Accessing the Canopy

Assessment of Biological Diversity and Microclimate of the Tropical Forest Canopy: Phase I

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SMITHSONIAN TROPICAL RESEARCH INSTITUTE

PARQUE NATURAL METROPOLITANO

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Collaborators

This report has been prepared by Dr S. Joseph Wright, principal investigator at the Smithsonian Tropical Research Institute, and consultant Marti Colley. Dr Wright assumed project directorship from the late Dr Alan Smith in June 1992.

In addition, Drs Stephen Mulkey, Klaus Winter, Kaoru Kitajima and Jorge Illueca provided valuable input.

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Introduction

by Elizabeth Dowdeswell, Executive Director of UNEP

Tropical forest canopies are thought to contain the greatest species diversity on earth, and yet we know so little about them. Because of the inaccessibility of most canopies, they are among the least explored of habitats. Much of the research that has been undertaken in the past has been on newly felled trees. However, UNEP's project *Assessment of Biological Diversity and Microclimate of the Tropical Forest Canopy* is a new venture to examine forest canopies by means of a tower crane.

UNEP is working closely with centres of excellence such as the Smithsonian Tropical Research Institute (STRI) to explore and assess the influence that forests have on both regional and global climates. At the local level, scientists are looking at plant and animal life in the canopies: their interdependence, their reactions to changes in the microclimate, their behaviour and much more. As many of the species of plants and animals are not found on the ground, scientists will be gathering new and valuable information which will be made available to the Secretariats of the Convention on Biological Diversity and the Framework Convention on Climate Change.

This initiative, to access tropical forest canopies by using tower cranes is just the beginning, and yet it has exceeded expectations. Our thanks must go to the many scientists who diligently worked under the skillful guidance of STRI and to the generous support of the governments of Finland, Germany and Norway as well as STRI, the Smithsonian Associates, the Smithsonian's Scholarly Studies and Visiting Investigators Programs, the Andrew W. Mellon Foundation, the National Science Foundation of the US, and the German Space Agency.

Accessing the Canopy is the first major report of the project's findings and it goes a long way towards showing us that the protection of the world's biodiversity can only really be accomplished if we continue to explore, assess and preserve it.

Introduction

by Ira Rubinoff, Director
Smithsonian Tropical Research Institute

Because of its inaccessibility, the canopy of a forest remains among the least explored of habitats. For many, only newly felled trees provide an opportunity to examine the rapidly growing upper section of a tree where most of the interchange of gases between the geosphere and the biosphere occurs. Our ability to study the influence that forests have on both regional and global climates is impeded by this inaccessibility and, of course, the study of epiphytes and most of the invertebrate and vertebrate organisms associated with forest canopies is likewise inhibited. This report summarizes the studies of a tropical forest canopy facilitated by the use of a construction tower crane. This crane has been permanently installed in a tropical forest for the exclusive long-term use of scientists. Scientists from more than 12 countries have participated in the pilot studies.

On-going studies include examinations of biodiversity, biotic interactions, energy exchange, microclimate and its effects on plant responses to variation, plant responses to variation in carbon dioxide and ultra-violet radiation.

The forest canopy access system has proved to be feasible and its immediate success in supporting research has exceeded our expectations. The crane is being used to its maximum capacity and there is a need for additional cranes installed in other types of tropical and temperate forests. The costs of these construction crane based access systems are great but nowhere approach that of a single space probe designed to describe the atmosphere of a distant planet.

We are particularly grateful to the Patronato of the Metropolitan Nature Park of the Republic of Panama for making the exclusive use of this section of forest available to science, to the Governments of Finland, Norway, and Germany who have helped finance these studies with donations through the Clearing House of the United Nations Environment Programme, and to members of the Smithsonian Institution's National Board whose individual financial donations made the final purchase of the crane a reality.

The canopy access initiative represents an excellent example of innovative use of technology developed for one industrial purpose to address important scientific questions. It also represents an example of the effective cooperation between the Smithsonian Tropical Research Institute, an organization with a pan-tropical mandate, the Government of Panama, the United Nations Environment Programme, and three developed nations with the resources and the vision to apply them to global problems beyond their borders. The participants also realize that the protection of the world's biodiversity cannot be accomplished without further understanding of how it works. Environmental management schemes developed without concomitant research often have led to sterile or counterproductive results. We must be prepared to admit that despite the many technological advances of the 20th century, we still do not understand fundamental processes on this planet.

Preface

This report responds to section 4.1(b) of the document elaborated for the joint United Nations Environment Programme/Smithsonian Tropical Research Institute project FP/610591-01 (2962) entitled *Assessment of Biological Diversity and Microclimate of the Tropical Forest Canopy: Phase 1.*

The project commenced in November 1990 and coincided with the international negotiations that led to the United Nations Convention on Biodiversity and the Framework Convention on Climate Change (1992). Both conventions recognised that tropical forests are among the world's most productive and biologically diverse habitats, that tropical forests play a significant role in regulating global climate[2], that tropical forests are disappearing at an alarming rate[3], and that research efforts need to be greatly and rapidly increased in order to establish essential baseline information while intact forests remain. Research carried out under this project is to be utilized by UNEP to support the implementation of both conventions[4].

The need for tropical forest research is nowhere greater than for the canopy. Biological activity and biodiversity are most concentrated in the uppermost strata of forests. There is more light here than in the shaded understory so that rates of photosynthesis (in which the leaves use energy from the sun to convert carbon dioxide into simple sugars) are more rapid. This permits more rapid production of new leaves, flowers and fruit, which in turn provide food for a diverse community of insects, birds, reptiles and many other animals that pollinate flowers and disperse seeds in the process of feeding. The upper canopy is also the interface between the biosphere and the atmosphere. It is the principal site for the interchange of heat oxygen, water vapour and the principal greenhouse gas, carbon

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[1] See chapter 1, Introduction to Tropical Forests and the Parque Natural Metropolitano.

[2] Nilsson, A., 1992, *Greenhouse Earth*, published on behalf of the Scientific Committee on Problems of the Environment (SCOPE), the International Council of Scientific Unions (ICSU) and UNEP by John Wiley & Sons, England, pp 154.

[3] Between 1950 and 1990 between 30-40% of tropical rainforest disappeared and it is projected that the same amount will disappear over the next 30-50 years. This could mean that some 2 million species (around 200 a day) may also face extinction (*Conserving Biodiversity: A Research Agenda for Development Agencies*, Report of a Panel of the Board on Science and Technology for International Development, US National Research Council, National Academy Press, Washington, DC, Preface, pp v.)

[4] See original project document, section 4.2(c).

dioxide. The forest canopy can therefore have a controlling influence on regional climate and plays an important role in processes of global climate change. Nonetheless, the physical difficulty and danger involved in accessing the tree tops in a dense tropical forest setting has meant that, up until now, the uppermost strata has remained largely unexplored.

Phase 1 of this project tested the feasibility of using a construction crane to access the upper canopy of a section of dry tropical forest in the Parque Natural Metropolitano, Republic of Panama. The success of this canopy access technique is demonstrated not only by the number of international scientists who have used, and continue to use the crane daily (in fact, research projects from the crane are already planned for the next two years) but also by the interest shown by the Norwegian Institute for Nature Research (NINA), the Austrian Academy of Sciences and the National Science Foundation of the USA, all of whom are planning to install similar construction cranes to access forest canopies[5]. Chapter 2 of this report explains how the crane greatly increases the possible range of canopy research and evaluates and compares this method with other canopy access techniques.

Phase 1 of the project also called for tropical forest canopy studies touching on the areas of biodiversity, biotic interactions, canopy energy balances, upper canopy microclimate and its effects on plant performance, physiological responses to variation in atmospheric carbon dioxide, and ultra-violet radiation effects on the upper canopy. Chapters 3 to 8 summarize completed and ongoing research projects in these areas.

Chapter 9 assesses project development against the achievement indicators of short-term objectives presented in section 3.2 of the original project document. The short-term objectives (section 3.1.2) were to: contribute to available data and information on microclimate patterns, canopy ecosystems and tropical taxa; to study the effects of structure and physiology of canopy trees on the transfer of heat and gases between the forest and atmosphere; and to measure the physiological responses of plants to experimental manipulations of the atmospheric environment.

Finally, a future work-plan is proposed in Chapter 10. This builds on the achievements to date and suggests how to improve and expand the project by implementing Phase 2 - to set up two canopy cranes in wetter and more diverse tropical forest sites in Panama. The work-plan also recommends that scientists who have studied tropical forest canopies, conservationists, climate change experts and appropriate UNEP staff be brought together at a conference to be organized jointly by UNEP and STRI and to be held in Panama in 1996. The aim of the conference is to consolidate research findings and methodologies with a view to streamlining research and setting priorities for the years ahead.

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[5] See chapter 9, *Achievement Indicators of Short-Term Objectives.*

Acknowledgments

STRI gratefully acknowledges the timely support of UNEP, the Smithsonian Institution's National Board, and the Governments of Finland, Germany and Norway through UNEP's Clearing House mechanism, all of whom provided funding to purchase the crane and without whom our scientists would never have gotten off the ground! In particular, STRI would like to mention Mikko Pyhala and Dan Rohrman of UNEP who provided welcome assistance and enthusiasm when it was most needed.

STRI would also like to thank the Andrew W. Mellon Foundation, National Science Foundation of the USA, Smithsonian Associates, the Governments of Finland, Germany and Norway, the German Space Agency and the Scholarly Studies and Visiting Investigators Programs of the Smithsonian Institution, all of whom have provided funding for canopy research projects carried out from the crane.

We wish to express our appreciation to the Board and Administration of the Parque Natural Metropolitano of Panama for their support and authorization of the first prototype crane in the Park. They also enthusiastically supported the longer term installation of a new system. We are also grateful for the support of the Park's Game Wardens Force in the continued protection of the crane.

In addition, STRI acknowledges the contribution and innovation of the late Alan P. Smith, former Assistant Director for Terrestrial Research at STRI who, with Michael C. Smith, conceived the original idea to use a construction crane to gain access to the upper canopy. The success of this project is largely due to Alan's exceptional abilities as both a visionary research biologist and an effective administrator. His role in opening up the tropical forest canopy to scientific exploration will be an enduring accomplishment. He is sadly missed.

Chapter 1:

Introduction to Tropical Forests and the Parque Natural Metropolitano

Tropical forests are among the planet's most productive, extensive and biologically diverse habitats. Gross primary production measured as the mass of carbon fixed by plants per unit land area per year is greater for tropical forests than for any other habitat with the exception of some wetlands[6]. Today, tropical forests cover some 6% of all terrestrial lands yet account for 46% of the carbon stored in terrestrial vegetation[6]. This productivity supports the most biologically diverse biota on the planet. Scientists have described some 1.8 million species more than half of which are found in tropical forests[7]. Many more species are undescribed, and it was recently estimated that more than 90% of all species are undescribed arthropods (primarily insects, spiders and mites) living in tropical forests[8].

Both primary production and biological diversity are distributed nonrandomly within tropical forests. From ground level up, tropical forests show five distinct (but overlapping) layers or strata of vegetative growth: herbaceous undergrowth, shrubs, a taller understory of shade tolerant trees and saplings, canopy[9] trees and emergents (i.e., trees that jut above the canopy). Biotic conditions vary radically between the different strata. The upper canopy is directly exposed to intense solar radiation. Mid-day temperatures are 5-8°C higher and relative humidities are 30% lower than on the cooler, shaded forest floor 30 or more metres below. The high light levels promote rapid rates of photosynthesis and production of new leaves, flowers and fruit that sustain the diverse animal community, giving rise to complex plant/animal interactions. The upper canopy is also the interface

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[6] Brown, S. and Lugo, A.E., 1982, The storage and production of organic matter in tropical forests and their role in the global carbon cycle, in *Biotropica,* no. 14, pp 161-187.

[7] Stork, N.E., 1988, Insect Diversity: Facts, Fiction and Speculation, in *Biological Journal of the Linnean Society,* no. 35, pp 321-337.

[8] Erwin, T.L., 1982, Tropical Forests: their Richness in Coleoptera and other Arthropod Species, in *Coleopterists Bulletin,* vol. 36, no. 1, pp 74-74.

[9] *Canopy* here means all the leaves in the crowns of the tallest trees - i.e., those above the understory layer.

between the biosphere and the atmosphere. Leaves are the principal site for the interchange of heat, oxygen, water vapour and carbon dioxide; and canopy trees, lianas and epiphytes account for at least 90% of tropical forest leaves. For these reasons the upper canopy can have a controlling influence on regional climate and plays an important role in processes of global climate change.

Despite the concentration of biological activity in the upper canopy of tropical forests, the upper canopy remains largely unexplored due to the difficulty of access. Traditional techniques provide limited manoeuverability, little safety and virtually no access to the outermost canopy where leaves, flowers, fruits and associated animals are concentrated. The use of a construction crane as a canopy access system described in the following chapter overcomes these limitations.

Widespread habitat destruction lends urgency to research in tropical forest canopies. Humans have removed some 40% of tropical forests world-wide and continue to cut and burn another 76,000 km^2 each year. The potential consequences for global fluxes of heat and carbon will remain a matter of conjecture until baseline measurements become available from the canopies of intact tropical forest. In turn, the impact of increasing atmospheric concentrations of carbon dioxide and possible global climate change on tropical forests will also remain a matter for conjecture until the appropriate experiments are conducted in the uppermost canopy. Tropical forests are also remarkably heterogeneous, and in many regions once extensive forest types have been reduced to small remnant patches (e.g., Brazilian Atlantic forest) or even eliminated (e.g., Pacific dry forest from northern Central America). The potential loss of genetic and species diversity will remain incalculable and effective conservation planning will remain a chimera until patterns of diversity in the critical upper canopy are known.

The Parque Natural Metropolitano[10]

The prototype construction crane is located in the Parque Natural Metropolitano. The Parque comprises an area of 270 hectares (666 acres) and is the only natural, undisturbed park in tropical Latin America located adjacent to a capital city. The Parque Nacional Sendero Las Cruces, a 5 km-wide forest corridor, connects the Parque Natural Metropolitano with the Parque Nacional Soberania, 17 km to the north east. The Parque Nacional Soberania is, in turn, contiguous with the Barro Colorado Nature Monument and the newly-created Parque Nacional Interoceanica. The total area of contiguous protected forests is 370 km^2.

The area now protected in the Parque Natural Metropolitano underwent

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[10] Extracted from the *Plan de Manejo del Parque Natural Metropolitano*, Asociación para la Investigación y Propagación de Especies Panameñas (AIPEP) in collaboration with the Comisión Nacional del Medio Ambiente of the Ministerio de Planificación y Política Económica, 1986.

substantial ecological modification beginning in pre-Colombian times but has remained largely undisturbed for the last eighty years during which time it reverted from abandoned pasture to secondary forest[11]. The Parque supports a dry, deciduous, lowland tropical forest that was once widely distributed along the Pacific coast of Meso-America from Mexico to Panama but that is now largely extirpated south of Mexico with the exception of a few remnant patches in Costa Rica and Panama.

This type of forest is very diverse. In Panama, the upper canopy is 25-35 metres high with emergent trees reaching 40 metres. More than 50 tree species and 20 canopy liana species have been identified beneath the canopy crane. Common tree species include *Calycophyllum candidissimum* (Rubiaceae), *Anacardium excelsum* (Anacardiaceae), *Astronium graveolens* (Anacardiaceae), *Spondias mombin* (Anacardiaceae), *Luehea seemannii* (Tiliaceae), *Antirrhoea tricantha* (Rubiaceae), *Castilla elastica* (Moraceae), *Annona spraguei* (Annonaceae), *Nectandra mexicanum* (Lauraceae), *Enterolobium cyclocarpum* (Leguminosae), and *Cordia alliodora* (Boraginaceae).

Annual rainfall averages 1,740 mm, with most precipitation falling during the rainy season between May and November (figure 1.1). Mean evapotranspiration exceeds mean rainfall by 431 mm during the dry season which begins in December and ends in April or May. The Curundu River and its tributaries which pass through the park are dry in March and April. Mean temperatures average 28°C. Wet-

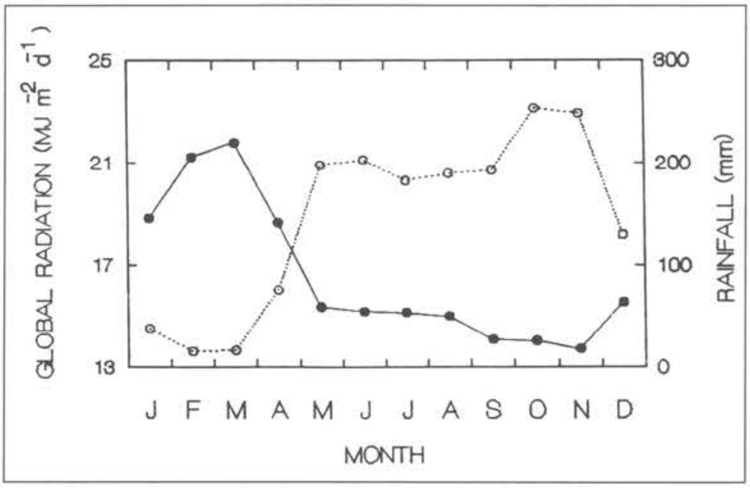

Figure 1.1: Mean monthly rainfall (open circles and dashed line) and global solar radiation in the Parque National Metropolitano, Panama. Note the sharp increase in solar radiation associated with reduced cloud cover during the five-month dry season.

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[11] Illueca Bonett, J., 1985, Demografía Historíca y Ecología del Istmo de Panamá, 1500-1945, Heckadon Moreno, S. and Espinosa, J., (eds), Instituto de Investigación Agropecuaria de Panamá and the Smithsonian Tropical Research Institute.

season cloud cover reduces canopy level solar radiation by 33% between May and November (figure 1.1). The Parque ranges in altitude between 10-138 metres above sea-level. Soils are characteristically of igneous extrusive origin, shallow, clay-like and brownish in colour.

The Parque provides a refuge for a diverse community of vertebrates - including such endangered species as the green iguana *(Iguana iguana)* and the native tamarin monkey *(Saguinus geoffroyi)*. Common mammals include agouti *(Dasyprocta punctata)*, armadillo *(Dasypus novemcinctus)*, northern anteater *(Tamandua mexicana)*, silky or pygmy anteater *(Cyclopes didactylus)*, South-American coati *(Nasua nasua)*, northern raccoon *(Procyon lotor)*, two-toed sloth *(Choloepus hoffmanni)*, three-toed sloth *(Bradypus variegatus)* and squirrel *(Sciurus variegatiodes)*. Tracks of ocelots (*Felix pardalis*) and white-tailed deer *(Odocoileus virginianus)* are occasionally seen along the river banks but sightings are rare. More than 200 bird species have been recorded, including a variety of tinamous, hawks, eagles, kites, parrots, owls, toucans, motmots, puffbirds, woodcreepers, antbirds and many others. Between April and September the Parque Natural Metropolitano is an important resting point for many north-American migratory species.

The Parque has been protected as a recreational and natural environmental area by law since July 1985. It is administered by a *Patronato* (foundation) presided over by the mayor of Panama City and a representative from each of the following organisations: the Institute of Natural Renewable Resources (INRENARE), National Commission on the Environment (CONAMA), Regional Inter-Oceanic Authority (ARI), Association for the Investigation and Propagation of Panamanian Species (AIPEP - a non-governmental organization), Smithsonian Tropical Research Institute, Panama-Pacific Soroptomist Club, United Civic Associations[12], and the Panama Audobon Society[13]. Private sector members have taken the lead in funding the Parque's management plan.

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[12] The last three are representative of civic and private sector organisations.

[13] Representing conservation groups.

Chapter 2:

Evaluation of the Prototype Construction Crane As a Canopy Access System

Background to the Crane

Funded by the Smithsonian Tropical Research Institute (STRI), the first, rented crane was installed in Panama's Parque Natural Metropolitano in late 1990 and measured 30 metres high with a 35 metre-long jib. Initial research results and engineering studies proved that the crane was an effective and safe canopy access method. Consequently, in November 1991 the lease on the crane was extended until April 1992, funded by the Government of Finland through UNEP's Clearing House.

The success of the preliminary research projects carried out from the crane led to STRI's decision to establish a permanent canopy biology programme. The STRI engineer strongly recommended the installation of a new crane to minimise possible safety problems. Consequently, in May 1992 the new, 42 metre-tall crane was leased and installed, still using funds from the Government of Finland. This crane was bought outright on 15 May 1993 for $255,000 with grants from Norway and Germany (administered through UNEP's Clearing House mechanism) and contributions from the Smithsonian National Associates. STRI currently pays the crane operator and maintenance costs out of its operating budget.

Phase I of the Project

Phase 1 of the project was a prototype study to determine the safety and utility of using a construction crane to access the upper forest canopy and to initiate research projects in the following areas: biodiversity; biotic interactions; canopy energy balance; effects of ultra-violet radiation on the upper canopy; upper canopy microclimate and its effects on plant performance; and physiological responses to variation in atmospheric carbon dioxide[14]. Completed and on-going research projects are described in the following chapters.

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[14] As defined in the original project document, Annex II.

Description of the crane

The canopy crane stands 42 metres high and has a horizontal jib 51 metres long (figure 2.1). The forest canopy under the crane ranges from 20-30 metres tall. The crane therefore provides researchers with access to 8,000 m^2 of upper canopy surface, and 28,000 m^3 of forest volume, including some 140 individual canopy trees. Researchers are raised up above, and then lowered into the canopy in a semi-open, capsule-shaped gondola suspended from the crane hook. The gondola is large enough to accommodate up to four investigators (fewer if they have research equipment) but small enough to provide flexible access into the canopy (1.2 m x 1.2 m footprint). Movement of the gondola is controlled by an operator stationed at a vantage point above the load. Separate electric motors adjust the azimuth of the jib, horizontal movements of the gondola along the jib and vertical movements of the gondola below the jib. A radio provides communication between the scientists, crane operator and ground-based staging area.

The total weight load of the fully-laden gondola is well within the crane's safe, maximum, lateral-load carrying capacity (up to 20 metric tonnes, depending on the gondola's distance from the tower). For additional safety and, in the event of mechanical breakdown or power failure, a separate safety line and descending system are available. The crane is not used during heavy rains, lightning storms or in very windy conditions.

The tower has outer dimensions of just 1.6 x 1.6 metres and so intrudes very little into the forest itself. It supports the horizontal jib, counterweights, motors and the operator's cab above the forest. The crane foot can be fixed either to a permanent concrete base (as in the Parque Natural Metropolitano) or, for even wider range, to a base that can move along a wide-gauge railway track.

