

WHAT'S UP?

THE NEWSLETTER OF THE INTERNATIONAL CANOPY NETWORK

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GLIDING ANTS IN TROPICAL FORESTS

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People who spend large amounts of time sitting on tree branches high above the forest floor unavoidably develop an interest in the way things fall. How long did that raindrop, fleeing lizard or fumbled carabiner take to hit the ground? What did it bump into along the way? Did it survive? Would I? This curiosity, combined with the ubiquity of ants in tropical forest canopies, led me to discover that workers of many neotropical ant species do not fall haphazardly when dislodged from tree crowns. Instead, they direct their aerial descent to land on the tree trunk with >80% success. This discovery was published in the journal *Nature* (Yanoviak et al. 2005a) with Drs. Robert Dudley (U. of California, Berkeley) and Mike Kaspari (U. of Oklahoma). Videos and links to related information are available at <<www.canopyants.com>>. The primary goal of this article is to provide additional background and details of the discovery. I also summarize the current status of our knowledge of this

behavior in ants, and future directions for research on this phenomenon.

LIFE AS A CANOPY ANT

Ants comprise a substantial portion of arthropod biomass and diversity in forest canopies of the lowland tropics. This is remarkable given that tree crowns offer relatively unstable substrates for insects like ants that are small, active, and wingless. Physical disturbances (e.g., wind, rain, passing primates, foraging birds) are common and unpredictable

in the tree tops, and may quickly dislodge an ant from a branch or leaf, ultimately dislocating it tens of meters. Indeed, ants fall or jump (Weber 1957) from trees with high frequency, often landing in the understory as "ant rain" (Haemig 1997, Longino & Colwell 1997).

Ants are social insects. Most individuals belong to the worker caste, whose primary functions include food gathering, brood care, nest maintenance and



Fig. 1. A typical *Cephalotes atratus* worker

defense. Ant workers that become lost while foraging or fighting must be replaced, and thus are costly to their colony. Whereas ground-dwelling ants use a variety of orientation techniques to find their way home (e.g., Hölldobler 1980, Wohlgenuth et al. 2001), the likelihood of a fallen canopy ant returning to its point of origin after landing in the unfamiliar and potentially hostile understory is presumably low. Thus, given the hazards inherent in canopy life and the dramatic change in conditions from the canopy to the understory, arboreal ants face a high risk of falling and of subsequently becoming lost. It follows that selection will favor traits that either prevent arboreal ants from falling, or prevent them from becoming lost when they do fall.

One trait that effectively reduces the chance of a fall is the ability to maintain a good grip on relatively smooth surfaces. Some ants (and other arboreal animals) achieve this with modified pretarsal structures having special adhesive properties (i.e., “sticky” tarsi; Orivel et al. 2001, Federle et al. 2002). However, even ants with sticky tarsi occasionally find themselves airborne. When faced with this circumstance, many other arboreal animals, especially vertebrates, use parachuting or gliding to control the speed or direction of their fall (e.g., Moffett 2000). Until the discovery of directed aerial descent (hereafter “gliding” for simplicity) in ants, this behavior was unknown in extant wingless arthropods (Dudley 2000).

BLUE MOSQUITOES AND GLIDING ANTS

I first noticed gliding in *Cephalotes atratus* ants in 1998 while working on a canopy ant project with Mike Kaspari on Barro Colorado Island (BCI) in Panama (Yanoviak & Kaspari 2000). I brushed a *C. atratus* worker off of my hand and watched

