understanding nitrogen cycling in forests will help us to predict the ultimate sustainability of natural, urban and agricultural ecosystems worldwide.

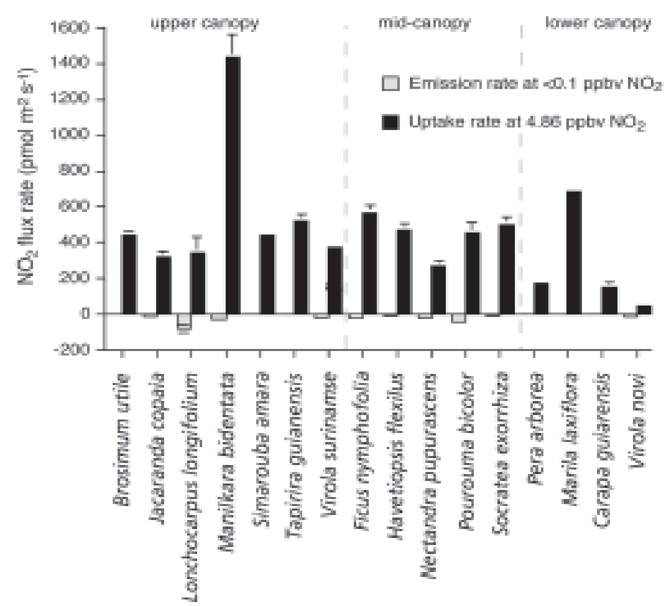

Fig. 101. Leaf NO_2 uptake and emission rates measured for sixteen tropical tree species. Each bar represents the mean of < 15 - 45 > measurements. Species are separated by dashed lines indicating relative canopy location. Error bars = ± 1 S. E. Error bars are not shown if smaller than the symbol used.

Table 23. Compensation points with respect to NO_2 (Γ_{NO2}; ppbv, F = 38.575, p < 0.0001, n = 10), average maximum photosynthetic rate (A_{max}; µmol CO_2 m^{-2} s^{-1}, F = 19.343, p < 0.0001, n = 9-34), and average leaf area specific nitrogen content (N_{leaf}; mmol N m^{-2}, F = 190.267, p < 0.0001, n = 8-130), for five tropical tree species. Letters indicate significant differences (SNK test, p < 0.05).

Species	Γ_{NO2}	A_{max}	N_{leaf}
Brosimum utile	0.52^a	7.75^b	157^a
Ficus nympholia	0.85^b	10.03^c	151^a
Nectandra pupurescens	1.09^c	4.12^a	148^a
Virola novi	1.23^c	4.08^a	241^c
Manilkara bidentata	1.60^d	8.09^b	224^b

Tropical forest phenologies and remote sensing

Stephanie A. Bohlman

Remote sensing of the world's forests has become increasingly important for various ecological applications including inputs to biogeochemical cycling (Field *et al.*, 1995). An important advantage to using remote sensing over point field studies is that it can provide continuous data on ecosystem variables that cannot readily be collected from the ground and it can monitor these parameters through time. Most field studies linking biophysical characteristics of the canopy to remotely sensed data have been performed in crop and temperate ecosystems (Gamon *et al.*, 1995). Few studies have been conducted that test the current interpretations of remotely sensed data in tropical forest canopies because of the difficulty in accessing the canopy. Our work at the Panama canopy cranes has provided important insights into how remote sensing can be used to measure deciduousness (Condit *et al.*, 2000), canopy light interception, and canopy structure and to identify tree canopy species (Cochrane, 2000) in seasonal tropical forests.

Remotely sensed images, which measure the amount of energy reflected from the forest canopy, track changes in leaf density between the wet and dry seasons, but only in the upper canopy, not the whole canopy profile. Remote sensing methods, such as the ubiquitous Normalized Difference Vegetation Index (NDVI) or spectral mixture modeling, can effectively quantify deciduousness in individual trees crowns, as well as the percentage of deciduous trees over the entire landscape of the Panama Canal watershed. Deciduousness in turns affects light absorption and carbon cycling in the canopy. Studies at the crane sites, where we can measure canopy light absorption in detail, show that dry season deciduousness affects the amount of light being absorbed, and thus available for photosynthesis, mostly in the upper strata of the canopy. Overall light absorption by the whole canopy remains high despite deciduousness in the overstorey. For carbon models that use remote sensing indices as a measure of canopy light absorption, the canopy should be represented by at least two layers, with only the upper strata receiving input from remote sensing data. Finally, work at the PNM canopy crane shows the potential for mapping individual species (Fig. 102). In the secondary forest of PNM, which has relatively low canopy species diversity and a large variety of phenological patterns in response to the severe dry season, we were able to map several tree species accurately in the dry season.

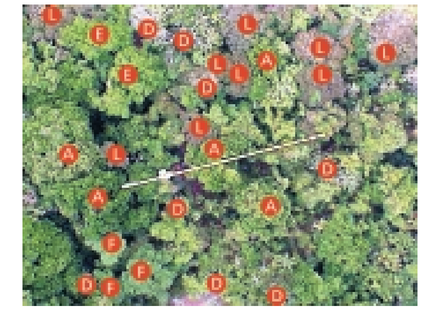

Fig. 102. Dry season, enhanced true colour image of the PNM canopy crane, showing contrast between different species. Letters indicate different species: A=*Anacardium excelsum*, D=*deciduous species*, E=*Enterolobium cyclocarpum*, F=*Ficus insipida*, L=*Luehea seemanii*.