The construction crane has proven to be a safe, effective and practical way to access the tropical forest canopy. The crane has been operated since September 1990 for up to 330 hours each month without an accident of any kind. The crane provides researchers with far greater scope for investigation, specifically for *in situ* measurements, than was previously possible. In particular, the crane permits repeated access to the tips of branches in the outer and uppermost canopy zone where photosynthesis, plant reproduction and insect life are concentrated and which, until now, has remained largely unexplored.

The crane has two additional advantages over other canopy access techniques. First, there is minimal impact on the vegetation because the gondola and investigators are suspended from above and not from the vegetation itself. As a consequence, phenomena that are disrupted by other canopy access techniques can be studied without interference. A second advantage of the crane is its manoeuvrability, stability and capacity for carrying scientific equipment - particularly heavy equipment - into the canopy.

Table 2.1 compares different canopy access techniques and evaluates their potential use for three types of research: observation, collection and *in situ* measurements and experimentation. Each type of research poses special problems for canopy investigators. Observational research requires sufficient proximity to locate and observe the study organism without disrupting its behaviour. Collections further require contact with the study organism. *In situ* measurements and experimentation are the most demanding, requiring direct manipulation of study organisms in the canopy. The crane has proven to be an excellent canopy access technique for all three types of research.

It is important to note that canopy cranes will complement rather than displace other canopy access methods. Canopy cranes are unique in providing access to extensive areas of the critical outermost canopy and in their ability to bring scientific instrumentation into the canopy. Cranes, however, are relatively expensive and fixed in space. Other, lower cost access technologies that can be moved easily among sites will continue to play an important role in canopy research.

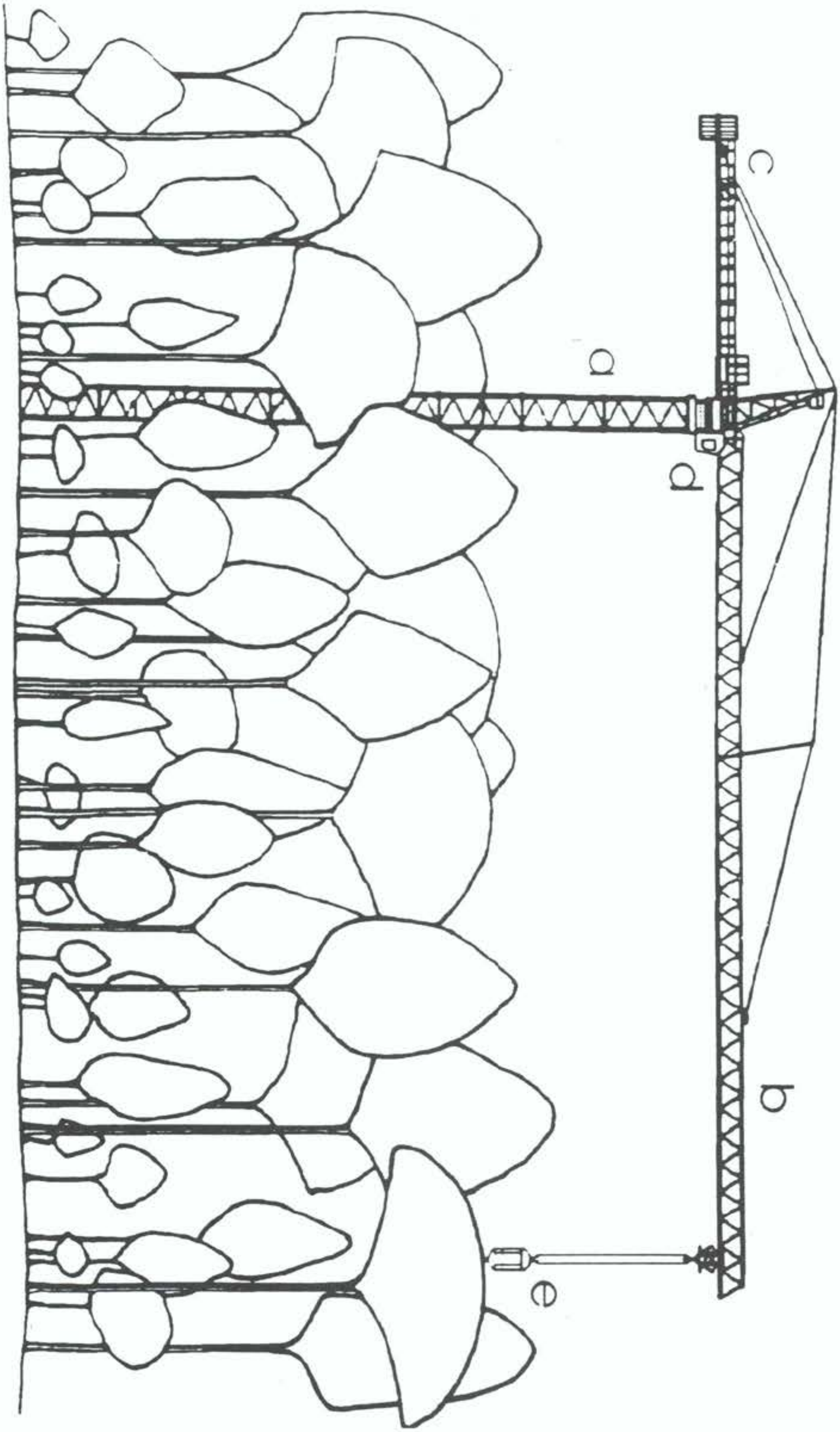

Figure 2.1: Schematic of the canopy crane operating over a tropical forest and showing the tower (a), jib (b), counterjib and counterweight (c), the operator's cab (d) and the gondola (e). The radius and height of the jib are 51 and 42 m. respectively.

Table 2.1: Comparison of Canopy Access Techniques

Technique	Description	Type of Research			Remarks
		Observation	**Collection**	***In Situ* Measurements and Experimentation**	
Tree climbing	Several methods - by hand, with ropes, ladders, pulleys or mountaineering equipment.	Allows observations across vertical strata within and beneath the tree climbed and into adjacent trees where intervening vegetation permits.	Allows collections from within reach of the tree trunk or rope climbed.	Allows *in situ* measurements within reach of the tree trunk or rope climbed. Limited to relatively light equipment.	Greatest strength - low cost and maximum flexibility. Greatest limitation - access to the outermost canopy is limited because a higher branch or trunk must support the investigator's weight.
Static towers	Structures of metal or scaffolding erected in gaps between trees or along tree boles. Often extended above the canopy.	Allows observations across vertical strata adjacent to the tower where intervening vegetation permits.	Allows collections from within reach of the tower.	Allows *in situ* measurements of microclimate and of organisms within reach of the tower.	Greatest strength - permanent platform for micro-climatic measurements across vertical strata. Greatest limitations - only allows study of organisms within reach of the fixed tower.

Table 2.1: Comparison of Canopy Access Techniques

Technique	Description	Type of Research			Remarks
		Observation	Collection	*In Situ* Measurements and Experimentation	
Platforms and walkways	Wooden or metal structures at the top of a single tree or connecting several trees.	Allows observations where intervening vegetation permits. Platforms accessed by climbing can be placed to facilitate observation at low cost.	Allows collections from within reach of structure.	Much improved stability and safety for researcher. Allows *in situ* measurements from within reach of structure.	Greatest strengths - platforms accessed by climbing provide maximum flexibility and low cost. Walkways can be hundreds of metres long providing access to extensive areas. Greatest limitations - access to the outermost canopy is limited because branches and trunks must support the weight of the structures plus investigators and their equipment.
Inflatable rafts	Inflatable rubber raft (the size of a tennis court) is raised above the canopy using an air ship and then lowered on to tree tops. Researchers climb up into the raft from the forest floor. Developed by the French Opération Canopée project led by Dr Francis Hallé.	Allows observation of the outermost canopy from the raft, a 600 m² platform.	Allows collections from within reach of the raft and over a larger area with an affiliated 'treetop' sledge which the air ship drags across the canopy.	Allows short-term *in situ* measurements. However, the raft must be moved regularly to prevent it from settling into the canopy and becoming stuck.	Greatest strengths - access is to the outermost canopy. Designed to be moved among sites. Greatest limitations - the weight of the raft and investigators is supported by the uppermost canopy which is perturbed accordingly. Costs are extremely high.

Table 2.1: Comparison of Canopy Access Techniques

Technique	Description	Type of Research			Remarks
		Observation	**Collection**	***In Situ* Measurements and Experimentation**	
Construction crane	Hammerhead crane with gondola that raises researchers above the canopy and then lowers them into forest (see chapter 2, *Evaluation of Canopy Crane*). The crane can be fixed or mounted on a wide-gauge railroad track.	Allows observations over a prolonged period over a large area of outermost canopy and also across lower forest strata wherever intervening vegetation permits entry of the gondola.	Allows collections from a large area of the outermost canopy and from lower forest strata wherever intervening vegetation permits entry of the gondola.	Allows long-term *in situ* measurements and experimentation. Repeated access to specific locations is safe and rapid. Numerous locations can be visited rapidly. Heavy equipment can be used.	Greatest strengths - first 'top-down' approach to canopy research. Gondola not in contact with tree so does not interfere with forest/atmosphere or biotic interactions. Large, heavier equipment can be easily transported to upper canopy. Safe and stable. Greatest limitations - initial installation requires a mobile crane or a cargo helicopter. Operation requires electricity and crane operator. Costs are high.

Chapter 3:

Biodiversity

The International Convention on Biological Diversity (June 1992) recognized the urgent need to document biodiversity in the face of ongoing world-wide habitat destruction[15]. The canopies of tropical forests are the planet's greatest reservoir of undocumented biodiversity[16, 17].

Estimates of the number of species inhabiting tropical forest canopies vary widely; however, all estimates are exceptionally high. In a now classical paper, Terry Erwin of the US National Museum stunned the scientific community with the hypothesis that 30 million undescribed arthropod species inhabit tropical forest canopies. By comparison, the number of scientifically-described species of all taxa is just 1.8 million. Erwin had hypothesized that more than 95% of the planet's species were arthropods (mainly insects, spiders and mites) inhabiting tropical forest canopies. This hypothesis has excited controversy. Nigel Stork of the British Museum provided upper and lower bounds for several extrapolations made by Erwin and estimated that tropical forest canopies may support as many as 80 million species of arthropods but not fewer than 10 million species[17]. At the other extreme, recent global estimates of the number of insect species derived from the number of described species and the proportion of undescribed species for selected groups range between two million and five million[18,19]. The canopy crane offers a unique opportunity to evaluate these widely-varying hypotheses[20].

In addition to arthropods, tropical forest canopies support diverse communities of micro-organisms, vertebrates, lianas and epiphytic plants such as orchids and bromeliads. In the only exhaustive tally of plants from a wet tropical

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[15] International Convention on Biological Diversity (June 1992), Article 7, Identification and Monitoring; and Article 12, Research and Training.

[16] Erwin, T.L., 1982, Tropical Forests: Their Richness in *Coleoptera* and other Arthropod Species, in *Coleopterists Bulletin,* vol. 36, no. l, pp 74-75.

[17] Stork, N.E., 1988, Insect Diversity: Facts, Fiction and Speculation, in *Biological Journal of the Linnean Society,* no. 35, pp 321-337.

[18] Gaston, K.J., 1991, The Magnitude of Global Insect Species Richness, in *Conservation Biology,* vol. 5, no. 3, pp 283-296.

[19] Hodkinson, I.D. and Casson, D., 1991, A Lesser Prediction for Bugs: Hemiptera (Insecta) Diversity in Tropical Rainforests, in'*Biological Journal of the Linnean Society,* no. 43, pp 101-109.

[20] See chapter 3.2: *Biodiversity and Host Plant Associations in the* Coleoptera *and* Homoptera *of a Tropical Forest Canopy.*

forest, 63 % of the individuals and 35% of the species were epiphytes found only in the canopy[21]. In contrast, a recent search of standard bibliographic databases located zero publications on tropical canopy microbes[22]. Again, the canopy crane offers access to these poorly studied groups.

Documentation of the many thousands of undescribed canopy species is important for several reasons. Description is a first step required for surveys for possible economic value, such as pharmaceuticals or in biotechnology. Changes in tropical forest biodiversity that result from direct human interference and from impending global climate change will go undetected unless natural patterns of species composition and abundance are known. This information will also enable forest managers and decision-makers to elaborate more effective conservation programmes.

3.1: Tropical Pollinators in the Canopy and Understory: Field Data and Theory for Stratum 'Preferences'

D.W. Roubik

This study tested the hypothesis that large bees pollinating tropical flowers show a marked preference for flowers produced in a single forest strata (i.e., understory, mid canopy or upper canopy). It has often been claimed, but never proved, that bees show stratum fidelity - i.e., they learn which strata of the forest is most rewarding and consistently return there - just as they show floral fidelity. This was the first study to be completed using the prototype canopy crane to gain access to the upper canopy strata. The success and flexibility of this canopy access technique largely paved the way for the more sophisticated and wide ranging study of canopy arthropod diversity described in chapter 3.2.

The study involved 20 bee species from the following ten genera: *Apis, Trigona, Eulaema, Centris, Euglossa, Scaptotrigona, Partamona, Megalopta, Rhinetula,* and *Oxytrigona.* The species vary in size from 70 mg to over one gramme. Two sets of insect traps were operated simultaneously, both at canopy height and in the understory, to test whether bees showed consistent stratum associations. The canopy crane was used to move the traps among a variety of sites throughout the canopy at two-week intervals for a one-year period.

Some 2,400 bees were captured during the study, only 26% of which arrived at canopy traps. One rare species, *Euglossa heterostica,* was restricted to the upper canopy. The most common species, *Eulaema nigrita,* was equally likely to be captured at all levels of the forest; eight other common *Euglossa* species were more likely to be captured in the understory. These nine common species showed

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[21] Gentry, A.H. and Dodson, C.H., 1987, Diversity and Biogeography of Neotropical Vascular Epiphytes, in *Annals of the Missouri Botanical Garden*, vol. 74, pp 205-233.

[22] David Hawksworth, personal communication.

clear seasonal differences in stratum fidelity, however, with captures being concentrated in the understory in the wet season and being more likely in the canopy in the dry season.

These results suggest that most bees are opportunistic and that stratum associations vary considerably among seasons. The ability of most species to forage over all vertical strata means that this first insect group examined does not display the degree of specialization required to sustain exceptionally high estimates of the numbers of insect species in tropical forest canopies.

3.2: Biodiversity and Host Plant Associations in the *Coleoptera* and *Homoptera* of a Tropical Forest Canopy

V. Rodriguez, D. Windsor and S.J. Wright

This study was initiated in May 1994 to refine estimates of the number of species of arthropods inhabiting tropical forest canopies. These estimates range from a low of 50% to a high of 95% of all species of all taxa inhabiting the planet[23]. The estimates share critical assumptions which can be uniquely tested with the canopy crane.

To appreciate those assumptions, one must be familiar with the components of current estimates of canopy arthropod diversity and the data used to approximate those components. In essence, the number of tropical forest canopy arthropods is estimated as the product of three numbers. The first is the number of arthropod species found in the canopy of a typical tropical tree species. The second is the proportion of those arthropod species that are host specific or that require the host tree species to reproduce successfully. The product of these two numbers estimates the number of host specific arthropod species found in the canopy of a typical tropical tree species. Finally, this product is multiplied by the number of tropical tree species (about 50,000) to generate a global estimate of tropical forest canopy arthropod diversity[24].

These global estimates have been controversial for two reasons. In practice, the number of species inhabiting tropical tree crowns has been estimated by broadcasting insecticide into the crown[24]. Many transients are captured, and this makes the estimate of the proportion of host specific arthropods critical. Uncertainty arises because the host specificity of canopy arthropods is unknown. In 1992, one expert[25] wrote:

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[23] See introduction to this chapter.

[24] Erwin, T.L., 1982, Tropical Forests: Their Richness in *Coleoptera* and other Arthropod Species, in *Coleopterist Bulletin,* vol. 36, no. 1, pp 74-75; May, R.M., 1988, How Many Species?, in *Philosophical Transactions of the Royal Society of London,* series B, no. 330, pp 293-304; and Stork, N.E., 1988, Insect Diversity: Facts, Fiction and Speculation, in *Biological Journal of the Linnean Society,* no. 35, pp 321-337.

[25] Basset Y., 1992, *Biological Journal of the Linnean Society, no. 47,* pp 115-133.

> *At the moment, no formal testing of the host specificity of arboreal and free-living folivores has been yet published. This is probably due to the formidable physical constraints upon insect sampling and canopy access in rainforest environments ... At this stage of research, we must rely on indirect information to hypothesize upon the host-specificity of rainforest herbivores.*

The canopy crane allows investigators to overcome these physical constraints and to take a completely different approach to estimate numbers of canopy arthropod species.

The canopy crane permits direct quantification of the number of canopy arthropod species dependent on a large number of host tree, liana and epiphyte species. Investigators are able to observe the behaviours and determine the life histories of canopy arthropods *in situ*. Arthropods feeding on the host plant are identified and transients are unequivocally eliminated. By screening large numbers of potential host plants for feeding arthropods, the degree of arthropod host-specificity is also determined with greater confidence. Direct diurnal and nocturnal observations of arthropod behaviour are being complemented with extensive measurements of leaf herbivory, pollination success and seed predation[26]. Preliminary observations suggest that current global estimates of tropical canopy arthropod diversity are too high by perhaps an order of magnitude. As an example, we have found fewer than 10 species of host-specific beetles in the same tree species that Erwin[24] estimated was host to more than 160 beetle species. Intensive observations over an entire annual cycle and additional canopy plants will be required to substantiate this preliminary result.

Current global estimates of tropical forest arthropod diversity also make a critical implicit assumption that remains untested. The implicit assumption is that host-specific plant/arthropod associations hold throughout the geographic ranges of both the host plant and the arthropod. This implicit assumption, which is required to extrapolate from local to global estimates of canopy arthropod diversity, is almost undoubtedly false. Many tropical trees have large geographic ranges that include forests with very different rainfall seasonality, while many tropical arthropods are highly sensitive to dry-season desiccation. Thus, it is unlikely that widespread plant species support the same host-specific arthropods throughout their ranges. This possibility may increase global estimates of canopy arthropod diversity substantially. Alternatively, a single insect species may have different host plants in different parts of its range. This would decrease global estimates of canopy arthropod diversity. An initial evaluation of these possibilities will be made possible by the installation of a second canopy crane in the Parque Nacional Interoceanica, an everwet forest on Panama's Caribbean slope, as part of phase II of the UNEP/STRI canopy biology project[27].

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[26] See chapter 4, *Biotic Interactions.*

[27] See chapter 10, *Future Perspectives,* and Annex V, *Proposed Sites in Panama for Future Installation of Construction Cranes to Access the Forest Canopy.*

Chapter 4:

Biotic Interactions

Biotic interactions shape tropical forests. Plants make animal life possible by converting the sun's light energy and carbon dioxide into simple carbohydrates. Animals feed on plants or on animals that feed on plants. Virtually all plants lose tissue to animal herbivores, however, many plants simultaneously benefit from symbiotic relationships with animals including pollinators and seed dispersers. These biotic interactions are critical to the functioning of tropical forests.

The recent history of the Las Tuxtlas Forest Reserve in Veracruz, Mexico, provides a concrete example of the dependence of forest function on biotic interactions. Las Tuxtlas has recently lost most species of herbivorous mammals to isolation, habitat fragmentation and poaching caused by an expanding human population. This has had a profound impact on forest regeneration. Dense monospecific carpets of seedlings now dominate the forest floor, interfering with regeneration of other tree species. In a nearby forest, where mammalian herbivores have not been disturbed, the seedling layer includes many more species and much lower densities of individuals[28]. The continued absence of browsing mammals will inevitably reduce the diversity of this rain forest plant community. The Las Tuxtlas example illustrates the decisive role that biotic interactions play in tropical forests. Conservationists and land-use managers will have a critical need for detailed understanding of biotic interactions as deforestation, forest fragmentation and isolation continue.

This need is nowhere greater than in the forest canopy. As outlined in the previous chapter, the tropical forest canopy is the cradle of biodiversity. The difficulty of access to the canopy means that biotic interactions that occur in the canopy are largely unstudied. Amongst upper canopy organisms, the greatest dearth of information is again for arthropods which, despite their small size, are

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[28] Dirzo, R., and Miranda, A., 1991, Altered patterns of herbivory and diversity in the forest understory: a case study of the possible consequences of contemporary defaunation, in *Evolutionary Ecology in Tropical and Temperate Regions,* John Wiley & Sons.

important in terms of biomass[29], numbers of individuals[30], and impact on forest ecology. The lack of basic taxonomic and behavioural information on canopy arthropod species hinders understanding of many critical biotic interactions. Research carried out from the crane in the Parque Natural Metropolitano aims specifically to probe biotic interactions, particularly those involving arthropods, within the upper forest canopy. Ongoing studies are examining the distribution, performance and behaviour of arthropod species on their plant (or animal) hosts[31], and the consequences for the host[32]. Defining the interactions between specific plants and animals will enhance our understanding of the factors that influence the distributions of individual species and the species composition of canopy communities. This will, in turn, provide insight for land-use managers and also advance understanding of why tropical forests, and the upper forest canopy in particular, are so rich in species.

4. 1 Herbivory

S.J. Wright and M. Samaniego

Insects, vertebrates and pathogens that consume leaf tissue have a tremendous impact on vegetation. Insects have caused greater economic loss to American agriculture than the combined effects of damage from drought and freezing and have caused greater tree mortality than does logging[33]. In the shaded understory of the tropical moist forest on Barro Colorado Island, Panama, insect herbivores consume 25% of all leaves produced[34]. Again, 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 construction 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 understory herbivory levels

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[29] For example, "(Ants) make up to 10-15% of the entire animal biomass in most terrestrial environments", Holldobler, B. and Wilson, E.O., 1990, *The Ants,* The Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA.

[30] "In the Amazon rainforest, for example, one hectare of soil contains more than eight million ants." (op. cit.)

[31] See chapter *3.1, Tropical Pollinators in the Canopy and Understory: Field Theory for Stratum 'Preferences',* and chapter *3.2, Biodiversity and Host Plant Associations in the* Coleoptera *and* Homoptera *of a Tropical Forest Canopy.*

[32] See chapter *4.2, Seed Predation* and chapter *6.16, Optimal Seed Size, Maternal Selection and Leaf Phenology of Two Neotropical Tree Species.*

[33] Coley, P.D., Bryant, J.L. and Chapin III, F.S., 1985, Resource Availability and Plant Anti-herbivore Defense, in *Science,* vol. 230, no. 4728, pp 895-899.

observed in nearby forests on Barro Colorado Island and elsewhere in the tropics[34]. 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[35]. 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 herbivòry of herbivory now suggest otherwise.

The current research programme will be further complemented by studies of morbidity in canopy leaves which are to be initiated by Dr Greg Gilbert of the Smithsonian Tropical Research Institute beginning in August 1994.

4.2 Seed Predation

C. Sánchez Garduño, S.J. Wright and C. Potvin

This study aims to identify the consumers of reproductive structures of canopy trees, lianas and epiphytes; to assess the percentage of each crop that is attacked; and to determine the degree of specialization of insects on single host plant species. The canopy crane is used to access reproductive canopy plants. Reproductive structures both with and without evidence of predation are systematically collected and returned to the laboratory where they are held in controlled environment chambers that maintain conditions similar to those in the field until eggs and larvae have hatched and grown into adult insects. Adults are then sent to Smithsonian entomologists for identification.

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 function,

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[34] Coley, P.D., 1983, Herbivory and defensive characteristics of tree species in a lowland tropical forest, in *Ecological Monographs,* no 53, pp 209-233.

[35] See chapter 6.5, *Modelling Carbon Gain in the Canopy of a Tropical Tree.*

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 predated upon 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.* Work in progress on other species will allow us to generalize these results and to determine levels of host plant specificity among insects and pathogens.

Chapter 5:

Canopy Energy Balance

Canopy energy balance measurements quantify the interchange of latent heat between forested ecosystems and the atmosphere. This interchange is important because it contributes to local and regional climates. Energy balance measurements are also a critical component of most methodologies used to measure the interchange of water vapour and carbon dioxide between forest strata and the atmosphere.

The prototype canopy crane is located in a forest reserve adjacent to Panama City. The proximity of the city limits the usefulness of the site for stand-level energy balance measurements. However, the following two studies have used canopy energy balance measurements at the level of individual branches and individual tree crowns and demonstrate the utility of the crane for energy balance measurements.

In phase II of the UNEP/STRI canopy biology programme, a second canopy crane erected over an everwet, evergreen Caribbean forest will permit stand-level canopy energy balance measurements (see chapter 10, *Future Perspectives).*

5.1 Stomatal and Environmental Control of Transpiration in a Lowland Tropical Forest Tree

F.C. Meinzer, G. Goldstein, N.M. Holbrook,
P. Jackson and J. Cavelier

The objective of this study was to probe the extent to which tropical forest trees control their own transpiration rates and to examine how external environmental factors, especially radiant energy, might affect transpiration rates. The limited data previously available indicated that temperate zone forest trees and horticultural crops showed stronger responses to external atmospheric changes than did tropical forest trees. This study was one of the first to measure directly the amount of daily water loss in the upper crown of a large tropical forest tree and was made possible by the construction crane which enabled scientists to have repeated access to terminal leaves and branches in all compass directions in the upper canopy. Such detailed measurements of changes in transpiration rates in response to changes in environmental conditions are required to evaluate the role of forests in regional water budgets.

The transpiration rate of the canopy emergent tree, *Anacardium excelsum,* was measured during daily fluctuations in evaporative demand under a variety of energy loads in both dry and wet seasons. Stomatal conductance of single leaves was measured using porometers. Simultaneously, transpiration by entire, intact branches was measured using stem heat balance methods. Transpiration that would occur in the absence of a boundary layer[36] was calculated from the total radiant energy balance of each branch. This permitted an estimate of the linkage between the canopy and the atmosphere for water vapour exchange.

In both the upper and lower canopy, leaf stomata rapidly closed to limit water vapour loss once high transpiration rates had been reached. These results coincide with the current theory that each stoma senses the tree's overall transpiration rate and responds to this, rather than being passively affected by fluctuating evaporative demand at the leaf surface. Had the stomata remained open during the dry season and allowed transpiration to continue at its maximum rate, then each leaf would have lost about twice as much water vapour overall. The stomata of upper canopy leaves were open more frequently during the wet season when evaporative demand is low. Consequently, the overall amount of water vapour transpired by *Anacardium* was about the same in both the dry and wet seasons. *Anacardium* exhibited an unusually high degree of stomatal control over its transpiration rate which suggests that some tropical forest trees have more control over transpiration than was previously realized.

5.2 Predicting Photosynthetic Carbon Fluxes From Spectral Reflectance of Leaves and Canopies

J.A. Gamon and S.S. Mulkey

This study explored the use of remote sensing techniques to monitor photosynthetic rates of the forest canopy. If these techniques can be shown to predict photosynthetic activity of the canopy, then canopy carbon fluxes could be measured by remote sensing. This is potentially a very powerful tool for understanding the carbon budget of whole stands of forest, and therefore for improving estimates of global carbon flux. These methods could enable scientists to evaluate the widely-accepted hypothesis that mature tropical forests emit the same amount of carbon as they

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[36] The relevant driving force for transpiration is always at the point where the water vapour molecules exit the stoma - i.e., in the boundary layer of motionless air directly at the leaf surface. As the plant transpires, the boundary layer gradually becomes more humid. Consequently, the driving force for evaporation in the boundary layer falls. In this way, the humid boundary layer creates a 'buffer' between the drier, outside atmosphere and the saturated leaf tissue.

absorb and are therefore in balance with the atmosphere. This hypothesis is in conflict with the observation that mature tropical forests export 0.2 billion metric tonnes of carbon per year to the oceans, an export rate greater than that of any other biome[37]. Photosynthetic data obtained from satellite monitoring could also be used to quantify the amount of carbon accumulated by secondary forests during tropical succession.

In this pilot study, the canopy crane was used to take a variety of conventional measures of leaf function that could be correlated with spectral characteristics determined from remote scans of the canopy. This permitted rapid determination of the 'ground truth' of the spectral signature and advanced the development of this exciting area of research much more rapidly than would otherwise have been possible.

First, a series of narrow-band spectral reflectance readings of a section of canopy were taken from the gondola at a height of a few metres above the canopy. During exposure to light, leaves undergo a biochemical shift (expoxidation of the xanthophyll pigments) that produces a spectral signature at 531 nanometers. This signature becomes greater with increasing light intensity. The xanthophyll conversion is highly correlated with the efficiency of light energy transfer for photosynthesis, which in healthy leaves is strongly correlated with overall photosynthetic efficiency. Immediately after the spectral scan, photosynthetic efficiency was independently assessed by measuring the level of chlorophyll fluorescence and instantaneous carbon gain with a portable fluorometer and a portable gas exchange system, respectively. Data from the spectral scan showed a strong relationship to both the chlorophyll fluorescence and the carbon gain per photon input. This preliminary evidence indicates that the spectral signature of xanthophyll conversion is predictive of the efficiency of carbon uptake and that remote sensing of the canopy can be used to predict carbon gain. This is the first step towards developing a capacity to use these techniques from aircraft and, possibly, satellites.

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[37] Brown, S. and Lugo, A.E., 1981, The Role of the Terrestrial Biota in the Global Carbon Dioxide Cycle, *in American Chem. Soc. Div. Pet. Chem*, no. 26, pp 1,019-1,025.

Chapter 6:

Upper-Canopy Micro-climate and its Effect on Plant Performance[38]

Light levels, air temperatures, humidity, atmospheric carbon dioxide concentrations, and soil fertility and water content all affect plant performance. These physical parameters vary in space and time. Light, humidity and temperature vary vertically among forest strata, diurnally, and seasonally with the position of the sun and, in Panama, with the latitudinal movements of the inter-tropical convergence zone. Micro-environmental conditions also fluctuate with seasonal changes in plant activity (e.g., leaf flush and fall, flowering and fruit production); biotic interactions, particularly herbivory[39]; and anthropogenic effects such as deforestation and the burning of forest fuels. Man has caused a 25% increase in atmospheric carbon dioxide concentrations since the beginning of the Industrial Revolution and it is widely believed that ongoing anthropogenic activities will lead to a shift in global climate with somewhat higher temperatures and substantially more severe dry seasons in the tropics. Detailed information on the temperature, carbon-dioxide and drought responses of tropical forest canopy plants is required to plan effective policies for tropical forest management in the face of a changing global climate and for the elaboration of more accurate global climate models.

The canopy crane has facilitated an extensive series of studies of the relations between plant performance and micro-climate. Prior to the crane, the difficulty posed by canopy access had largely limited studies of tropical forest plant performance to forest floor conditions. The upper canopy remains a critical site for such studies because micro-climatic conditions are very different from lower forest strata. Temperatures are often 5° to 8°C higher, humidities can be 30% lower,windspeeds an order of magnitude higher and light levels two orders of magnitude higher in the canopy than on the forest floor[40].

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[38] Annex II of the original project document called for research to be initiated into the physiological effects of drought on canopy plants. Scientists implementing the UNEP/STRI canopy project felt that it was critically important to study integrated plant responses to covarying environmental conditions, and this chapter was perforce expanded to include the physiological effects of co-variation in light intensity, water availability and other factors.

[39] See chapter 4, *Biotic Interactions.*

[40] See chapter 1, *Introduction to Tropical Forests and the Parque Natural Metropolitano.*

Many of the investigations summarized in this chapter have used a combination of controlled and natural experiments to provide mechanistic insight into plant-environment responses in the canopy. Controlled experiments manipulate one environmental factor while others are held constant; natural experiments monitor plant performance in response to simultaneous variation in a variety of micro-climatic conditions that occur diurnally, seasonally or along vertical gradients. Together, the combination of controlled experiments to isolate plant responses to single environmental factors and natural experiments to elucidate integrated plant responses to natural variation in a complex of environmental factors has provided rapid increases in our understanding of canopy plant performance. This chapter concentrates on plant responses to drought and radiation in photosynthetically active wavelengths. Summaries of research into the effects of ultra-violet-B radiation on the upper canopy, and the physiological responses of trees to changes in atmospheric carbon dioxide are presented in chapters 7 and 8.

Tropical Forest Water Cycles

Forest water cycles have a direct effect on local and global climate. For example, in the Amazon basin, 75% of rainfall is derived from forest evapotranspiration[41]. Little is known, however, about the mechanisms of evapotranspiration; how much is attributable to evaporation from soil and wet leaf surfaces and how much is a direct result of transpiration by the vegetation. Nor is it known how different plant species contribute to the total amount of forest transpiration, or how transpiration rates may vary throughout the seasons. This information is required to evaluate the role of forests in seasonal water budgets, to construct more accurate models of local and global weather patterns and to predict the effects of deforestation on global climate. The canopy crane has facilitated such studies[42] by making possible non-intrusive access to the interface between the upper forest strata and the atmosphere.

Effects of Light Variation on the Upper Canopy

Plants depend on light energy from the sun for photosynthesis and growth. Excessive solar radiation can, however, damage leaf chlorophyll and permanently reduce photosynthetic capacity. Light levels vary by two orders of magnitude between forest strata and are always most intense on the exposed upper canopy.

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[41] Salati, E. and Vose, P.B., 1984, Amazon Basin: A System in Equilibrium, in *Science, vol.* 225, no. 4658, pp 129-137.

[42] See chapter 6.13, *Mechanisrns of Long-Distance Water Transport in Plants: A Re-Examination of some Paradigms in the Light of New Evidence;* and chapter 6.14, *Whole-Tree Transpiration: Linking Stand Structure, Composition and Phenology with Watershed Hydrology.*

Leaves exposed to excess sunlight activate different mechanisms which either facilitate the dissipation of excess absorbed light as heat or prevent light energy from being absorbed. These mechanisms limit photosynthesis (i.e., induce photoinhibition) and so limit plant growth and the plants's ability to act as a carbon sink. However, photoinhibition is reversible; and it is currently believed that photoinhibition is a regulatory mechanism to protect the plant, rather than an indication of tissue damage. The canopy crane has facilitated studies of the mechanisms by which leaves of the exposed upper strata are able to cope with the extreme solar intensity[43].

Paradoxically, many trees are light limited at the whole canopy level by a combination of heavy cloud cover, self-shading of lower leaves, lateral shading by neighbouring trees and shading by encroaching lianas[44], even while their sun-exposed leaves are susceptible to photoinhibition. This possibility motivates a number of studies from the crane that seek an integrated understanding of plant responses to seasonal changes in light and water availability in the canopy[45].

6.1: Light Quality and Distribution Within The Canopy of a Neotropical Forest

S.S. Mulkey, S.J. Wright, R.W. Pearcy and J. Gamon

The most important variable resource for carbon gain in the forest canopy is light and thus the study of light was the starting point for canopy studies with the crane. Clearly the distribution of light in even the most simple canopies can be dynamically variable in time and space. Although canopies of small forests and plants have been studied in some detail, because of limited access, few studies have quantified light in the canopies of tall tropical forest. During 1993, a series of studies were conducted to assess the quantity and quality of light in the canopies of trees growing near the crane. The goals of this work were to document (i) the vertical variation in light penetration and foliage density (figures 6.1.1, 6.1.2 and

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[43] See chapter 6.7, *Photosynthesis and Photoinhibition;* chapter 6.9, *Day-Courses of Two Light Activated Calvin-Cycle Enzymes: Field Measurements on a Tropical Forest Tree,* Ficus Insipida; chapter 6.10, *Xanthophyll Cycle Pigrnents in Tropical Forest Species: A Comparative Field Study of Canopy Trees, Gap and Understory Species;* chapter 6.11, *Photoinhibition and Xanthophyll Cycle Activity in Young and Mature Canopy Leaves of Tropical Rainforest Plants;* and chapter 6.12, *Mechanisms of Long-Distance Water Transport in Plants: A Re-Examination of Some Paradigms in the Light of New Evidence.*

[44] Wright, S.J. and Van Schaik, C.P., 1994, Light and the Phenology of Tropical Forest Trees, in *The American Naturalist,* vol. 143, no. 1, pp 192-199.

[45] See chapter 6.1, *Light Quality and Distribution Within the Canopy of a Neotropical Forest;* chapter 6.2, *Leaf Area Seasonality in a Tropical Forest;* chapter 6.3, *Variation in Resource Availability and Consequences for Interdependent Physiological and Morphological Leaf Traits in Neotropical Canopy Trees;* chapter 6.4, *Assessment of the Effects of Microsite Factors on Liana Physiology;* chapter 6.5, *Modelling Carbon Gain in the Canopy of a Tropical Forest;* and chapter 6.6, *Storage Carbohydrates in Tropical Forest Trees.*

6.1.3), (ii) vertical variation in light spectral quality, and (iii) the distribution of direct light (sunflecks) and diffuse light in the canopies of selected species. Because of the fundamental importance of light, these data provide the cornerstone by which all other work from the crane will assess the energy available for biological processes in the canopy.

The crane allowed the documentation of light by permitting radiation sensors to be placed with great precision throughout the canopy in a highly-organized and repeatable sequence. First, a series of transects were made from above the canopy to the ground by dropping a quantum sensor (detecting radiation only for the photosynthetically-active wavelengths) mounted on a gravity-balanced platform. A reading was taken every half metre while within the canopy of a tree, and every one metre thereafter until the sensor platform rested on the ground. A pin attached to the base of the sensor was used to record the number of leaf interceptions and thus quantify the foliage density. These data and the total available sunlight

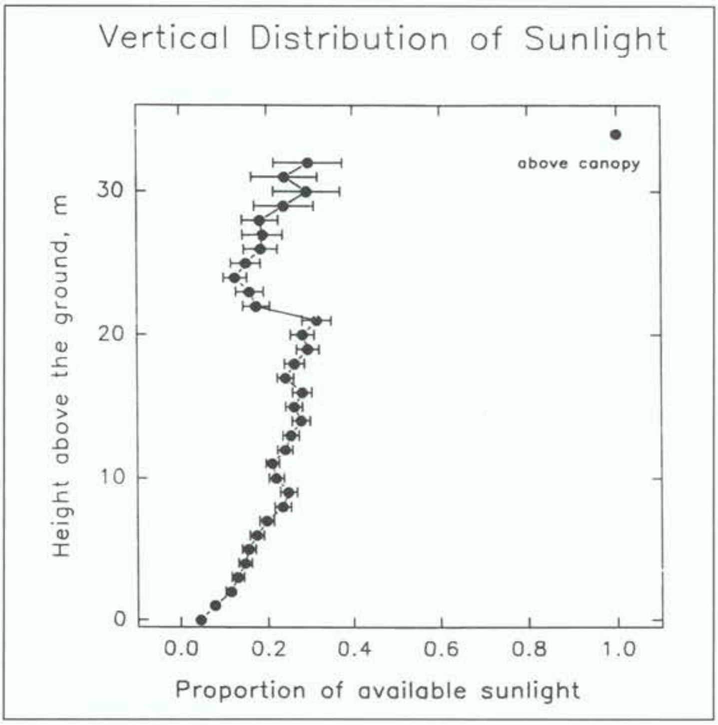

Figure 6.1.1: The distribution of sunlight at 1-m intervals along vertical transects through the canopies of selected tropical tree species. Note the increase due to diffuse side light at 20 metres which corresponds with the bottom of the canopy of most species. Values are means ± one standard deviation for a total of 7,100 light determinations.

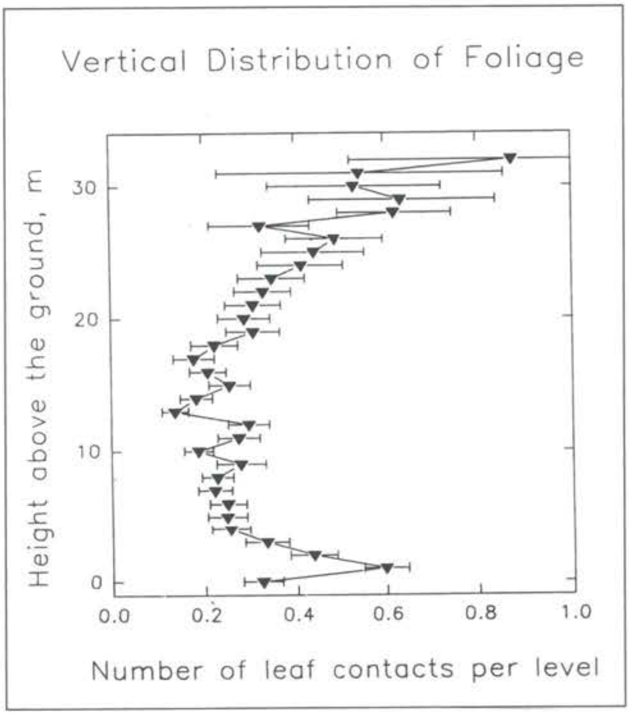

Figure 6.1.2: The distribution of foliage at 1-m intervals along vertical transects through the canopies of selected tropical tree species. The abscissa or x-axis presents the mean number of leaves contacted by a 1-m long 'pin'. Error bars represent one standard deviation for a total of 7,100 leaf counts.

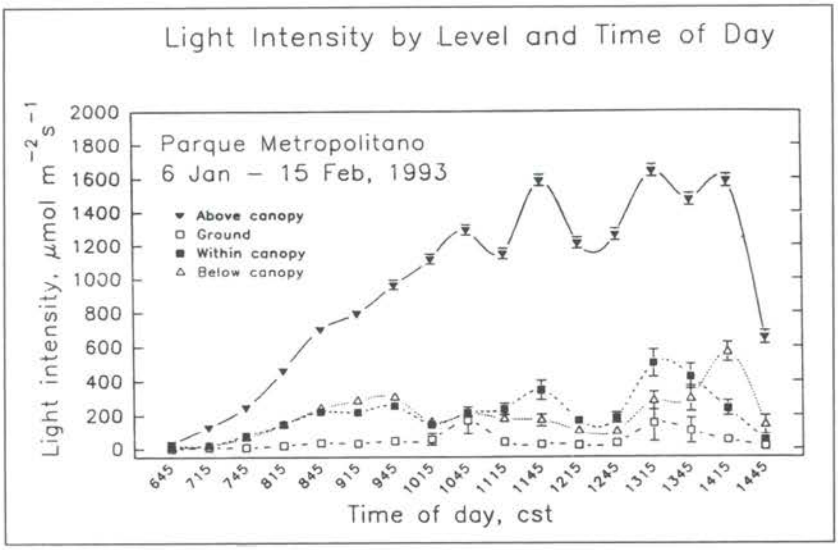

Figure 6.1.3: Light intensity by forest strata and time of day. Note the relatively low light intensities observed within tree crowns (filled squares) where large numbers of leaves are located (compare with figure 6.1.2). This suggests that self-shading will limit photosynthesis for many canopy leaves. Values are means ± one standard deviation for a total of 7,100 light determinations.

(measured by a sensor above the canopy) were simultaneously recorded by a data logger so that the proportion of light penetrating the canopy could be calculated. Spectral scans of the reflected light over vertical gradients were made using a portable spectral/radiometer lowered through the canopy to the ground[46]. Sunfleck distribution at various levels within the canopies of selected species was determined using a horizontal array of 80 light sensors.

The distribution and quality of light throughout the forest canopy around the crane was found to be extremely heterogeneous. Over the first two metres of transect from above the canopy, there was often a drop of light intensity of greater than two orders of magnitude. In contrast, gaps in the canopy permitted direct sunlight to penetrate to the forest floor with little interception by foliage. Especially dense canopies were encountered below lianas that were invading the canopy from these gap edges. In many cases, light was somewhat greater immediately beneath a tree canopy than within the canopy because of an increase in diffuse side light (note the increase at 20-metre height in figure 6.1.1). Light within and beneath the canopy was relatively enriched in far-red wavelengths due to the spectral character of light reflected from green leaves. Diffuse light reaching the forest floor was the most enriched in far-red wavelengths. Of all the measures, the distribution of sunflecks within the canopy was the most heterogeneous because of the effect of wind on leaf flutter and the change in sun angle over the course of a day. Relative to diffuse light, sunflecks accounted for the majority of light energy in the canopy.

The forest around the crane is similar in structure, species composition and height to many humid successional forests in Central America and Amazonia. Accordingly, these data will provide a basis for extrapolating the distribution and quality of light in these developing forests. This data base is the most comprehensive and detailed ever collected and it unambiguously documents spatial and temporal variation in the quantity and quality of light available for carbon gain. From this, a paper will be published detailing (i) the penetration of light through canopies of contrasting architecture and foliage density, (ii) the relative contribution of far-red light to the overall energy environment in the understory, (iii) the potential effect of sunflecks on total carbon within the canopy. In combination with other projects from the crane[47], these data will permit estimates of the potential for carbon gain in a wide array of microenvironments throughout and beneath the forest canopy.

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[46] See chapter *5.2, Predicting Photosynthetic Carbon Fluxes From Spectral Reflectance of Leaves and Canopies.*

[47] See chapter *5.2, Predicting Photosynthetic Carbon Fluxes From Spectral Reflectance of Leaves and Canopies* and chapter *6.5, Modelling Carbon Gain in the Canopy of a Tropical Forest.*

6.2: Leaf Area Seasonality in a Tropical Forest

S.J. Wright, S.S. Mulkey and K. Kitajima

Canopy leaf area is generally assumed to be maximal throughout the rainy season in tropical forests[48]. The canopy crane made possible the first quantitative leaf counts from a tropical forest canopy. Leaf area seasonality was much more complex than expected. Each species examined had a unique seasonal pattern of canopy leaf numbers. This unexpected seasonality will modify individual allocation strategies, interspecific interactions and forest carbon fixation.

Leaves were counted each month for 100 randomly chosen branches from the uppermost canopies of the seven most abundant tree and liana species of closed-canopy forest and the two most abundant tree species of treefall gaps. The censuses included 31,639 leaves.

Leaf numbers cycled annually for all nine species (figure 6.2.1). *Anacardium excelsum, Luehea seemannii* and *Bonaemia maripoides* exchanged leaves in January, June and July, respectively; the six remaining species became deciduous during the dry season and renewed leaf production in April and May with the first rains. The proportion of the canopy re-established in this initial burst of leaf production was unexpectedly low in six species (figure 6.2.1). After two months[49] of renewed leaf production, canopy leaf number averaged more than 85% of its maximum value in three species, but less than 70% in the remaining six species and less than 50% in three of these species (table 6.2.1).

The latter six species required from three to six months after the initiation of leaf production to attain maximum leaf numbers. The increase in leaf number was linear with time for all species except *Cecropia longipes* and *Luehea*. New leaves produced after the initial burst of leaf production invariably represented extension growth on existing branches or on newly formed sub-branches. Most new leaves were sun exposed and shaded older leaves.

Net reductions in canopy leaf numbers also occurred before the rainy season ended. In the final months of the wet season as five species reached maximum canopy leaf numbers, the four remaining species were steadily losing leaves. In the final month of the rainy season, these species averaged as little as 58% of maximum canopy leaf numbers (table 6.2.1).

These dynamic changes in canopy leaf numbers have implications for several levels of forest organization. At the level of individual leaves, the investment in new leaves may change seasonally in species with prolonged leaf production. Photosynthetic enzymes may be degraded in older leaves that become shaded and

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[48] Raich, J.W. and eight others, 1991, Potential Net Primary Productivity in South America: Application of a Global Model, in *Ecological Applications,* vol. 1, pp 339-429.

[49] Two months is used to eliminate the possibility that the first census artificially split a discrete period of leaf production.

reinvested in new, sun-exposed leaves. Leaves produced in different seasons may also have different morphologies suitable for the wet, cloudy conditions of the rainy season or the dry, sunny conditions of the dry season[50].

At the level of the individual, seasonal carbon gain must vary widely among species. Prolonged linear increases in leaf numbers with time suggest that new photosynthate is required to complete canopy leaf complements in four species. The May dip in *Cecropia* leaf numbers which was observed in two years (second-year data not shown) may indicate extreme depletion of energy reserves. This possibility is consistent with observations that levels of stored carbohydrates are much lower in many tropical trees than in their temperate zone counterparts[51]. In contrast, stored carbohydrates must play a more important role in the two lianas and one tree species that produce complete leaf crops in a short time.

The seasonal timing of reproduction and seasonal changes in irradiance are also important[52]. The greatest reproductive energy sink occurs when fruit are filled. For five species, this coincided closely with maximum leaf area (figure 6.2.1). For the two lianas, fruit were filled well after maximum leaf areas were observed, again suggesting a role for stored carbohydrates. For *Antirrhoea* and *Castilla,* fruit were filled well before leaf area reached its maximum. Two species, *Anacardium* and *Luehea,* had large numbers of young leaves with maximum photosynthetic potentials and maximum canopy leaf areas and filled seeds during the dry season when irradiance is maximal (figure 6.2.1). These species have deep roots to access deep soil water reserves and are adapted to take advantage of the dry season irradiance peak[52]. Seasonal leaf dynamics will also affect interspecific interactions. Lianas shade their hosts and displace host leaf area[53] while trees cast shade laterally on their neighbours. 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.

Finally, seasonal leaf dynamics will affect annual carbon gain and water vapour loss at the level of forest stands. Current models of forest carbon gain

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[50] Mulkey, S.S., Smith, A.P., Wright, S.J., Machado, J.L. and R. Dudley, 1992, Contrasting Leaf Phenotypes Control Seasonal Variation in Water Loss in a Tropical Forest Shrub, in *Proceedings of the National Academy of Science (USA),* no. 89, pp 9,084-9,088.

[51] Christian Korner, unpublished data.

[52] Van Schaik, C., Terborgh, J. and Wright, S.J., 1993, The Phenology of Tropical Forests: Adaptive Significance and Consequences for Primary Consumers, in *Annual Review of Ecology and Systematics,* no. 24, pp 353-377; Wright, S.J. and Van Schaik, C., 1994, Light and the Phenology of Tropical Forest Trees, in *American Naturalist,* no. 143, pp 192-199.

[53] Ogawa, H., Yoda, K., Ogino, K. and Kira, T., 1965, Comparative Ecological Studies on Three Main Types of Forest Vegetation in Thailand II: Plant Biomass, in *Nature and Life in South-East Asia,* no. 4, pp 49-80.

assume that the photosynthetic capacity of tropical deciduous forests increases seasonally with actual evapotranspiration[48]. To the extent that leaf area contributes to forest-level carbon gain, these models are wrong. Accurate models of the contribution of tropical forest to global carbon balances will have to include accurate estimates of leaf area seasonality.

Table 6.2.1: Analyses of seasonal changes in canopy leaf number

Post hoc tests based on repeated measures analyses of leaf counts were used to determine the number of months in which leaf counts increased and to determine whether maximum counts were significantly greater than leaf counts in the second month after the initiation of leaf production and in the final month of the rainy season (November). The mean proportion of maximum leaf count present in the second month was calculated after synchronizing the initiation of leaf production for all conspecifics.

Species	Months to build canopy leaf area	Proportion of maximum leaf count two months after initiating leaf crop	Proportion of maximum leaf count in November
Anacardium excelsum	5	.700[*]	.749[*]
Annona spraguei	4	.674[*]	.903[nt]
Antirrhoea trichantha	6	.512[*]	.935[nt]
Bonaemia maripoides	<2	.850[nt]	.912[nt]
Castilla elastica	6	.492[*]	.897[nt]
Cecropia longipes	3	.403[*]	.718[*]
Combretum fruticosum	<2	.950[nt]	.580[*]
Luehea seemannii	6	.484[*]	.884[nt]
Urera caracasana	<2	.834[nt]	.596[*]

$p < .01$
No test performed because month of maximum leaf area falls in the first or second month after leaf initiation or in November or later.

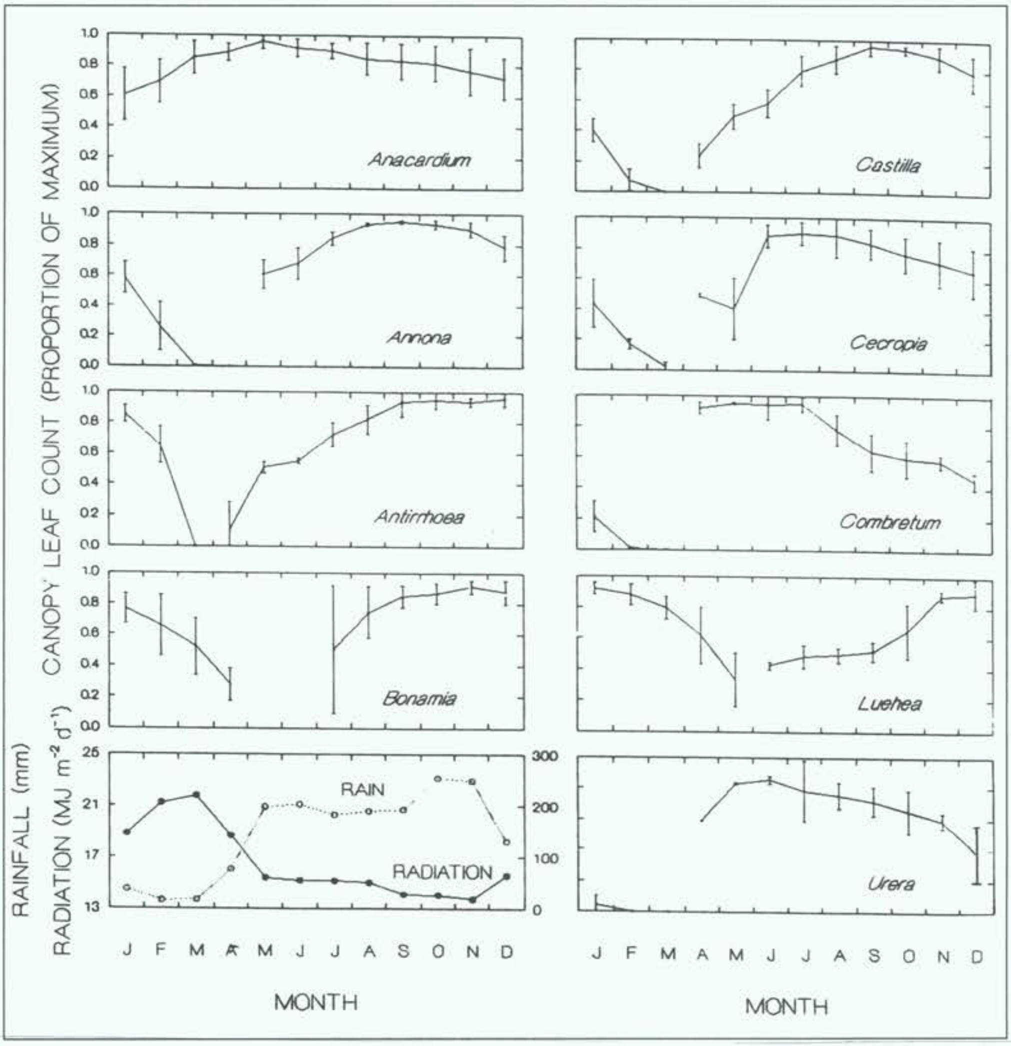

Figure 6.2.1: Leaf number seasonality for sun-exposed branches of nine common tree and liana species from a tropical dry forest. Leaf counts are standardized to a proportion of the maximum observed for each census branch. Values are means ± one standard deviation of this proportion. For comparison, the lower, left panel presents mean monthly rainfall and solar radiation.

6.3: Variation in Resource Availability and Consequences for Interdependent Physiological and Morphological Leaf Traits in Neotropical Canopy Trees

S.S. Mulkey, S.J. Wright and K. Kitajima

This research project examines the hypothesis that plant resources are allocated to maximize carbon gain and leaf production during seasonal variation in rainfall and light intensity. The aim is to determine if leaf lifespan and construction costs reflect predictable variation in resources, and to document suites of interdependent functional leaf and plant characteristics (a) over the resource gradients within the canopy of two mature evergreen tropical tree species with contrasting leaf phonologies, and (b) among seedlings of the same species grown in an experimental common garden with contrasting levels of resource availability.

To date, owing to the difficulties in accessing the uppermost canopy, very little is known about how the leaves of mature tropical forest trees are adapted to the microenvironmental conditions of the upper strata which are so different from the microenvironmental conditions in which the tree initially developed.

In this project the form, structure, function and vital processes of leaves from different micro-environments within the canopy are studied *in situ*. This is the first time that a systematic evaluation of within-canopy seasonal variation in physiological responses to irradiance and water availability has been made. This data will be compared and contrasted with similar data derived from seedlings and saplings growing in an experimental garden plot and the understory and used to draw up the first comprehensive economic conceptual model of resource allocation in tropical forest trees using methodologies developed in temperate zone forests.

This research project has been made possible by the canopy crane which allows researchers repeat access to numerous and wide-ranging locations within tree canopies. Selection of species that exhibit different phenologies for leaf and fruit production will permit an understanding of how the opportunity for carbon gain is correlated with reproduction. To determine phenology and leaf longevity, new leaves and reproductive structures are marked each month with a date-specific tag on three sun-exposed and three shaded branches for four individuals of each species. Tagged leaves are censused each month to estimate leaf survivorship. This is the first time that leaf ages have been recorded for such a comprehensive sample of tropical forest canopy leaves. Reproductive buds are tagged when they first become visible to the naked eye and transitions to anthesis and fruit production are noted. In addition, supplementary qualitative data based on a three-point scale of development for leaf flush, leaf fall, flowering and fruiting is collected from the ground each month from 10 additional individuals of several species.

To study leaf construction costs and nutrient content, leaves of known age from nonreproductive branches in strata with varying light level (low, intermediate, high) are collected from four individuals of each tree species during both the dry season (February, before leaf fall) and wet season (July and again in November). In addition, a small number of leaves are collected during early leaf flush for each species (April and December). Construction costs are assessed and nutrient analysis is performed on the same leaves using established methodologies to determine nitrogen, phosphorous, sulphur and ash content. A subsample of the leaves collected during the second year will be submitted for carbon stable isotope analysis which will indicate the leaf's water-use efficiency. Measurements of relative growth rate and leaf area ratio using established techniques are determined at the same time as leaf collection.

Spot measurements of the diurnal course of photosynthesis, transpiration and temperature under ambient conditions are made with a portable gas analyzer each month using leaves of known age and taking readings at two-hour intervals from just after dawn until dusk. Dark respiration is also measured periodically to obtain a qualitative understanding of instantaneous carbon maintenance requirements. The *in situ* photosynthetic capacity of three individuals of each species is determined using leaves of known age during the early and late dry season, and again during the early and late wet season. In addition, photosynthetic rates of leaves growing in each light environment are measured with an oxygen electrode to determine maximum photosynthetic capacity and so monitor how photosynthetic potential changes according to fluctuations in resource availability. Similarly, sun leaves in the outer canopy are shaded to imitate light conditions deep within the canopy and then measured for photosynthetic ability.

Environmental data on temperature, humidity, rainfall, windspeed and radiation intensity are logged continuously above the upper canopy. In addition, radiation intensity, windspeed and humidity are measured at five heights throughout the canopy in three individual of each species. These are monitored randomly for two days during early, middle and late dry season and again during the early, middle and late wet season.

Preliminary results to date show that emergent species with large canopies show considerable variation among leaves as a function of light availability. Resource allocation to leaves of contrasting light environments varies considerably in some cases *(Luehea sernannii, Antirrohea tricantha)* and very little in others *(Anacardium excelsum)*. Photosynthetic capacity parallels this variation in nutrient allocation. Thus, canopies with little variation in photosynthetic capacity have remarkably similar leaf morphology and function, regardless of a leaf's position in the canopy, and *Anacardium* shows particularly low rates of photosynthesis throughout. This is associated with a high degree of shading within branches because of the overlap of leaves[54]. Interestingly, this pattern of leaf arrangement reduces transpiration during the dry season. In contrast, *Luehea* shows much higher rates of gas exchange and considerable contrast in carbon gain between sun and shade leaves. Allocation of essential nutrients such as nitrogen and phosphorous parallel this variation between sun and shade in this species. To date, it appears that allocation of nutrients to photosynthetic function is maximal in newly-mature leaves but declines slightly during the remainder of a leaf's functional life. Data concerning the relationship of leaf function to sexual reproduction are presently being collected.

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[54] See chapter 6.5, *Modelling Carbon Gain in the Canopy of a Tropical Forest.*

Ultimately, it is expected that this multi-level evaluation of leaf development will show how leaf structure and function vary according to the different resources available. This study is also expected to show the extent to which leaves growing under a wide range of available resources have suites of functional characteristics linking photosynthetic capacity to the potential for plant growth. It will also clarify which components of leaf structure and function have been influenced by natural selection to maximize carbon gain and growth.

It is essential to document the coordination of suites of leaf and canopy features during acclimation if we are to understand general syndromes of response to different stresses. It is expected that the results of this research can be applied to species with similar leaf characteristics in contrasting ecosystems. This may help to clarify how global climate change affects developmental processes in different forest ecosystems.

This research will also provide crucial information about the limits to acclimation and the potential for natural selection to produce coordinated responses to short-term and long-term environmental variation. This information is vital for environmental planners and managers, particularly with regard to reforestation projects and prediction of the consequences of impending global climate change.

6.4: Assessment of the Effects of Microsite Factors on Liana Physiology

G. Avalos, S.S. Mulkey and S.J. Wright

Lianas are woody climbing plants that root in the soil and clamber up host trees to reach the forest canopy. Lianas are a critical component of tropical forests where they are ten times more abundant than in temperate-zone forests[55]. Lianas influence tropical forest dynamics in several important ways. First, they compete for light with their host trees and displace foliage of the host tree. The decrease in host tree foliage approximately equals the amount of liana foliage[56] and lianas comprise between 10 and 30% of total leaf biomass in tropical forests[57]. Lianas may also directly damage or even strangle their host trees and when a single liana spreads over more than one tree crown, may pull down several neighbouring trees whenever any one host tree dies and falls. Despite their importance, lianas

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[55] Gentry, A.H., 1983, Lianas and the 'paradox' of contrasting latitudinal gradients in wood and litter production, in *Tropical Ecology*, no. 24, pp 63-67.

[56] Ogawa, H., Yoda, K., Ogino, K. and Kira, T., 1965, Comparative Ecological Studies on Three Main Types of Forest Vegetation in Thailand II: Plant Biomass, in *Nature and Life in South-East Asia*, no. 4, pp 49-80.

[57] Putz, F.E., 1983, Liana biomass and leaf area of a 'tierra firma' forest in the Rio Negro basin, Venezuela, in *Biotropica*, vol 15, pp 185-189.

have received little study in tropical forests due to their inaccessibility in the uppermost canopy[58].

This on-going study explores the hypothesis that lianas allocate resources to maximize carbon gain in a spatially and temporarily varying environment. Lianas display very different physiologies and plasticity from their host plants, being built for climbing, flexibility and long-distance water transport, rather than for rigidity and structural support. Throughout their ascension from the understory towards the canopy lianas experience sharply different physical conditions. Strikingly different habitats are found over short changes in height. These habitats also change seasonally due to seasonal climatic changes and colonization or overshadowing by other canopy plants. Little is known about the micro-climatic conditions that influence developmental shifts in leaf and stem tissues, and reproductive status [59] or the specific energetic constraints that influence these changes. Nor is it known how much each leaf stage contributes to the liana's overall carbon budget, or the influence on carbon economy of seasonal variation in physical factors at each microsite. However, extreme temporal and spatial variation in the environment must have acted as a strong evolutionary force for the selection of highly plastic plants able to respond quickly to variation in the physical environment.

The study has two components. First, the same liana species will be compared in different microclimates along the vertical gradient from forest floor to upper canopy. Second, two liana species with contrasting phenologies will be compared to elucidate physiological mechanisms underlying different responses to a common seasonality.

The canopy crane is being used to study two liana species, *Combretum fruticosum* (Combretaceae) and *Bonaemia maripoides* (Convolvulaceae) growing in the uppermost strata of canopy trees during part of the 1994 wet season (May to August), and part of the 1995 dry season (mid January-mid February). *Combretum* produces new leaves with the first rains in April, begins to lose leaves in the middle of the rainy season in August, flowers in December, and disperses ripe fruit, loses its final leaves and becomes deciduous in January. *Bonaemia* produces new leaves in the middle of the rainy season in July, flowers in December, disperses ripe fruit in March and is briefly deciduous in the third month of the rainy season in June. These phenologies suggest very different physiologies that

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[58] Putz, F.E. and Mooney, H.A., 1991, *The Biology of Vines,* Cambridge University Press, Cambridge.

[59] Putz, F.E. and Windsor, D.M., 1987, Liana phenology on Barro Colorado Island, Panama, in *Biotropica,* vol. l9, no. 4, pp 334-341; Hegarty, E.E., 1990, Leaf life-span and leafing phenology of lianas and associated trees during a rainforest succession in *Journal of Ecology,* no. 78, pp 30-312; and Lee, D.W. and Richards, J.H., 1991, Heteroblastic development in vines, pp 205-243, in F.E. Putz and H.A. Mooney, *The Biology of Vines,* Cambridge University Press, Cambridge.

permit different responses to a common seasonality.

The working hypothesis is that mature *Bonaemia* possesses a suite of physiological characteristics that permit dry-season activity. The suite of hypothesized characteristics includes high maximum photosynthetic potentials to take advantage of high dry-season light levels and a variety of physiological adaptations to acquire and conserve water. Collectively, the data being collected will provide insight into the physiological plasticity of tropical lianas in a spatially- and temporarily-varying environment and fill gaps in some of the most poorly known aspects of liana biology, including water relations and photosynthetic efficiency.

A second complementary study to be initiated in late 1994 will document the dynamics of liana and tree growth and liana-tree interactions by mapping the species composition of the uppermost canopy at one metre resolution at annual intervals.

6.5: Modelling Carbon Gain in the Canopy of a Tropical Forest

K. Kitajima, S.S. Wright and R.W. Pearcy

The ability to scale up from leaf-level to whole-canopy measures of carbon gain has proved logistically difficult because of the huge numbers of micro-environments occupied by leaves within the canopy of most tree species. In theory, measures of photosynthesis and respiration at the leaf level could be used to calculate the carbon exchange for an entire canopy simply by multiplying these numbers by the number of leaves in the canopy. However, this can produce large errors as numerous small errors are compounded in the process of adding up the total carbon budget. One approach to this problem is to carefully determine the carbon budget for a subunit of the canopy, such as a branch, and then apply these results to the whole canopy. Even this approach is fraught with difficulty because different branches grow in different microclimates determined by such factors as solar orientation, which varies with season, and shading by neighbouring trees. A shortcut is made possible by intensively studying a few branches and then incorporating these results into a simulation which includes information about light availability for branches in different microclimates. Kitajima will be responsible for applying an empirical model, developed by Pearcy, to branches in a variety of locations on individuals of *Anacardium excelsum* and *Luehea semannii*. The model will be used to predict the carbon gain potential for these different microhabitats. With extensive measurements of the variation in light over the canopy, an estimate of whole-canopy carbon gain will be possible.

The model allows the determination of photosynthetic carbon gain of any assemblage of leaves attached to a central branch and its subbranches based on available sunlight. The available sunlight is obtained from a hemispherical photograph of the sky above the branch to assess shading by neighbouring plants. This image is digitized and the solar track for any specified time of the year is used to define the amount of diffuse and direct irradiance arriving at a branch. These photos will be taken from a boom-mounted camera extended from the gondola. The model uses the photo to generate the available energy to drive photosynthesis, and a carbon budget is then calculated for each leaf based on the amount of self-shading within the branch, a typical photosynthetic response curve, night-time respiration, light absorption of the leaf, and leaf age. The values for the leaves of each branch are summed. This will permit a robust estimate of daily carbon gain for branches from an array of microclimates over the canopy of an individual tree, provided that these microclimates can be identified and quantified. These data will be provided by rapid measures of available light using the new technology provided by the LAI-2000 canopy analyzer. In addition, photosynthetic light response curves must be constructed for leaves of varying ages and light environments. A total canopy carbon budget can be calculated for any specified time of year by adding up the estimated carbon budget for all branches of different microenvironments in the canopy. Output from the model will be scaled for branches with varying numbers of leaves and subbranches. This work will commence in August 1994.

The importance of obtaining a whole-canopy estimate of carbon gain cannot be overstated. Once a representative group of species have been added to a database, rapid assessments of carbon flux of entire regions of a forest will be possible. Although only two species will be studied initially, this approach will be applied to a range of species available from the existing crane and the crane to be erected in the Parque Nacional Interoceanica. These data will be fundamental for assessing the effect of canopies of differing successional status on regional atmospheric carbon flux. In turn, this information is essential to parameterize global circulation models used to predict the extent of climate change as our planet becomes warmer.

6.6: Storage Carbohydrates in Tropical Forest Trees

E. Newell, S.J. Wright, S.S. Mulkey and K. Kitajima

This research project examines the seasonal and within-canopy dynamics of carbohydrate storage in *Anacardium excelsum, Luehea seemannii, Urera caracasana* and *Cecropia longipes.* When more carbohydrates are produced through photosynthesis than are used immediately by the plant for maintenance, growth, defense or reproduction the excess is stored as sugar or starch in leaves, stems and roots. Stored carbohydrates are used to replace or repair damaged tissue and to build new leaf canopies in drought-deciduous species. They are also metabolized whenever available resources are insufficient to meet immediate needs (e.g., when low light, water shortage, or other factors limit the plant's ability to photosynthesise). Storage of carbohydrates is therefore an important component of maximised productivity under constraints imposed by seasonal changes in resource availability.

Information regarding carbohydrate storage in woody species of the tropics is very scarce. It is not known how rates of carbohydrate storage vary in response to changes in carbon gain resulting from fluctuating levels of light and moisture availability. Nor is it known if the ratio by which carbohydrates are allocated to growth and storage is a fixed or plastic characteristic in tropical tree species. In addition, more information is needed on the patterns of carbohydrate allocation for successful plant reproduction. Storage carbohydrates may also be an important sink for excess carbon fixed in response to anthropogenic increases in atmospheric carbon dioxide concentrations. For all these reasons, knowledge of storage carbohydrate dynamics is important to an understanding of tropical forest dynamics and to predictions of the possible effects of global climate change.

In this research the construction crane will be used to access and take samples of the outermost leaves and stems in at least five trees of each species. Samples will be made once a month during both wet and dry seasons and analysed in the laboratory for starch and sugar concentrations. Similar analyses will also be made of trunk and root tissue samples. These data will be combined with measurements of photosynthesis and observations of leaf production and reproductive phenology[60] to help to clarify how seasonal variations in photosynthetic rates, leaf production and the timing of reproduction affect concentrations of stored carbohydrates.

It is expected that drought-deciduous species will exhibit seasonal fluctuations in carbohydrate storage because the energy needed to rebuild their leaf canopies must come from storage. *Urera* and *Cecropia* are both drought-deciduous. However, *Urera is* leafless for fairly long periods during the dry season and is therefore expected to store more carbohydrates than *Cecropia* which looses its leaves for only a short period (figure 6.2.1).

Species with rapid growth rates and short life spans are expected to preferentially allocate energy to growth rather than to storage. Species with long-lived leaves are expected to allocate more energy to storage to ensure survival in the face of unpredictable demand (e.g., herbivory, branch damage from storms). *Anacardium* and *Luehea* are slower growing and have longer-lived leaves than *Urera* and *Cecropia*. Therefore it is expected that *Anacardium* and *Luehea* will

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[60] See chapter 6.1, *Leaf Area Seasonality in a Tropical Forest;* chapter 6.2, *Light Quality and Distribution Within the Canopy of a Neotropical Forest;* chapter 6.3, *Variation in Resource Availability and Consequences for Interdependent Physiological and Morphological Leaf Traits in Neotropical Canopy Trees;* chapter 6.4, *Assessment of the Effects of Microsite Factors on Liana Physiology;* and chapter 6.5, *Modelling Carbon Gain in the Canopy of a Tropical Forest.*

have higher concentrations of storage carbohydrates overall than *Cecropia* and *Urera*.

Leaf, stem and root samples will also be taken from seedlings of the same four species growing under controlled conditions of light and moisture. Samples will be analysed as above. This will help to clarify the patterns of carbohydrate storage in young understory plants that are dependent on light gaps created by tree or branch falls or seasonal changes in the canopy overhead (i.e., when deciduous species shed their leaves). Most understory plants appear to give growth a high priority when light availability increases. However, allocation of carbon to storage is also critical to survival as eventually the canopy will once again close over understory plants. To date, this role of storage has not been examined in tropical forest trees.

6.7: Photosynthesis and Photoinhibition

K. Winter and A. Virgo

To learn more about the carbon dioxide and water vapour fluxes between tropical rainforest plants and their surrounding atmosphere, we have previously used a 40-metre tall tower and a metal ladder system on Barro Colorado Island to perform photosynthesis measurements on a limited number of canopy species differing in life form. These studies revealed a linear relationship between the integrated 24-hour carbon gain of leaves and the maximum rate of net carbon dioxide uptake, Amax[61]. Furthermore, for the canopy tree *Ceiba pentandra,* as well as for one hemi-epiphytic and two epiphytic species, annual leaf-carbon budgets were derived from 24 integrals of carbon gain determined at regular intervals throughout the year. We found a linear relationship between leaf nitrogen content and annual leaf carbon budgets in these plants[62]. These findings represent a remarkable example of functional convergence between plants. Moreover, the practical implications of the linear Amax/carbon gain relationship and the annual carbon gain/nitrogen relationship may prove to be of considerable value for scaling from individual leaves to whole plants and ecosystems. Such considerations become increasingly important as we face the challenge of understanding the responses of plants to global climatic changes.

These previous studies included only one rainforest tree species. To assess further the biological and practical significance of these results, measurements need to be extended to more tropical trees from different habitats, with particular attention to leaf longevity and leaf position within the canopy. Using the canopy

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[61] Zotz, G. and Winter, K., 1993, Short-Term Photosynthesis Measurements Predict Leaf Carbon Balance in Tropical Rainforest Canopy Plants, in *Planta,* no. 191, pp 409-412.

[62] Zotz, G. and Winter, K, in press, Predicting Annual Carbon Balance from Leaf Nitrogen, in *Naturwissenschaften.*

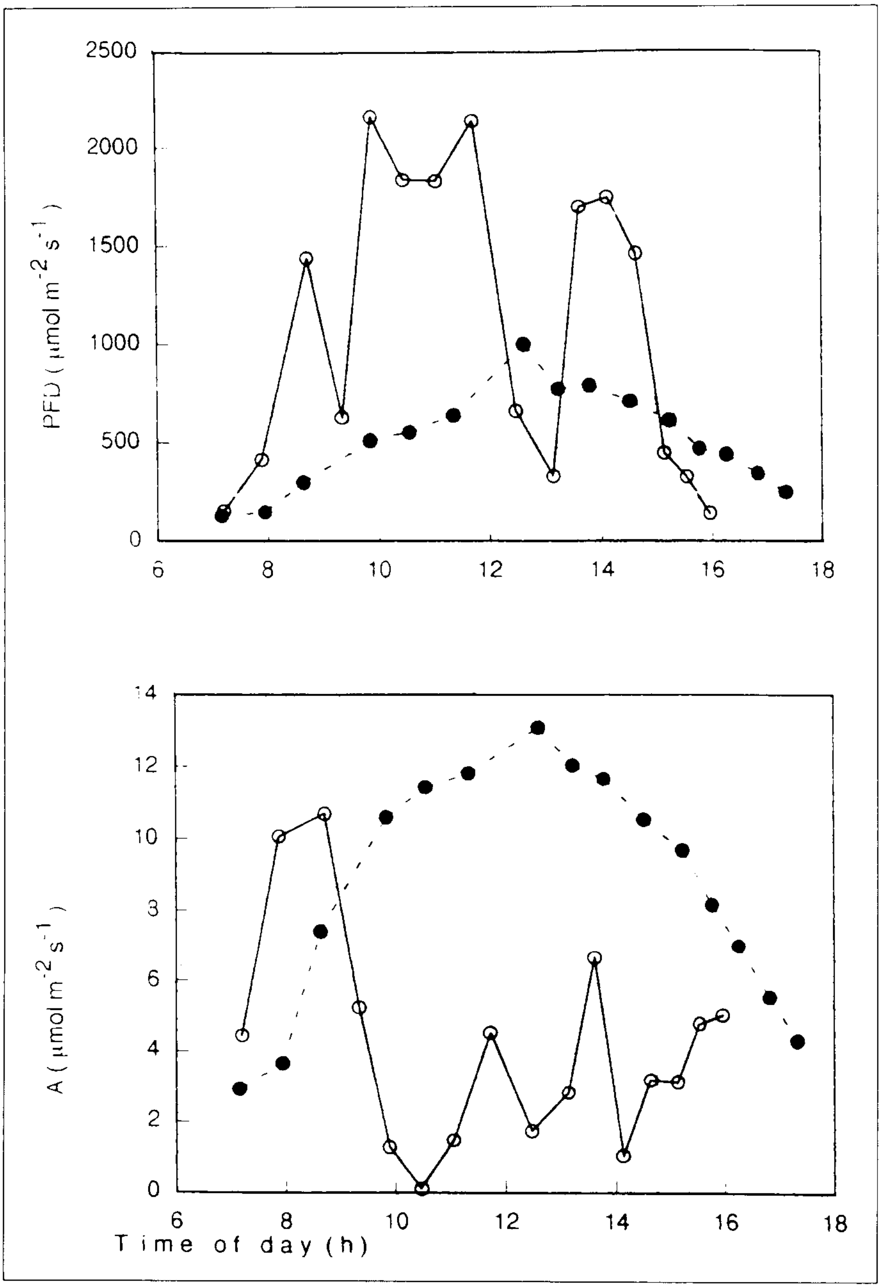

Figure 6.7.1: Photosynthetic rates (A, lower panel) and light intensity (PFD, upper panel) for sun-exposed leaves of *Pseudobombax septanatum* on an overcast and a sunny day. Photosynthesis was limited by stomatal closure after 10 am on the sunny day (open circles, solid line). In contrast, photosynthesis was much greater on the overcast day (filled circles, dashed line).

crane in the Parque Natural Metropolitano, in January 1994 we began to test the carbon gain/nitrogen relationship for sun and shade leaves of several additional canopy trees[63]. At bi-weekly intervals, measurements of diurnal carbon dioxide exchange are combined with measurements of photosynthetic oxygen evolution to obtain information about diurnal carbon gain, *in situ* rates of Amax, as well as Amax under conditions of carbon dioxide and light saturation. Annual carbon budgets will be estimated from determinations of daily carbon budgets and compared with leaf nitrogen levels throughout the growing season. The study will greatly advance our understanding of seasonal changes in photosynthetic carbon dioxide fluxes of tropical trees and provide essential information on the extent to which point measurements of carbon dioxide exchange and leaf nitrogen allow us to scale up to annual carbon budgets of rainforest species.

Our previous and current photosynthesis measurements on outer-canopy leaves of tropical trees show that photosynthetic carbon dioxide uptake is saturated at less than 50% of full sunlight in most species. In fact, direct exposure to sunlight can markedly increase leaf temperatures and lead to stomatal closure thereby decreasing carbon dioxide uptake. Recent studies with the canopy tree *Pseudobombax septenatum* from the canopy crane showed that daily leaf carbon gain was much greater on overcast than on bright days (figure 6.7.1). Thus leaves of canopy trees often absorb much more light than is used in photosynthesis. Absorbance of excess light can cause photoinhibition, i.e. a reversible reduction in photosynthetic competence. It is currently believed that photoinhibition is a regulatory mechanism to protect the plant from sustained photodamage, rather than an indication of tissue damage. In a long-term study of two canopy trees, *Anacardium excelsum* and *Ficus insipida,* which began in September 1993, sustained decreases in the chlorophyll fluorescence parameter F_V/F_M that are characteristic of photoinhibition were regularly observed after bright days. These measurements will be extended to more species and will yield quantitative information on how daily light doses and photoinhibition are related in various trees throughout the dry and wet season.

The mechanisms of photoinhibition and how they vary both between species and within leaves of a single tree growing in different light conditions within the canopy are little understood. Two studies carried out from the canopy crane investigated the role of chloroplast carotenoid pigments - particularly the xanthophyll cycle pigments violaxanthin, antheraxanthin and zeaxanthin - in protecting uppermost canopy leaves from photodamage, especially during the dry season when water stress exacerbates the effects[64]. The carotenoids of the

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[63] See also chapter *6. 8, Photosynthesis and Carbon Gain of the Tropical Pioneer Tree,* Ficus insipida.

[64] See chapter 6.10, *Xanthophyll Cycle Pigments in Tropical Forest Species: A Comparative Field Study of Canopy Trees, Gap and Understory Species* and chapter 6.11,

xanthophyll cycle, particularly antheraxanthin and zeaxanthin, have been implicated in the photoprotective de-excitation of chlorophyll. When light becomes excessive, violaxanthin is de-epoxidized to zeaxanthin through the intermediate antheraxanthin. The photoprotective process that accompanies the accumulation of zeaxanthin provides an alternative pathway for the dissipation of energy. This prevents the excess light from bleaching the chlorophyll pigments which would limit the plant's photosynthetic potential on a long-term, if not permanent, basis.

Comparatively little is known about another mechanism of photoinhibition - the turnover of the D1 protein in photosystem II of the electron transport chain of the chloroplast thylakoid membrane. It is postulated that rapid degradation of the Dl protein under high light conditions may protect the leaf from further photooxidative damage. The role of the D1 protein could thus be compared to that of a fuse.

The relative role of both xanthophyll cycle pigments and D1 protein turnover in regulating photoinhibition under natural conditions is poorly understood. New research will be initiated from the crane in August 1994 to investigate these basic biochemical mechanisms in young and mature sun and shade leaves of canopy trees[65]. The ultimate goal of our photosynthesis and photoinhibition studies is to quantitatively assess the dual role of light - the driving force of photosynthetic carbon dioxide uptake but also reducing the photesynthetic capacity when in excess - in relation to the primary productivity and growth of rainforest trees.

6.8: Photosynthesis and Carbon Gain of the Tropical Pioneer Tree, *Ficus insipida*

G. Zotz, G. Harris, M. Königer and K. Winter

This study tested the hypothesis (established in the 1980s) that photosynthetic rates of tropical trees are similar to those of temperate zone trees. A limited number of measurements have been made of *in situ* carbon dioxide fluxes from static towers in the last decade but we are still far from a full understanding of the gas-exchange properties of tropical forest trees. Once again, the primary limitation has been the difficulty involved in making *in situ* measurements in the uppermost strata of the forest canopy where photosynthetic rates are expected to be higher than elsewhere in the forest.

This research project used the canopy crane to access the outer canopy leaves of three mature specimens (20-25 metres) of *Ficus insipida* to study *in situ* diurnal courses of carbon dioxide gas exchange, transpirational water loss, light, temperature and humidity. Data were collected for fully mature leaves with east and west exposures at intervals of 20-50 minutes from shortly before dawn until

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[65] See chapter 6.12, *Mechanisms of Photoinhibition in Leaves of Tropical Plants.*

dusk on nine days in a seven month period beginning early in the dry season (January 1993) and ending in the middle of the wet season (July 1993).

F. insipida had higher *in situ* rates of net carbon dioxide uptake (and, therefore, of photosynthesis) than any other rainforest tree reported to date. Observed rates (33.1 μmol $m^{-2} s^{-1}$ in the early dry season) were comparable with those recorded for fertilized, irrigated crop plants. During the dry season there were sharp reductions (mid-day depressions) in net carbon dioxide uptake and stomatal conductance at noon, similar to patterns previously described for plants of deserts and semi-arid lands. However, daily carbon gain and wateruse-efficiency (the ratio of carbon dioxide uptake to water vapour loss) did not differ between seasons. East-exposed leaves that received direct sunlight during early morning hours showed higher carbon dioxide uptake rates and lost less water per carbon dioxide fixed than did west-exposed leaves. As previously demonstrated for several canopy species on Barro Colorado Island[66], the maximum daily rate of carbon dioxide uptake in F. *insipida* was an excellent predictor of daily carbon gain.

6.9: Day-Courses of Two Light Activated Calvin-Cycle Enzymes: Field Measurements on a Tropical Forest Tree, *Ficus insipida*

G.C. Harris, M. Königer, G. Zotz and K. Winter

This study investigated the *in situ* effects of light on two important enzymes that enable plants to transform carbon dioxide absorbed from the atmosphere into carbohydrates. These enzymes (phosphoribulokinase and NAD(P)H glyceraldehyde-3-phosphate dehydrogenase) are known to be activated by light but the explicit biochemical mechanism by which this occurs is little understood. To date, virtually all investigations of the light activation of these enzymes have been carried out on herbaceous species under laboratory conditions and have involved light transitions from complete darkness to full illumination. No information is available on changes in the activation state of these enzymes during normal daily variations in light intensity for tropical forest species studied in the field. Understanding the mechanisms by which Calvin-cycle enzymes are activated is important because these enzymes largely determine the plant's photosynthetic efficiency and so affect its growth rate and ability to act as a carbon sink.

The canopy crane was used to gain access to and sample leaves in the uppermost crown of a mature *Ficus insipida*. This uppermost layer experiences the greatest light intensity and greatest daily variation in light intensity of all forest strata. Samples were taken at various times of the day at the beginning of

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[66] Zotz, G and Winter, K., 1993, Short-Term Photosynthesis Measurements Predict Leaf Carbon Balance in Tropical Rain-Forest Plants, in *Planta,* no. 191, pp 409-412.

the dry season (January 1993). The leaves were excised from the canopy and immediately plunged into liquid nitrogen where they were stored until processing. Small sections of frozen leaf pieces were analysed for enzyme activity in the laboratory, using established methodology. At the same time carbon dioxide gas exchange and incident light intensity were monitored in neighbouring canopy leaves in a similar developmental state and position to those sampled.

Results showed substantial phosphoribulokinase activity in leaves harvested before sunrise (approximately 50-65% of fully activated levels) which confirmed previous laboratory findings that phosphoribulokinase can exist in the dark in a relatively high state of activation. Following sunrise, the enzyme's initial activity increased slowly, prior to carbon dioxide assimilation, and then continued to increase steadily and in parallel with carbon assimilation throughout the late morning and early afternoon. This correlation between phosphoribulokinase activity and carbon assimilation rates was no longer evident by late afternoon when the light was fading, or when light levels were temporarily reduced by passing clouds. Overall, phosphoribulokinase activity reached its maximum observed activation state and appeared to saturate at much higher light intensities (in excess of 1,000 μmol photons $m^{-2} s^{-1}$) than previous studies have shown. It is possible that the changes observed here over several hours represent a different phenomenon than the short-term stimulation seen in most laboratory experiments which generally last just minutes. For example, protein synthesis may have contributed to the increased phosphoribulokinase activity and the slow rate of saturation.

NAD(P)H glyceraldehyde-3-phosphate dehydrogenase showed little or no evidence of light activation. In 90% of the samples taken throughout the day the activation state of NAD(P)H glyceraldehyde-3-phosphate dehydrogenase was 40% or less and this changed little.

6.10: Xanthophyll Cycle Pigments in Tropical Forest Species: A Comparative Field Study on Canopy Trees, Gap and Understory Species

M. Königer, G. Harris, A. Virgo and K. Winter

This research project examined the role of xanthophyll-cycle pigments - particularly violaxanthin and zeaxanthin - in protecting the leaves of a variety of tropical forest trees acclimated to different light environments from damage caused by excess light.

The construction crane was used to access upper- and inner-canopy leaves of seven canopy trees in the Parque Natural Metropolitano during the rainy season (May-December) in 1992. The kinetics of zeaxanthin production and degradation were studied under various light conditions in the field, both during normal diurnal cycles (dawn to dusk) and during rapid fluctuations in light intensity (e.g., passing clouds, sunflecks, etc). Photosynthetic capacity, light intensity and ambient and leaf temperature were measured *in situ*. Sun-exposed leaves of six canopy tree species were harvested prior to dawn after a sunny day and analysed for chlorophyll a fluorescence to determine the photochemical efficiency of the leaves' photosystem II reaction centre (where light energy is harvested and photoinhibition takes place). At the same time, leaf samples were taken from the various forest strata and frozen immediately in liquid nitrogen. Pigments were later extracted and analysed in the laboratory using High Performance Liquid Chromatography (HPLC) to determine the pool size of both carotenoid (xanthophyll and carotene) and chlorophyll a and b pigments. Results from this study were contrasted with results obtained using similar methodology on leaves of eight gap species and fourteen understory species on Barro Colorado Island.

It was found that sun-exposed leaves of canopy trees showed the highest photosynthetic capacities and largest xanthophyll-cycle pools. In high-light conditions, canopy leaves rapidly converted up to 96% of their violaxanthin into zeaxanthin. The conversion from zeaxanthin back into violaxanthin occurred much faster in low light than in total darkness. At the end of the night, zeaxanthin still accounted for an average of 14% of the total xanthophyll-cycle pigments.

Leaves of gap plants showed moderate photosynthetic capacity and a 43% lower total carotenoid content than canopy leaves. Under high light conditions, gap plants converted up to 86% of the xanthophyll-cycle pigments into zeaxanthin. Following a decrease in light levels the conversion from zeaxanthin back into violaxanthin was much slower. At the end of the night, on average, zeaxanthin accounted for 7% of the xanthophyll-cycle pigments of gap plants.

Understory plants showed the lowest photosynthetic capacity and the smallest xanthophyll-cycle pool (fully 75% lower than in canopy leaves). The conversion of xanthophyll-cycle pigments into zeaxanthin was negligible, except when sunflecks exceeded five minutes in duration. Prior to dawn, leaves of understory plants rarely contained any detectable zeaxanthin.

Overall, there was an inverse relationship between the extent to which plants engage in the xanthophyll cycle and their photosynthetic capacity. The finding that on bright days leaves of canopy trees convert almost 100% of violaxanthin into zeaxanthin shows that these plants experience severe light stress and indicates that xanthophyll pigments play a significant role in the photo-protection of these tropical forest trees.

6.11: Photoinhibition and Xanthophyll Cycle Activity in Young and Mature Canopy Leaves of Tropical Rainforest Plants

G.H. Krause, A. Virgo and K. Winter

This research investigated the role of chloroplast pigments, particularly the yelloworange-red xanthophyll cycle pigments and alpha-carotene, in protecting young and mature canopy sun leaves from photoinhibition. Tropical forest trees frequently produce young canopy leaves on the distal tips of branches where light intensity is greatest. Young leaves differ markedly in their pale-green appearance to dark-green, mature canopy leaves. It was predicted that these young, pale-green, upper canopy leaves would exhibit different biochemical and physiological protective mechanisms to the effects of high irradiance to mature, dark-green canopy leaves.

The canopy crane was used to take *in situ* measurements of photosynthetic gas exchange and chlorophyll fluorescence (i.e., the amount of light absorbed by the leaf) in mature and developing sun-exposed canopy leaves of seven tropical forest tree species. Chlorophyll fluorescence was also measured in detached leaves which were exposed to high light (1.8 mmol photons m^{-2} s^{-1}) in controlled-environment chambers at the Smithsonian Tropical Research Institute. Sampled leaves were also analysed in the laboratory using High Performance Liquid Chromatography to determine the amount of xanthophyll cycle, carotene and chlorophyll pigments.

Results showed that young canopy leaves were significantly more susceptible to photoinhibition than were mature canopy sun leaves. Young leaves had about half the concentration of chlorophyll a and b pigments of mature leaves. Young leaves also exhibited a strongly lowered alpha-carotene content, and a higher content of xanthophyll cycle pigments, particularly zeaxanthin under strong illumination. Both mature and young leaves recovered quickly from photoinhibition in low light conditions.

The results suggest that the high degree of reversible photoinhibition observed in young sun leaves represents a dynamic regulatory response that protects the leaves' photosynthetic apparatus from severe damage by excess light.

6.12: Mechanisms of Photoinhibition in Leaves of Tropical Plants

A. Thiele, G.H. Krause and K. Winter

This research will begin in late 1994 and will be the first study to assess the relative role of two biochemical mechanisms in photoinhibition/photoprotection in tropical plants under natural conditions. Investigations will assess the relative role of xanthophyll cycle pigments and alpha-carotene, together with turnover of the D1 protein in the photosystem II reaction centre in photoinhibitory processes in young and mature canopy leaves.

Preliminary studies carried out from the canopy crane have shown that young, usually extremely sun-exposed leaves are much more susceptible to photoinhibition than mature leaves and that young leaves exhibit a higher content of xanthophyll cycle pigments per unit chlorophyll than mature leaves[67]. However, the role of the D1 protein in young and mature leaves is not understood[68]. Possibly the xanthophyll cycle pigments provide initial photoprotection when leaves undergo the early stage of excess light conditions whereas the D1 degradation mechanism is activated later.

In this research, the canopy crane will be used to access and sample young and mature sun and shade leaves of several species of canopy trees. Photoinhibition and recovery will be studied and manipulated *in situ* during the course of the day, using streptomycin to inhibit D1 protein synthesis and dithiothreitol (DTT) to prevent zeaxanthin formation in leaves. Chlorophyll fluorescence and gas exchange measurements will be made to characterize photosynthetic activity.

These *in situ* measurements will be complemented by laboratory analyses of the size of xanthophyll pigment pools in sampled leaves using High Performance Liquid Chromatography. Particular attention will be paid to changes in the level of alpha-carotene whose role in photo-protection is not yet understood. The turnover of D1 protein will be analyzed by electrophoresis and Western blotting methods.

Results from this research will be compared with results of similar research carried out on plants growing in temperate zone climates. This research will help to determine the physiological reasons for the differences in photosensitivity between young and mature canopy leaves and will help to clarify how D1 protein turnover and xanthophyll cycle pigments interact under natural conditions during photoinhibition.

6.13: Mechanisms of Long-Distance Water Transport in Plants: A Re-Examination of some Paradigms in the Light of New Evidence[69]

U. Zimmermann, A. Hasse, D. Langbein and F. Meinzer

This study used the canopy crane to test several predictions of the cohesion theory of the ascent of sap. This theory proposes that sub-vacuum tensions are created in the plant during the process of transpiration which effectively draw water up from the plant roots, through the xylem to the leaves. This theory has been the standard text-book explanation for the ascent of sap in tall plants since it was introduced by Scholander *et al* in 1965[70]. The research group led by Dr Prof U.

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[67] See chapter 6.10, *Xanthophyll Cycle Pigments in Tropical Forest Species: A Comparative Field Study of Canopy Trees, Gap and Understory Species* and chapter 6.11, *Photoinhibition and Xanthophyll Cycle Activity in Young and Mature Canopy Leaves of Tropical Rainforest Plants.*

[68] See chapter 6.7, *Photosynthesis and Photoinhibition.*

[69] This research was published by the *Philosophical Transactions of the Royal Society of London,* series B (1993), no. 341, pp 19-31.

[70] Scholander, P.F., Hammel, H.T., Bradstreet, E.D. and Hemmingsen, E.A., 1965, Sap Pressure in Vascular Plants, in *Science,* no. 148, pp 339-346.

Zimmermann questions the cohesion theory because the predicted negative pressures in the plant xylem have never been measured directly. Dr Prof Zimmermann and his associates have developed a micro-pressure transducer that can be introduced into minute xylem elements in leaf tissue to make possible the first direct measurements of plant water potentials.

The canopy crane was used to access leaves 30 metres above the ground. Raw height provided a crucial test of the cohesion theory because a negative tension of 3 atmospheres (or -3 bars or -0.3 MPa) is required to pull water up 30 metres against gravity. The cohesion theory further predicts that water tensions can only become more negative as the plant transpires. Water tensions of -20 to -30 bars are commonly observed in transpiring trees using the generally-accepted, indirect methods to measure plant water tensions.

The investigators found that xylem pressure probe measurements in the leaves of tall individuals of *Anacardium excelsum* were sub-atmospheric or slightly negative. Xylem pressures decreased throughout the day as the transpiration rate increased due to rising temperatures and decreasing humidity and, in the rainy season, xylem pressures decreased more strongly when a light breeze arose, which is probably also a result of increased transpiration. Although internally consistent, the xylem pressure probe measurements were one to two orders of magnitude greater than standardly-accepted, indirect measurements and impossible to reconcile with the cohesion theory of the ascent of sap.

The results suggest that the cohesion theory is wrong. However, this conclusion is controversial. Other plant water relations experts believe that the micro-pressure transducer makes an imperfect seal as the leaf xylem element is punctured and that this permits equilibration of tensions within the xylem element and the atmosphere. Future experiments will resolve this controversy. In any event, this research provided a rigorous test of the crane as a canopy access system. The gondola was sufficiently stable to introduce a microcapillary into a microscopic leaf xylem vessel and hold it in place for up to five hours.

6.14: Whole-Tree Transpiration: Linking Stand Structure, Composition and Phenology with Watershed Hydrology

R. Oren and R. Zimmermann

This study examined seasonal changes in whole plant water vapour transpiration by upper canopy tropical trees. Whole tree transpiration was calculated by applying a known amount of heat to the lower trunk and monitoring its flux up the trunk with the transpirational water stream. Similar studies conducted by the same authors in Belize showed that, at the stand level, the dry-season reduction in transpiration per ground area achieved by some species which shed their leaves was more than compensated by the increase in transpiration by other species - species whose transpiration rate increased in direct relation to atmospheric vapour pressure deficits. In this way the transpiration rate on a ground-area basis was maintained during the dry season at the same level, or increased relative to the wet season.

In Panama, the canopy crane was used to access upper canopy leaves for simultaneous measurement of several water relations parameters, including leaf water potential, conductance to water vapour and whole tree transpiration. These measurements, combined with phenological observations, permitted an unambiguous characterization of the integrated responses of several tropical tree species to seasonal changes in their environment.

Results showed that tropical trees respond to drought in one of three ways. The three types of responses were: (a) shedding foliage; (b) reducing transpiration through stomatal regulation; and (c) continuing to transpire in direct relation to the atmospheric demand, resulting either in a reduction in tissue water content or water potentials, or both. Most species combined all three types of responses to different degrees. Their range of responses indicates that plant phenology (e.g., the rate of leaf expansion and senescence), plant water relations (e.g., stomatal response to saturation vapour pressure deficit and to plant water potential) and tissue (mostly stem) water storage must be incorporated into stand-level estimates of seasonal transpiration and water budgets.

6.15: Carbohydrates and Osmotic Adjustment in Canopy Leaves

M. Popp and K. Winter

This research project is investigating the quantity and type of carbohydrates produced by leaves of various tropical forest trees growing in different microenvironments within the canopy. All plants have different photosynthetic rates and produce different types and amounts of carbohydrates according to their genetic structure and environmental conditions. These carbohydrates include fructose, glucose, sucrose and insoluble starch. The aim of this research is to assess which type of carbohydrates accumulate diurnally in each species. to assess whether the type of carbohydrate that accumulates during the daytime varies according to photosynthetic rates and to investigate how leaf carbohydrate content is reduced overnight.

This research will also investigate the role of certain carbohydrates (pinitol and inositol) that have been postulated to play an important role in leaf osmotic adjustment and turgor maintenance under conditions of drought stress. The presence or absence of these carbohydrates may indicate the extent to which these leaves undergo daily and/or sustained leaf water deficits during the dry and wet season.

The canopy crane was used to take *in situ* measurements of photosynthetic gas exchange at different times of the day and night in leaves of 10 species of tropical forest trees growing in different light environments within the canopy. At the same time, leaf samples were collected and returned to the laboratory for analysis of carbohydrate content. Leaf samples are still being analysed using High Performance Liquid Chromatography but preliminary data indicate that, depending on the species, leaves contain considerable levels of either pinitol or inositol during the dry season.

6.16: Optimal Seed Size, Maternal Selection and Leaf Phenology of Two Neotropical Tree Species

C. Potvin

This project completed in 1994 examined the mechanisms by which individual trees adjust their reproductive output in response to spatial variation in light availability within their crowns. Two alternative hypotheses were considered. The first hypothesis was that trees would selectively abort fruit in shaded branches to maintain equal quality seeds regardless of local light availability. The second hypothesis was that trees would produce seeds of higher quality in the uppermost, fully sun-exposed branches and seeds of lower quality on lower shaded branches.

The canopy crane was used to monitor sun and shade branches on five individuals of two tree species, *Anacardium excelsum* and *Luehea seemannii,* throughout their reproductive period. Careful measurements of light levels, total leaf area, representative photosynthetic rates and numbers of developing fruit were made to determine the ratio of carbon resources to seeds produced for each branch. Seed mass (carbon content) and nitrogen concentrations were used to estimate seed quality.

The clear result was that both tree species produced seeds of similar quality on all branches. Selective abortion of developing fruit and initiation of fewer inflorescences were the primary mechanisms that permitted the production of reduced numbers of seeds of similar quality on shaded branches.

Chapter 7:

Physiological Responses to Variation in Atmospheric Carbon Dioxide

Carbon dioxide is essential for plant growth. During photosynthesis, plants convert atmospheric carbon dioxide and light energy into simple sugars (carbohydrates). These carbohydrates are used by the plant for maintenance, defense and reproduction, as well as growth. Before the industrial revolution carbon dioxide accounted for 265-280 molecules per million molecules of air (265-280 ppm). Since then, the atmospheric concentration of carbon dioxide has increased to 353 ppm, largely due to anthropogenic activities (burning of fossil fuels, etc), and a further increase to 700 ppm is anticipated in the next century. The consequences of this immense increase in atmospheric carbon dioxide for plants is an area of intense investigation. Experiments with increased levels of atmospheric carbon dioxide on grain crops grown with ample nutrients, light and water have shown an increase of 36% in marketable yield. However, it is not clear what the consequences of increases in atmospheric carbon dioxide will be for plant growth for natural vegetation where other essential resources (such as nutrients, light and water) are often limiting. The construction crane in the Parque Natural Metropolitano permits researchers for the first time to study and manipulate *in situ* the interchange of carbon dioxide between the atmosphere and the upper forest canopy where more than 90% of forest leaves are concentrated.

7.1: Total Non-Structural Carbohydrate Pools in Tropical Forest Trees

Chr. Körner, M. Würth and K. Winter

This study is testing the hypothesis that the size of a plant's non-structural carbohydrate pool is indicative of the degree of the plant's carbon saturation. If this is so, screening for the size of such pools in tropical forests may indicate the extent to which trees have been affected by the large increase in atmospheric carbon dioxide since the industrial revolution[71]. It may also clarify the remaining

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[71] Nilsson, A., 1992, *Greenhouse Earth,* Published on behalf of the Scientific Committee on Problems of the Environment (SCOPE), the International Council of Scientific Unions (IUCN), and the United Nations Environment Programme (UNEP) by John Wiley & Sons, Chichester, England, pp. 24-25.

potential of tropical forests to absorb increasing amounts of atmospheric carbon dioxide and so help to predict the future role of forests in controlling processes of global warming.

Total non-structural carbohydrates (TNC) represent a significant fraction of plant biomass. TNC accumulate in leaves when the plant's rate of photosynthesis exceeds its immediate needs. These stored carbohydrates are largely dissipated at night (when the plant is unable to photosynthesise) and metabolized for growth and other life processes. In experiments carried out in greenhouses in Switzerland, plants grown under optimal conditions of water, light and nutrients, but subjected to elevated levels of carbon dioxide, had large pools of un-metabolized carbohydrates at the end of the night. This suggests that they fixed more carbon than either the leaf or the whole plant could use. The presence of similarly large carbohydrate pools in tropical forest trees may indicate the degree to which tropical forests have already been affected by increases in atmospheric carbon dioxide. On the other hand, the presence of small TNC pools would not necessarily mean that tropical forests have not been affected by increased atmospheric carbon dioxide. It may be that, in natural conditions, plants are able to regulate their uptake of carbon dioxide in accordance with other available resources and their carbohydrate needs.

The only way to test the carbon-dioxide response of individual plants in their natural environment is to subject them *in situ* to artificially manipulated levels of atmospheric carbon dioxide and to measure their corresponding rates of photosynthesis and the size of their carbohydrate pools. Until now, this has not been possible for tropical forest trees owing to their height and the consequent problems involved in accessing the uppermost forest strata where natural photosynthetic rates are highest. This study has therefore largely been made possible by the construction crane is enabling researchers to access the canopy of six species of tropical forest tree during the peak rainy (November) and dry (March/April) seasons during 1994.

Parts of leaves will be exposed, *in situ,* to elevated carbon dioxide and photosynthetic measurements will be made. High levels of carbohydrate pools in exposed leaf tissue would suggest that individual cells limit the rate at which accumulated carbohydrates are dissipated, rather than being a reflection of the plant's overall degree of carbon saturation. The size of the TNC pool in whole leaves will be compared and contrasted under several light regimes, both natural and manipulated, within the canopy. Previous experiments have shown that in conditions of elevated carbon dioxide, plant growth rates increase with increased levels of light. However, it may also be that this is a plant defense against photodamage: higher photosynthetic rates under strong light may dissipate the excess energy that would otherwise cause photodamage. Study of the relationship between carbon dioxide levels and leaf position within the canopy may explain how light variation affects the accumulation of mobile carbohydrates.

The leaf-level analyses of TNC pools will be complemented by whole plant, species and community-level analyses of TNC. TNC will be determined for typical storage tissues such as stems, branches and older roots, as well as for leaves. Repeated measurements will be made throughout the year to determine the degree to which carbohydrate pools are depleted during periods of high demand, such as during developmental phases of the tree (leafing, flowering, fruiting). This may cast light on the connection between TNC and sink activity.

At the community (stand) level, TNC pools will be examined on a unit land area basis. Species will be weighted by their abundances to merge species-level carbohydrate pools to give an overall community estimate. This will be the first community-level estimate of TNC pools for a tropical forest and will permit a global-level comparison of TNC pools across major biomes of contrasting temperatures.

The whole plant-, community- and global-level analyses will provide insight into the growth and developmental dynamics of tropical trees and the potential responses of natural vegetation to increasing atmospheric concentrations of carbon dioxide. This comparison will provide insight into global trends for forest responses to increases in atmospheric carbon dioxide and may reveal how forest-level carbon dioxide responses are related to temperature, latitude and altitude.

Chapter 8:

Effects of Ultra-Violet Radiation on the Upper Canopy

Plant growth is dependent on photosynthetically active radiation - light energy in the 400-700 nm wavelength to which photosynthesis is sensitive. Ultra-violet-B radiation is light energy in the 280-320 nm wavelength which cannot be used for photosynthesis and which damages the DNA in plant and animal tissues. Throughout the world the amount of ultraviolet-B radiation that reaches earth is increasing due to the damage caused to the atmospheric ozone layer by man-made sources of pollution (chlorofluorocarbons, halons, etc).

The biological implications of ultra-violet B radiation and its effects on vegetation are not fully understood. Experiments carried out on agricultural crops grown in monoculture showed that plant growth rates were unaffected by increased levels of ultra-violet B radiation. However, when wheat and wild oats were grown together and subjected to enhanced ultraviolet-B radiation, there was a marked change in the competitive balance between the two species, mostly because of altered plant morphology.

It is not known how ultra-violet-B radiation affects the competitive balance between the numerous plant species that make up diverse tropical forests, or whether increasing levels of ultra-violet-B radiation will cause long-term changes to the forest ecosystem. Even without ozone depletion, levels of ultra-violet-B radiation are higher in the tropics (up to 400 μmol m^{-2} s^{-1}) than elsewhere because the sun's rays strike the earth more directly and so pass through less radiation-absorbing atmosphere than at higher latitudes. Experiments carried out on the leaves of shade-tolerant and gap-pioneering forest tree seedlings growing in an experimental garden on Panama's Barro Colorado Island showed that tropical vegetation responds to natural, present-day levels of ultra-violet-B radiation. Leaves of plants that were exposed to ultra-violet-B radiation were shorter and overall plant height was reduced, particularly in shade-tolerant species that were suddenly exposed to near-ambient ultra-violet-B. In addition, exposed leaves often exhibited increased ultra-violet-B-absorbing compounds and increased leaf mass per area[72]. These results suggest that even minor ozone layer depletion in the

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[72] Searles, P.S., Caldwell, M.M. and Winter, K., 1994, Response of Five Tropical Species to Natural Solar Ultra-Violet-B Radiation, awaiting publication.

tropics may have significant biological implications for forest ecosystems. Already a marked ozone reduction has been detected within 15° of the equator by the Total Ozone Mapping System for the years 1979-1992[73].

Sun leaves of the uppermost tropical forest canopy are exposed to higher levels of solar radiation (and therefore of ultra-violet-B radiation) than shaded leaves at lower forest strata. Using the canopy crane to gain access, researchers will investigate *in situ* how leaves of this most-exposed of forest strata respond to natural and manipulated levels of ultra-violet-B radiation and will explore the defense mechanisms by which plants are able to protect themselves from excessive absorption. This information will help to clarify the degree to which tropical forest growth and regeneration has been and may continue to be affected by ongoing damage to the ozone layer.

8.1: The Response of Five Tropical Plant Species to Natural Solar Ultra-Violet-B Radiation

M.M. Caldwell, P.S. Searles and K. Winter

A project will be initiated in late 1994 to study *in situ* ultra-violet-B radiation responses of canopy leaves from the canopy crane. Results will be compared with the responses of seedlings studied under different ultra-violet-B regimes in Barro Colorado Island. The results of this initial seedling study completed in 1993 indicate the potential importance of ultra-violet-B radiation in the canopy.

The effects of ultra-violet-B radiation on photosynthesis, growth rates and leaf concentrations of ultra-violet-B absorbing compounds were studied for tree seedlings of five tropical tree species. Previous studies of the effects of ultra-violet-B radiation have been carried out on temperate zone agricultural crops grown in glasshouses and subjected to artificially high light levels. This was the first study to be carried out on native woody tree species growing outdoors under the natural light conditions of the tropics. Ultra-violet-B irradiance levels are significantly higher in the tropics than at higher latitudes.

Seedlings were grown under polyester filters to block out all ultra-violet-B radiation and also under ambient light. Ambient levels of ultra-violet-B radiation reduced plant height growth and altered leaf morphology in climax, shade-tolerant species and also in pioneer, high-light-demanding species. Ambient levels of ultra-violet-B radiation also induced higher concentrations of ultra-violet-B absorbing compounds in four of the five species. This may reflect the importance of these compounds in preventing photosynthetic damage.

These results provide the first evidence of the potentially adverse effects of present day, natural ultra-violet-B radiation on tropical forest vegetation. Ambient

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[73] Murali, N.S. and Gruijl, F.R., 1993, Skin Cancer and UV Radiation, in *Nature*, no. 366, pp 23.

levels of ultra-violet-B radiation may reduce growth in some species and may alter interspecific competitive relationships and, as a consequence, forest species composition. Increases in ultra-violet-B levels due to damage to the ozone layer will exacerbate these effects, particularly in the tropics where plants are already exposed to high background levels of ultra-violet-B radiation. The data suggest that minor ozone depletion in the tropics may have biological implications.

8.2: Ultra-Violet-B Absorbing Substances in Canopy Leaves

M. Veit and K. Winter

This research project is investigating the quantity and type of ultra-violet absorbing compounds in leaves of various tropical forest species growing in different light environments. Phenolic substances, including the flavonoids, have long-been discussed as protecting leaves against the damaging effects of high ultra-violet-B radiation. Using the canopy crane, samples have been taken from leaves of a large number of canopy tree species for High Performance Liquid Chromatography analysis of leaf phenolics. The study will identify the different substances that may be employed by different species in ultra-violet-B protection in young and mature, sun and shade leaves. The study will also reveal information about possible short-term fluctuations of these compounds in response to daily variation in light conditions. Samples have been taken from leaves of rainforest gap and understory plants for comparison. The samples are currently being analysed and the data will be contrasted with those obtained from studies on temperate zone plants. This is the first investigation to broadly survey the content and chemical characteristics of ultra-violet-B absorbing compounds in tropical plants. The data can be used to further evaluate the extent to which tropical forest canopy plants are already affected by natural ambient levels of ultra-violet-B radiation.

Chapter 9:

Achievement Indicators of Short-Term Objectives

Section 3.2 of the original project document listed four achievement indicators of short-term objectives. These were:

a): *Increased scientifically tested and management oriented data and information on tropical forest biological diversity, including: (i) on micro-climate patterns, (ii) physiological responses, (iii) canopy ecosystems, and (iv) number of tropical taxa assessed and their biology understood using the methodology developed by this project.*

(b) *Scientists draw on the publications to design strengthened tropical forest biological biodiversity conservation programmes at the national, sub-regional and regional levels.*

(c). *The catalytic impact of the publications will be gauged through their citation in the scientific literature and through their role in promoting closer interaction and cooperation with other scientific organizations and management authorities which are addressing problems of conservation of tropical forest biological diversity.*

(d) *Number of countries that will have adopted the use of the Canopy Access System.*

This chapter discusses how far phase I has fulfilled each of these achievement indicators.

The preceding chapters provide brief overviews of the 25 research projects that have been conducted or recently initiated from the canopy crane. Collectively, this body of work represents a revolution in our knowledge of ecological and physiological processes in tropical forest canopies.

It is premature to apply the second and third achievement indicators at this time. These indicators are based on the impact of crane-based research publications on conservation planners (indicator *b)* and on the scientific community (indicator c). These impacts are necessarily limited at this time because the canopy crane was installed late in 1990, the first methodological publication appeared in 1992 and publications including scientific results only began to appear in 1993 (Annex IV). The great majority of crane-based research projects were initiated after 1992, data collection is still in progress and publications will appear in a timely manner. In the future, these publications will have a tremendous impact on the international scientific community. In addition, a UNEP-funded conference is proposed for phase II of the project to bring conservation planners and canopy investigators together to explore interactions[74].

The final achievement indicator (d) has been fulfilled. Three countries are now installing canopy crane access systems. In the United States, Drs Jerry Franklin, Nalini Nadkarni and David Shaw have received funding to install a canopy crane in Douglas Fir/Ponderosa Pine forests of the Wind River area of the Thomas Munger Reserve in Washington state. In Austria, Dr Wilfried Morawetz has received funding to install a crane in lowland tropical forest at La Esmeralda, Venezuela. And in Norway, scientists at the Norwegian Institute for Nature Research plan to install a crane in coniferous forest. In addition, scientists from a consortium of six European countries recently (July 1994) completed an initial planning workshop to create a Tropical Canopy Programme which will install a canopy crane at a tropical forest site to be identified[75]. Representatives of all four research groups have visited the prototype crane funded by UNEP/STRI in Panama. Active contact is being maintained with all four groups so that research comparable to that conducted in Panama can be initiated as their cranes are installed.

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[74] See chapter 10, *Future Perspectives.*

[75] See Annex VI: *Other Canopy Research Developments.*

Chapter 10:

Future Perspectives

The development and success of the tropical forest canopy project has surpassed initial expectations. The canopy crane has proven to be an effective instrument facilitating long-term monitoring and research in biodiversity and microclimate in what was previously an inaccessible strata of the tropical forest. The crane is being utilized to maximum capacity. The quality of the monitoring and research carried out in the project is reflected in the number of articles already published (and awaiting publication) in leading scientific and environmental journals throughout the world (see Annex IV). The planned initiation of similar projects in Washington state, USA, Venezuela and Norway (see Annex IV) is an indicator of the receptivity that the canopy access system tested in Panama is having worldwide. A major contribution of the project has been the number of researchers and scientists from the developing world, primarily from Latin America, who under the guidance of STRI scientists, have been trained in tropical forest canopy biology.

Given these successes, it is proposed that a second phase of activities be initiated in which the overall objectives of the project remain unaltered. The key elements of the phase two proposal are to install a second crane in a contrasting everwet tropical forest and to organise a joint UNEP/STRI conference on the Biodiversity and Ecology of the Tropical Forest Canopy.

A second canopy crane will augment the UNEP/STRI canopy biology programme in several ways. First, the prototype crane is oversubscribed and several important research projects have been postponed indefinitely and others have been delayed. Second. the prototype crane is located in a forest reserve adjacent to Panama City and the proximity of the city limits the usefulness of the site for some types of studies[76]. Most important, however, is the heterogeneity of tropical forests. The general significance of scientific findings from a single tropical forest is unclear until parallel research is conducted in contrasting tropical forests. Moreover, many scientific questions have an explicit geographic component. For example, accurate estimates of the number of canopy arthropod species will require hard data on the degree of constancy of arthropod/lhost plant associations across

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[76] See chapter 5, *Canopy Energy Balance.*

contrasting forests[77]. For all of these reasons, it is proposed that a second canopy crane access system be installed in a contrasting everwet forest in Panama.

The Panamanian isthmus provides an ideal gradient for contrasting canopy studies. Throughout the lowland tropics, the amount and seasonality of rainfall cause the clearest gradients in forest structure and biodiversity[78]. Along a gradient of increasing rainfall and decreasing rainfall seasonality, dry, closed-canopy deciduous forests are replaced by taller, semi-deciduous forests and finally by evergreen, perhumid forests[79]. The biodiversity of plants increases by five-to-tenfold along such rainfall gradients[80]; changes in biodiversity of arthropods remain unstudied.

The prototype canopy crane is located in a dry, deciduous forest on Panama's Pacific coast where annual rainfall averages 1,740 mm. The crane site is connected by 370 km2 of contiguous forest reserves and national parks to an evergreen forest on the Caribbean coast where annual rainfall averages 3,400 mm. This forest in the newly-created Parque Nacional Interoceanica is proposed as the site for a second canopy crane.

These two contrasting, lowland forest sites separated by just 70 km offer an ideal comparison for canopy studies. Many plant species are shared between the two sites; many more are restricted to just part of the isthmian rainfall gradient and are found at just one of the extreme sites. This presents an ideal situation to compare and contrast the host plant ranges of canopy arthropods. Two critical questions need to be answered. Does the same tree species play host to different canopy insect species in forests with contrasting rainfall regimes? And, does a single insect species specialize on different host plant species in different parts of its range? Answers to these questions are urgently required by conservationists attempting to maximise biodiversity in protected areas and will also lead to refinements of estimates of global canopy arthropod diversity. The canopy crane to be erected in Venezuela (see Annex IV) will not elucidate these critical questions because few plant species are shared between Central America and the Guyana shield. A second canopy crane access system in Panama will allow studies of a host of other scientific questions with an explicit geographic component, relieve the severe oversubscription of the prototype crane, be suitable for eddy-correlation analyses of canopy-atmosphere energy and

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[77] See chapter 3, *Biodiversity.*

[78] Wright, S.J., 1992, Seasonal Drought, Soil Fertility and the Species Density of Tropical Forest Plant Communities, in *Trends in Ecology & Evolution,* vol. 7, no. 8, pp 260-263.

[79] Holdridge, L.R., Grenke, W.C., Hatheway, W.H., Liang, T. and Tosi jr, J.A., 1971, *Forest Environments in Tropical Life Zones,* Pergamon Press; and Koppen, W. and Geiger, R., 1930, *Handbuch der Climatologie,* Teil I D, Borntraeger, Berlin.

[80] Gentry, A.H., 1988, Annals of the Missouri Botanical Gardens, no. 75, pp 1-34; Hall, J.B. and Swain, M.D., 1981, *Distribution and Ecology of Vascular Plants in a Tropical Rain Forest: Forest Vegetation in Ghana,* Geobotany series, vol. I; and Gentry, A.H., and Dodson, C.H., 1987, Diversity and Biogeography of Neotropical Vascular Epiphytes, in *Annals of the Missouri Botanical Gardens,* vol. 74, pp 205-233;

gas exchange, and allow validation and generalization of findings made from the prototype crane.

The second key element of phase II of the UNEP/STRI canopy biology programme is a conference proposed to bring canopy scientists, conservationists and global change specialists together. Given the volume and complexity of the studies carried out in phase I of the project, the fact that many of these projects were carried out independently of one another, and the long time lag between data collection and publication in the appropriate scientific journals, it is felt that greater effort is required to interpret the relevance of the findings with regard to decision-making and management. At the same time, attention should be given to future monitoring and research priorities within the framework of an open-minded philosophy for advancing scientific knowledge.

Therefore, it is proposed that STRI, in collaboration with UNEP, organize a conference on the Biodiversity and Ecology of the Tropical Forest Canopy for November 1996. This conference is timed to follow two years after the Canopy Biology Symposium to be held at the Marie Selby Botanical Gardens in November 1994 (see Annex IV) and will take a pan-tropical approach to developments in canopy biology. The four main objectives of the conference will be to: (i) review the findings of the project's studies, (ii) promote dialogue and exchange of ideas among tropical forest canopy researchers, (iii) assess the relevance of the studies to decision-making and environmental management, and (iv) recommend areas of monitoring and research which require greater attention.

It is expected that 30-40 persons will be invited, to include the following (in addition to Smithsonian investigators):

- experts involved in tropical forest canopy monitoring and research who will present papers at the Conference;
- relevant UNEP/headquarters staff to be determined by the organisation;
- a representative of the Secretariat of the Biodiversity Convention;
- a representative of the Secretariat of the Climate Change Convention;
- the Coordinator of UNEP's Environmental Assessment Sub-programme for Latin America and the Caribbean;
- a representative from each of the USA, Venezuelan, Norwegian and European Community canopy crane projects (see Annex V);
- a climate change scientist to be recommended by UNEP;
- two tropical forest/biodiversity experts recommended by UNEP; and
- a representative of the Scientific Committee on Problems of the Environment (SCOPE) .

The Proceedings of the above Conference will be published and widely distributed to the appropriate policy-makers, scientists and environmental managers by STRI and UNEP in collaboration. In addition, Drs S. Joseph Wright and Klaus Winter will edit a second book with the objective of integrating the wide variety of projects conducted at the prototype crane to provide a uniquely integrated view of ecological and physiological process in a tropical forest. The editors of the Academic Press (New York, New York, USA) have already expressed interest in this contribution which could be published along the lines of the SCOPE publications funded by UNEP.

Phase II of the project would also include the following additional elements:

i As in phase 1, research findings in phase II would continue to be published in leading scientific and environmental management journals throughout the world.

ii Through UNEP, phase II of the project would periodically inform the Secretariats of the Biodiversity and Climate Change conventions of research findings and, where applicable, highlight findings of particular importance to decision-makers and environmental managers.

iii The programme for training developing world scientists, environmental managers and decison-makers will be intensified in phase II of the project.

iv Application of global positioning system to locate the gondola precisely in three-dimensions in the canopy.

v In 1998 a follow-up conference will be held on tropical forest canopy biodiversity and atmospheric interactions, which will be organised jointly by UNEP and STRI.

Annex I: Summary of Canopy Biology Research Projects, Investigators and Funding Sources

Summary of Canopy Biology Research Projects, Investigators and Funding Sources

Name	Citizen of	Institution	Name of Research Project (chapter.section)	Dates	Funding
Avalos, Gerardo	Costa Rica	University of Missouri, St Louis, USA	Assessment of the effects of microsite factors on liana physiology (6.4)	May-July 1994 June-March 1995	Andrew W. Mellon Foundation
Caldwell, Martyn M.	United States	Utah State University, Utah, USA	The response of five tropical plant species to natural solar ultra-violet B radiation (8.1)	1994-1995	Andrew W. Mellon Foundation
Cavelier, Jaime	Columbia	Universidad de Los Andes, Bogotá, Columbia	(Goldstein collaborator - 5.1)	1991-1993	Smithsonian Institution pre-doctoral and Andrew W. Mellon Foundation
Gamon, John A.	United States	California State University, Los Angeles, USA	Predicting photosynthetic carbon fluxes from spectral reflectance of leaves and canopies (5.2) (Mulkey collaborator - 6.1)	April 1994	Smithsonian Institution Short-term Fellow
Goldstein, Guillermo	Argentina	University of Hawaii, Honolulu, Hawaii, USA	Stomatal and environmental control of transpiration in a lowland tropical forest tree (5.1)	1991-1993	Andrew W. Mellon Foundation
Haase, A.	Germany	Universität Würzburg, Würzburg, Germany	(Zimmermann collaborator - 6.13)	1993	Graduiertenkolleg NMR HA 1232/8-1 and Deutsche Forschungsgemeingschaft HA 1232/3-1
Holbrook, N. Michelle	United States	Harvard University, Cambridge, MA, USA	(Goldstein collaborator - 5.1)	1991-1993	Andrew W. Mellon Foundation
Hongliang, Tong	China	University of California, Davis, USA	(Pearcy post-doctoral student - 6.1)	March and June 1993	National Science Foundation
Harris, Gary	United States	Wellesley College Wellesley, USA	Day-courses of two light-activated Calvin-cycle enzymes: field measurements on a tropical forest tree, *Ficus insipida* (6.9) (Königer collaborator - 6.10) (Zotz collaborator - 6.8)	1992-1993	Smithsonian Tropical Research Institute visiting scientist and Wellesley College

Summary of Canopy Biology Research Projects, Investigators and Funding Sources

Name	Citizen of	Institution	Name of Research Project (chapter.section)	Dates	Funding
Jackson, Paula	Venezuela	University of California, Los Angeles, USA	(Goldstein collaborator - 5.1)	1991-1993	Andrew W. Mellon Foundation
Langbein, D.	Germany	Batelle Institute, Frankfurt, Germany	(Zimmermann collaborator - 6.13)	1993	German Space Agency
Kitajima, Kaoru	Japan	Smithsonian Tropical Research Institute, Panama City, Panama	Modelling carbon gain in the canopy of a tropical forest tree (6.5) (Mulkey collaborator - 6.3) (Newell collaborator - 6.6) (Wright collaborator - 6.2)	1994-1996	Smithsonian Institution Scholarly Studies, National Science Foundation and Andrew W. Mellon Foundation
Königer, Martina	Germany	University of California Davis, USA	Xanthophyll cycle pigments in tropical forest species: a comparative field study on canopy trees, gap and understory species (6.10) (Harris collaborator - 6.9) (Zotz collaborator - 6.8)	1992-1993	Smithsonian Tropical Research Institute visiting scientist
Körner, Christian	Switzerland	Basel University, Basel, Switzerland	Total non-structural carbohydrate pools in tropical forest trees (7.1)	1993-1995	Andrew W. Mellon Foundation
Krause, G. Heinrich	Germany	Heinrich Heine Universität, Düsseldorf, Germany	Photoinhibition and xanthophyll cycle activity in young and mature canopy leaves of tropical rainforest plants (6.11) (Thiele collaborator - 6.12)	1993-1994	Smithsonian Institution Short-term Fellow
Meinzer, Frederick C.	United States	Hawaiian Sugar Planter's Association, Aiea, Hawaii, USA	(Goldstein co-principal investigator - 5.1) (Zimmermann collaborator - 6.13)	1991-1993	Andrew W. Mellon Foundation

Summary of Canopy Biology Research Projects, Investigators and Funding Sources

Name	Citizen of	Institution	Name of Research Project (chapter.section)	Dates	Funding
Mulkey, Stephen S.	United States	University of Missouri, St Louis, USA	Variation in resource availability and consequences for interdependent physiological and morphological leaf traits in neotropical canopy trees (6.3) Light quality and distribution within the canopy of a neo-tropical forest (6.1) (Avalos collaborator - 6.4) (Gamon collaborator - 5.2) (Kitajima collaborator - 6.5) (Newell collaborator - 6.6) (Wright collaborator - 6.2)	1992-1996	National Science Foundation
Newell, Elizabeth	United States	Hobart and William Smith Colleges, New York, USA	Storage carbohydrates in tropical forest trees (6.6)	1994-1995	National Science Foundation
Oren, Ram	Israel	Duke University, Durham, USA	Whole-tree transpiration: linking stand structure, composition and phenology with watershed hydrology (6.14)	May 1993	Smithsonian Institution Short-term Fellow
Pearcy, Robert	United States	University of California, Davis, USA	(Kitajima collaborator - 6.5) (Mulkey collaborator - 6.1)	March and June 1993	Smithsonian Institution and National Science Foundation
Popp, Marianne	Austria	Universität Münster, Münster, Germany	Carbohydrates and osmotic adjustment in canopy leaves (6.15)	April 1994 (preliminary visit)	Smithsonian Tropical Research Institute Plant Physiology Programme and German funding
Potvin, Catherine	Canada	McGill University, Montreal, Canada	Optimal seed size, maternal selection and leaf phenology of two neotropical tree species (6.16)	1994-1995	Sabbatical
Rada, Fermin	Venezuela	Universidad de los Andes, Merida, Venezuela	(Goldstein collaborator - 5.1)	1991-1993	Andrew W. Mellon Foundation

Summary of Canopy Biology Research Projects, Investigators and Funding Sources

Name	Citizen of	Institution	Name of Research Project (chapter.section)	Dates	Funding
Roubik, David	United States	Smithsonian Tropical Research Institute, Panama City, Panama	Tropical pollinators in the canopy and understory; field data and theory for stratum 'preferences' (3.1)	1990-1994	Smithsonian Tropical Research Institute
Rodriguez, Viterbo	Panama	Smithsonian Tropical Research Institute, Panama City, Panama	Biodiversity and host plant associations in the *Coleoptera* and *Homoptera* of a tropical forest canopy (3.2)	1994-1995	Andrew W. Mellon Foundation
Samaniego, Mirna	Panama	University of Panama, Panama City, Panama	(Wright technician)	1990-1996	Smithsonian Institute Scholarly Studies
Sánchez Garduño, Cecilia	Mexico	University of Mexico, Mexico City, Mexico	Seed predation in a neotropical forest canopy (4.2)	Feb-August 1994	Andrew W. Mellon Foundation
Searles, Peter S.	United States	Utah State University, Utah, USA	(Caldwell post-doctoral student - 8.1)	1994-5	Andrew W. Mellon Foundation
Thiele, Alexandra	Germany	Heinrich Heine University of Düsseldorf, Düsseldorf, Germany	Mechanisms of photoinhibition in leaves of tropical plants (6.12)	1994-5	Smithsonian Institution Short-Term Fellow
Veit, Markus	Germany	Universität Würzburg, Würzburg, Germany	Ultra-violet-B absorbing substances in canopy leaves (8.2)	March 1994	Smithsonian Tropical Research Institute Plant Physiology Programme and German funding
Virgo, Aurelio	Panama	University of Panama, Panama City, Panama	(Winter technician)	Since 1992	Smithsonian Tropical Research Institute
Windsor, Donald	United States	Smithsonian Tropical Research Institute, Panama City, Panama	(Rodriguez co-principal investigator - 3.2)	1994-1995	Andrew W. Mellon Foundation

Summary of Canopy Biology Research Projects, Investigators and Funding Sources

Name	Citizen of	Institution	Name of Research Project (chapter.section)	Dates	Funding
Winter, Klaus	Germany	Smithsonian Tropical Research Institute, Panama City, Panama	Photosynthesis and photoinhibition (6.7) (Caldwell collaborator - 8.1) (Harris collaborator - 6.9) (Königer collaborator - 6.10) (Körner collaborator - 7.1) (Krause collaborator - 6.11) (Popp collaborator - 6.15) (Thiele collaborator - 6.12) (Veit collaborator - 8.2) (Zotz collaborator - 6.8)	Since 1991	Smithsonian Tropical Research Institute
Wright, Joseph	United States	Smithsonian Tropical Research Institute, Panama City, Panama	Herbivory (4.1) Leaf area seasonality in a tropical forest (6.2) (Avalos collaborator - 6.4) (Kitajima collaborator - 6.5) (Mulkey collaborator - 6.1 and 6.3) (Newell collaborator - 6.6) (Rodriguez collaborator - 3.2) (Sánchez Garduño collaborator - 4.2)	1992-1996	Smithsonian Institution Scholarly Studies, National Science Foundation and Andrew W. Mellon Foundation
Würth, Mirjam	Switzerland	Basel University, Basel, Switzerland	(Körner post-doctoral student - 7.1)	1993-1995	Andrew W. Mellon Foundation

Summary of Canopy Biology Research Projects, Investigators and Funding Sources

Name	Citizen of	Institution	Name of Research Project (chapter.section)	Dates	Funding
Zimmermann, Reiner	Germany	Jet Propulsion Laboratory, Pasadena, USA	(Oren co-principal investigator - 6.14)	January 1992 May 1993	Smithsonian Institution Short-term Fellow and NASA
Zimmermann, Ulrich	Germany	Universität Würzburg, Würzburg, Germany	Mechanisms of long-distance water transport in plants (6.13)	1993	Sonderforschungsberiech 251 and Graduiertenlokkeg NMR HA 1232/8-1
Zotz, Gerhard	Germany	Universität Wurzburg, Germany	Photosynthesis and carbon gain of the tropical pioneer tree, *Ficus insipida* (6.8) (Harris collaborator - 6.9)	Jan-July 1993	Smithsonian Tropical Research Institute Plant Physiology Programme

Annex ll: Alphabetical Listing of Researchers with Contact Addresses

Gerardo Avalos
Department of Biology
University of Missouri
St Louis
Missouri, 63121
USA

Martvn M. Caldweil
Department of Range Science and the Ecology Center
Utah State University
Logan
Utah, 84322-5330
USA

Jaime Cavelier
Departamento de Ciencias Biologicas
Universidad de Los Andes
Bogota
Colombia

John Gamon
Department of Biology and Microbiology
California State University, Los Angeles
5151 State University Drive
Los Angeles
California, 90032-8201
USA

Guillermo Goldstein
Department of Biology
Honolulu
Hawaii, 96822
USA

N. Michelle Holbrook
Department of Botany
Harvard University
Cambridge
Massachusetts
USA

Tong Hongliang
Department of Botany
University of California, Davis
California, 95616
USA

A. Haase
Lehrstuhl für Experimentelle Physik B
(Biophysik)
Am Hubland
University Wurzbürg
D-97074, Wurzbürg
Germany

Gary Harris
Biology Department
Wellesley College
Wellesley
Massachussetts 02181
USA

Paula Jackson
Laboratory of Biomedical and
Environmental Sciences
University of California, Los Angeles
California 90024
USA

Kaoru Kitajima
Smithsonian Tropical Research Institute
Apartado 2072
Balboa Ancon
Panama City
Panama

D. Langbein
Batelle Institut
Am Römberhof 35
D-60486 Frankfurt aM
Germany

Martina Königer
Department of Plant Biology
University of California,
Davis California, 95616
USA

Christian Korner
Department of Botany
University of Basel
CH-4056 Basel
Switzerland

G. Heinrich Krause
Institute of Plant Biochemistry
Heinrich Heine University Düsseldorf
Universitätsstrasse 1
D-4000, Düsseldorf 1
Germany

Frederick C. Meinzer
Hawaiian Sugar Planter's Association
PO Box 1057
Aiea
Hawaii, 96701
USA

Stephen S. Mulkey
Department of Biology
University of Missouri
St Louis
Missouri 63121
USA

Elizabeth Newell
Department of Biology
Hobart and William Smith Colleges
Geneva
New York, 14456
USA

Ram Oren
School of Forestry and Environmental Sciences
Duke University
Durham
NC, 27706
USA

Robert Pearcy
Department of Botany
University of California,
Davis California, 95616
USA

Marianne Popp
Institut für Angewandte Botanik
Universität Münster
Hindenburgplatz 55
D-48143 Münster
Germany

Catherine Potvin
Department of Botany
McGill University
Montréal Quebec
Canada

Fermin Rada
Universidad de los Andes
Merida Venezuela

David Roubik
Smithsonian Tropical Research Institute
Apartado 2072
Balboa Ancon
Panama City
Panama

Viterbo Rodriguez
Smithsonian Tropical Research Institute
Apartado 2072
Balboa Ancon
Panama City
Panama

Mirna Samaniego
Smithsonian Tropical Research Institute
Apartado 2072
Balboa Ancon
Panama City
Panama

Cecilia Sánchez Garduño
Centro de Ecología
Interacción Planta Animal
University of Mexico
Apartado 70-275
Mexico City, 04510
Mexico

Peter S. Searles
Department of Range Science and the Ecology Center
Utah State University
Logan Utah, 84322-5230
USA

Alexandra Thiele
Heinrich Heine University of Düsseldorf
Institute of Plant Biochemistry
Geb. 26.03
Universitätsstrasse 1
D-40225 Düsseldorf
Germany

Markus Veit
Lehrstuhl Pharmazeutische Biologie
Universität Würzburg
Mittlerer Dallenbergweg 64
D-97082 Würzburg
Germany

Aurelio Virgo
Smithsonian Tropical Research Institute
Apartado 2072
Balboa Ancon
Panama City
Panama

Donald Windsor
Smithsonian Tropical Research Institute
Apartado 2072
Balboa Ancon
Panama City
Panama

Klaus Winter
Smithsonian Tropical Research Institute
Apartado 2072
Balboa Ancon
Panama City
Panama

S. Joseph Wright
Smithsonian Tropical Research Institute
Apartado 2072
Balboa Ancon
Panama City
Panama

Mirjam Würth
Department of Botany
University of Basel
CH-4056 Basel
Switzerland

Reiner Zimmermann
Jet Propulsion Laboratory
4800 Oak Grove Drive
Pasadena, California, 91109
USA

Ulrich Zimmermann
Lehrstuhl für Biotechnologie
Biozentrum
Am Hubland
Universität Würzburg
D-97074 Würzburg
Germany

Gerhard Zotz
Smithsonian Tropical Research Institute
Apartado 2072
Balboa Ancon
Panama City
Panama

Annex III: List of Researchers By Nationality

Argentina	Guillermo Goldstein
Austria	Marianna Popp
Canada	Catherine Potvin
China	Tong Hongliang
Colombia	Jaime Cavelier
Costa Rica	Gerardo Avalos
Germany	A. Haase D. Langbein Martina Königer G. Heinrich Krause Alexandra Thiele Marcus Veit Klaus Winter Reiner Zimmermann Ulrich Zimmerman Gerhard Zotz
Israel	Ram Oren
Japan	Kaoru Kitajima
Mexico	Cecilia Sánchez Garduño
Panama	Viterbo Rodriguez Mirna Samaniego Aurelio Virgo
Switzerland	Christian Körner Mirjam Würth
United States	Martyn M. Caldwell John Gamon Gary Harris N. Michelle Holbrook Frederick C. Meinzer Steven S. Mulkey Elizabeth Newell Robert Pearcy David Roubik Peter S. Searles Donald Windsor S. Joseph Wright
Venezuela	Paula Jackson Fermin Rada

Annex IV: Publications and Scientific Presentations Based on Canopy Crane Research Publications

Popular Press and Crane Reviews in Technical Sources

Anderson, A., 1990, The View From the Top, in *Nature,* vol. 347, no. 6288, pp 5.

Anonymous, 1993, A Crane With a View, in *Science,* vol. 260, no. 5108, pp 619.

Illueca, J.E. and Smith, A.P., 1993, Exploring the Upper Tropical Forest Canopy, in *Our Planet,* the magazine of the United Nations Environment Programme, vol, 5, no.3, pp 12-13

Joyce, C., 1991, A Crane's Eye View of Tropical Forests, in *New Scientist,* vol 131, no. 1787, pp 40-42.

Moffet, M., 1994, *The High Frontier: Exploring the Tropical Rainforest Canopy,* Harvard University Press, Cambridge, MA, USA.

Pennisi, E., (in press), How Flora and Fauna Structure Tropical Forests, in *Science News.*

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Films

The Forest Canopy: The Last Frontier, a 60-minute documentary filmed in part from the canopy crane by the Japanese Public Broadcasting Company (NHK) (filmed in 1992; first aired in Japan in 1993).

Tropical Forest Bees, a 30-minute documentary filmed in part from the canopy crane by Oxford Scientific Films for the British Broadcasting Company (filmed in 1994).

The Tropical Forest Canopy, a 30-minute documentary narrated by UN Goodwill ambassador Olivia Newton John and filmed entirely from the canopy crane by Beyond Productions for the Australian Broadcasting Corporation (filmed in March 1994).

Annex V: Proposed Sites In Panama for Future Installation of Construction to Access the Forest Canopy

The initial phase I project document[81] called for a second phase in which two crane access systems were to be established on Barro Colorado Island, Panama. Scientists implementing the project now believe that the first priority for a second crane should be more humid forests on Panama's Caribbean slope in the newly-created Parque Nacional Interoceanica. Barro Colorado Island, with rainfall and a forest biome intermediate between the prototype crane site and the Parque Nacional Interoceanica is proposed as the site for a third canopy crane. A brief justification for additional canopy crane sites can be found in chapter 10, *Future Perspectives*. This annex describes the Parque Nacional Interoceanica and Barro Colorado Island. The Parque Natural Metropolitano which is the site of the prototype canopy crane is described in chapter 1, *Tropical Forests and the Parque Natural Metropolitano.*

Parque Nacional Interoceanica

The forests of the Parque Nacional Interoceanica have been protected within the boundaries of Fort Sherman, a military installation operated by the United States since the completion of the Panama Canal in 1914. Under the terms of the 1977 Panama Canal Treaty, Fort Sherman is to return to the control of the Republic of Panama in 1996. Anticipating this change, the Panamanian legislature created the Parque Nacional Interoceanica in 1993. The Parque Nacional Interoceanica completes a contiguous series of forest reserves and national parks that extends from the Caribbean to the Pacific and includes 370 km^2 of forest, the prototype crane site and the two proposed canopy crane sites.

These protected forests incorporate a strong rainfall gradient that extends across the Panamanian isthmus from Pacific to Caribbean. At the prototype crane site within site of the Pacific, annual rainfall averages 1,740 mm, there is a severe five-month dry season and the forest is largely dry-season deciduous. Seventy kilometres to the north in the Parque Nacional Interoceanica, annual rainfall averages 3 400 mm, monthly rainfall averages less than 100 mm for just two months and the forest is evergreen.

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[81] See *Assessment of Biological Diversity and Microclimate of the Tropical Forest Canopy: Phase 1,* 1991, United Nations Environment Programme Decision Sheet, Project no. CD/6105-91-01(2962)

High rainfall promotes high plant diversity throughout the tropics[82]. In a comparison of forest sites that began in a dry forest immediately adjacent to the prototype crane and ended in a wet forest less than two thirds of the way to the Parque Nacional Interoceanica, Gentry[83] found that the numbers of species of trees and lianas increased by 85%. The diversity of other plant life forms, in particular canopy epiphytes, increases much more rapidly with rainfall than does the diversity of trees and lianas[84]. Preliminary comparisons of the forests in Parque Nacional Interoceanica and at the prototype canopy crane site indicate that canopy epiphytes are more than two orders of magnitude more abundant in the Parque Nacional Interoceanica. Although there have been no botanical surveys of the newly-formed Parque Nacional Interoceanica, the evidence indicates that the number of species of trees and lianas will more than double and the number of species of canopy epiphytes may increase ten-fold relative to the prototype crane site. Canopy access in contrasting dry and wet forests across a strong, pantropical biodiversity gradient is critical to advance our understanding of canopy processes and tropical forest biodiversity.

There are two additional reasons to site the second canopy crane in the Parque Nacional Interoceanica. First, the Parque Nacional Interoceanica includes extensive areas of forest on level ground. It is proposed to take advantage of this by siting the second crane on a wide-gauge track using standard 'off-the-shelf' technology. The track will extend 300 metres through the forest, increasing the area of accessible canopy to 3.8 hectares. A second advantage of the Parque Nacional Interoceanica is that the Center for Tropical Forest Science centred at the Smithsonian Tropical Research Institute has received independent funding to map all trees and saplings in a six hectare plot in the Parque Nacional Interoceanica. This plot will be centred on the second canopy crane. Center for Tropical Forest Science personnel will remap the plot at regular intervals which will permit integrated analyses of tree dynamics and canopy processes.

Barro Colorado Island

Barro Colorado Island holds the best studied tropical forest in the world. The flora and fauna have been described in more than 2,000 scientific publications, with

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[82] Wright, S.J., 1992, Seasonal Drought, Soil Fertility and the Species Density of Tropical Forest Plant Communities, in *Trends in Ecology & Evolution,* vol. 7, no. 8, pp 260-263; Gentry, A.H., 1988, *Annals of the Missouri Botanical Gardens,* no. 75, pp 1-34; and Hall, J.B. and Swain, M.D., 1981, *Distribution and Ecology of Vascular Plants in a Tropical Rain Forest: Forest Vegetation in Ghana,* Geobotany series, vol. 1.

[83] Gentry, A.H., 1982, Patterns of Neotropical Plant Species Diversity, in *Evolutionary Biology,* vol. 15, pp 1-84, Penum Press, New York, New York, USA.

[84] Gentry, A.H., and Dodson, C.H., 1987, Diversity and Biogeography of Neotropical Vascular Epiphytes, in *Annals of the Missouri Botanical Gardens,* vol. 74, pp 205-233.

the first having appeared in 1918. In recent years, there have been more than 70 scientific publications based on research conducted on Barro Colorado Island each year. Unique intellectual resources available on Barro Colorado Island include published floras of the cryptogams[85] (lichens and mosses), the vascular plants[86] and the pollen[87]; a complete onsite herbarium; long-term data on the population fluctuations and phenologies of many insects, vertebrates and plants collected by the Smithsonian's Environmental Science Program and Centre for Tropical Forest Science since 1971; and the additional scientific insight that accrues from 75 years of intensive study. Physical facilities include modern laboratories, and dining and housing for 40 scientists. Collectively, these resources make Barro Colorado Island an ideal site for a third canopy access system.

Annual rainfall averages 2,600 mm on Barro Colorado Island and there is a strong four-month dry season. The forest biome (tropical moist forest in the Holdridge Life Zone System[88]) is intermediate between the tropical dry and wet forests of the Parque Natural Metropolitano and the Parque Nacional Interoceanica, respectively. Comparisons made possible by canopy-access systems in these three lowland forest biomes will greatly advance understanding of the tropical forest canopy.

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[86] Croat, T.B., 1978, *Flora of Barro Colorado Island,* Stanford University Press, Stanford, California, USA.

[87] Roubik, D.W. and Moreno, P.J.E., 1991, Pollen and Spores of Barro Colorado Island, *Missouri Botanical Gardens: Monographs in Systematic Botany.*

[88] Holdridge, L.R., Grenke, W.C., Hatheway, W.H:, Liang, T. and Tosi jr, J.A., 1971, *Forest Environments in Tropical Life Zones,* Pergamon Press.

Annex VI: Other Canopy Research Developments

Additional canopy research developments include a major symposium to be held in November 1994, and the organization of canopy research networks in Europe and North America. The symposium, entitled *Forest Canopies: Ecology, Biodiversity and Conservation,* will be held at the Marie Selby Botanical Gardens in November 1994. Dr S. Joseph Wright of the Smithsonian Tropical Research Institute has organized a session entitled *Canopy Processes.* The symposium will bring together 200 canopy investigators from around the world.

In North America, Drs Nalini Nadkarni (Evergreen State College, Olympia, WA, 98505) and Geoffrey Parker (Smithsonian Environmental Research Center, Edgewater, MD, 21038) have received National Science Foundation funding to organize a canopy research network. Activities include building an international communication network (electronic and conventional), developing and standardizing three-dimensional data processing capabilities for canopy applications and developing appropriate bibliographic databases. Subscriptions to their canopy electronic bulletin board are accepted at "CANOPY-REQUEST@LTERNET.EDU". STRI's Drs Mulkey and Wright will participate in an initial meeting to advance three dimensional data processing capabilities planned for January 1995.

In Europe, a coalition of investigators from seven nations is establishing a *Programme in Tropical Canopy Research.* An initial planning conference was held in July 1994 in Austria. Dr Nadkarni presented the UNEP/STRI canopy crane project. Conferees discussed the establishment of from one to three tropical canopy research sites with a canopy crane at each site. A committee was formed to prepare a proposal for the European Science Foundation. Committee members include Prof. E. Linsenmair (Lehrstuhl Zoologie III, Univ. Wurzburg, Biozentrum Am Hubland, 8700 Wurzburg, Germany), Dr H. Balslev (Aarhus Univ., Department of Systematic Botany, Herbariet-Bygn 137, 8000 Aarhus, Denmark) and Dr N. Stork (Department of Entomology, Natural History Museum, Cromwell Road, London SW7 5BD, England). UNEP/STRI conferences proposed for 1996 and 1998 in Panama interdigitate with canopy conferences proposed for 1995 and 1997 by this coalition. Further coordination is being explored.

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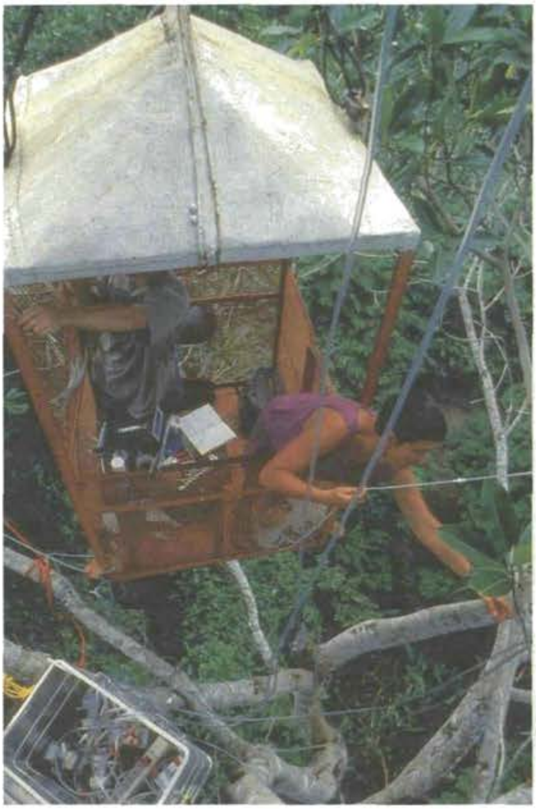
Accessing the Canopy
Assessment of Biological Diversity and Microclimate of the Tropical Forest Canopy: Phase 1

The uppermost tropical forest canopy is the principal site for the interchange of heat, oxygen, water vapour and carbon dioxide between atmosphere and biosphere. In addition, rapid rates of photosynthesis and production of new leaves, fruits and flowers that sustain a diverse animal community give rise to complex plant/animal interactions. The difficulty and danger involved in accessing the forest canopy mean that, until now, it has remained largely unexplored.

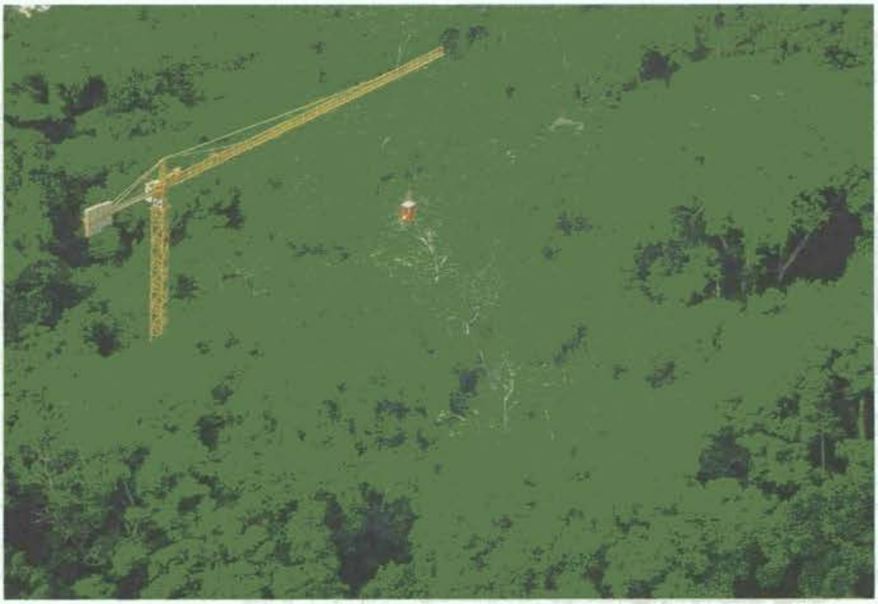
Researchers are raised up above and then lowered into the canopy in a gondola suspended from the crane hook. The gondola is not in contact with the tree so does not interfere with forest atmosphere or biotic interactions.

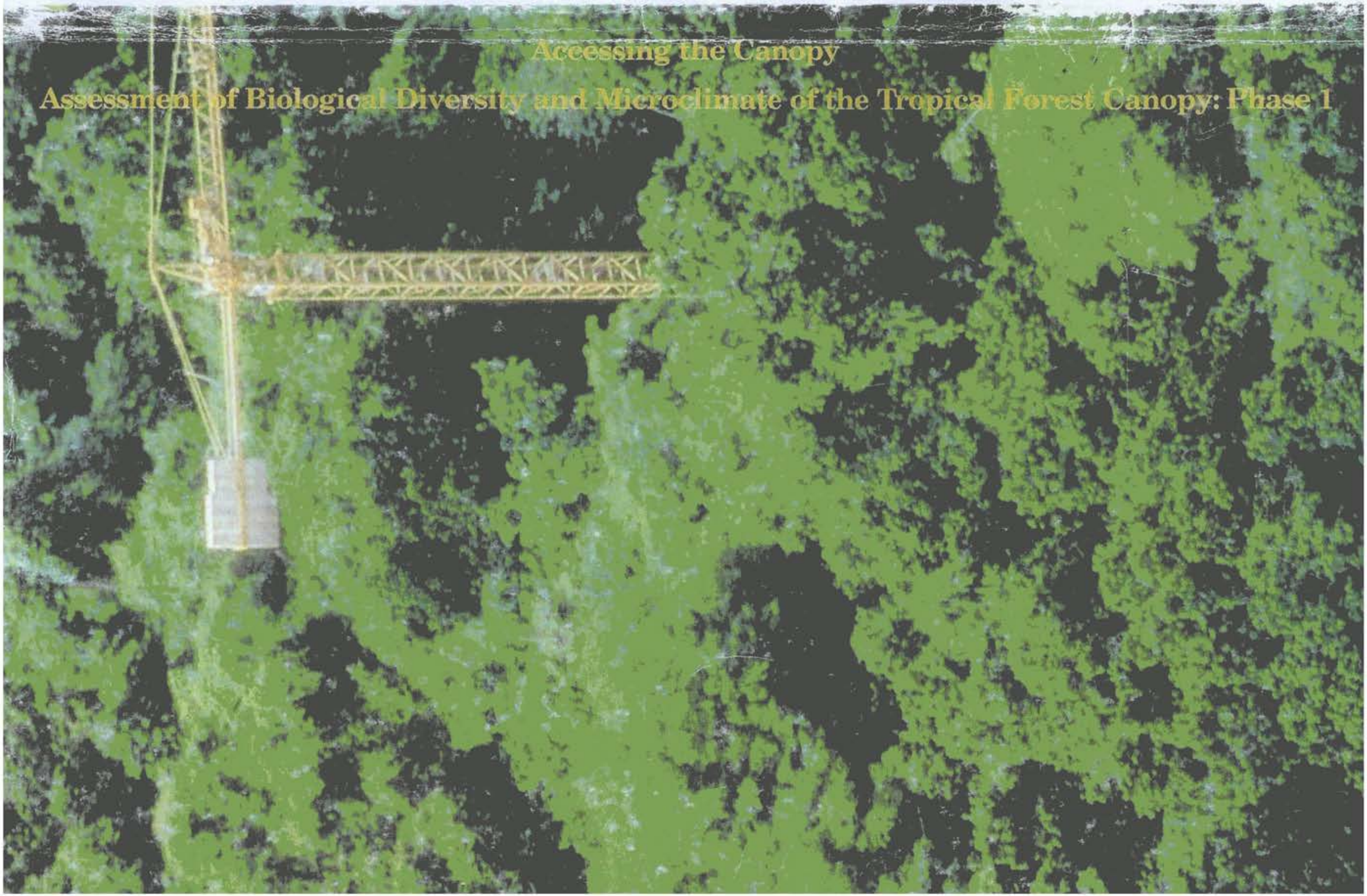
The crane facilitates long-term measurements and experimentation and provides repeated access to specific locations safely and rapidly. Scientists can be carried easily and efficiently between numerous locations within the area accessible from the crane.



The construction crane opens up the tropical forest canopy to scientific exploration by enabling scientists to access the leaves of canopy trees, lianas and epiphytes which account for at least 90 per cent of tropical forest leaves. In the Parque Natural Metropolitano, scientists now have access to 8,000 m^2 of upper canopy surface and 28,000 m^3 of forest volume, including some 140 individual canopy trees.

The crane allows for scientific equipment - particularly large, heavy equipment - to be carried into the canopy. It is more manoeuvrable, safer and stable than other canopy access techniques.





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