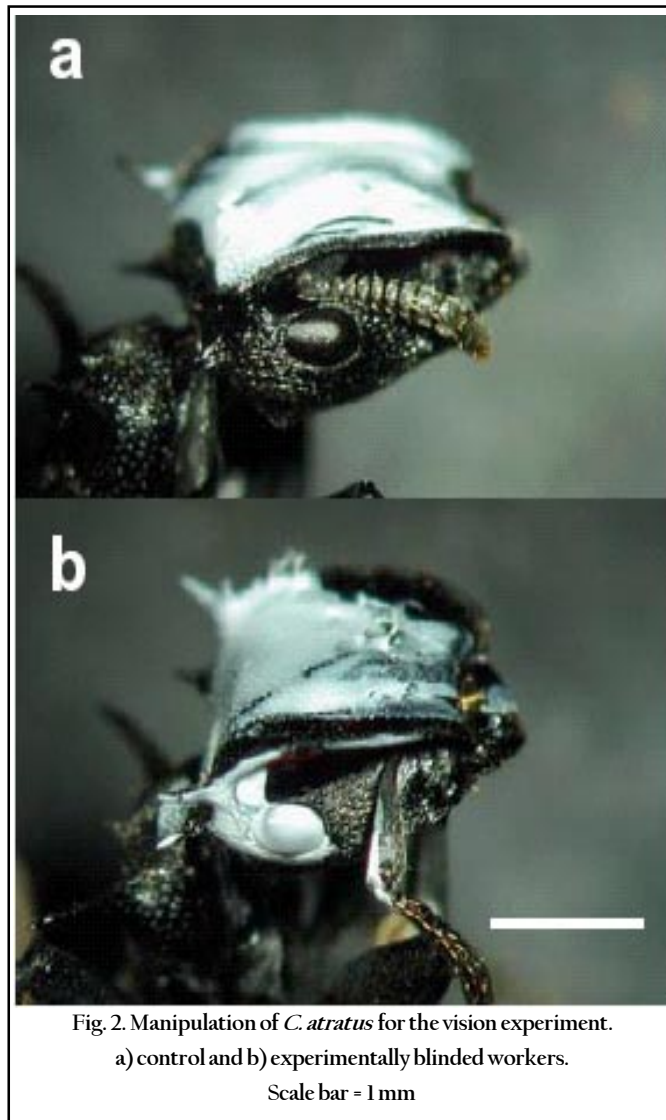


Fig. 2. Manipulation of *C. atratus* for the vision experiment. a) control and b) experimentally blinded workers. Scale bar = 1 mm

in amazement as it seemed to glide a considerable horizontal distance instead of falling straight to the ground as I had expected. Four years later I was climbing trees in the Peruvian Amazon in search of metallic blue mosquitoes (*Haemagogus janthinomys*). The goal was to collect blood-fed females and take them (live) back to our lab in Iquitos for a project examining the effects of deforestation on transmission of Venezuelan equine encephalitis and related diseases (Aguilar et al. 2004, Yanoviak et al. 2005b). While waiting for the mosquitoes to arrive, I was attacked by hundreds of *C. atratus* workers that were nesting inside the branch I was sitting on. These ants are rather large, and they have a hard exoskeleton and dorsal spines that will easily puncture skin (Fig. 1). Needing an ant-free place to put my hand, I brushed 20-30 *C. atratus* workers off of the branch. To my surprise, the falling ants followed a distinct J-shaped trajectory leading directly back to the tree trunk about

6m below me. I recalled my prior observation in Panama and realized that there was definitely something interesting going on. Since then, I have spent most of my free time dropping ants out of trees.

DROPPING ANTS

My first tasks were to develop a basis for quantifying the ants' glide success (i.e., frequency of trunk contact after a fall), and to rule out other possible explanations for what appeared to be a novel behavior. After a review of basic physics, a simple quantitative null model emerged (Yanoviak et al. 2005a) and opened the door to some hypothesis testing. I began by marking individual ants with white paint so that I could see their glides better against the dark understory. That led to the realization that the ants were gliding backwards and were climbing back up into the crown after landing on

the trunk. I then moved ants from their home trees and dropped them from trees 50 km away to see if gliding success was somehow linked to characteristics of individual trees. I found that prior experience with a given tree had no effect on the ants' performance. This facilitated further experimentation because it enabled me to collect ants from readily accessible colonies and drop them from the best climbable trees. In the last set of experiments, I dropped ants from opposite branches within trees and in different relative positions at the time of release. Results of these trials showed that location within a tree and starting position with respect to the trunk do not influence the behavior. Thus, the gliding behavior was not an accident or the result of observer bias.

After ruling out these basic alternative hypotheses, I next investigated the sensory and morphological mechanisms behind gliding in *C. atratus*. By experimentally blinding the ants with paint (Fig. 2), I was able to show that they locate the tree in a fall using visual cues. Tropical tree trunks are often light in color, and further trials showed that the ants cue in on and glide to almost any light-colored column appearing against a darker background. But how do the ants adjust their trajectories in mid-air? Results of preliminary experiments showed that the shape and orientation of the ants' appendages play an important role in determining glide success.

For me, one of the most memorable moments in this project was when I dropped a second, much smaller species, *Cephalotes umbraculatus*, from a *Dipteryx* tree on BCI. Not only did it glide, it seemed to do so with greater speed and precision than *C. atratus*. I started dropping every species of ant I could find in the canopy, and we sought a way to quantify their performance. Now we know that smaller *Cephalotes* species tend to glide better than larger species (i.e., they land on the trunk over shorter vertical drop distances). We also know that gliding occurs in at least five ant genera in three subfamilies (Myrmicinae, Pseudomyrmecinae, and Formicinae), but appears to be completely absent in ponerimorphs and Dolichoderinae. The formicine genus *Camponotus* is especially interesting because it contains both gliding and non-gliding species.

NEXT STEPS (OR DROPS)

We continue to work on this system and are making new discoveries with ants and other gliding canopy insects almost daily. Currently we are focused on four principal topics: 1) determining the taxonomic distribution of gliding behavior in arboreal arthropods, 2) testing for associations between gliding and other ecological and behavioral characteristics, 3) documenting the abundance, species composition, and fate of arboreal insects that fall to the understory in

tropical forests, and 4) identifying and quantifying the morphological and aerodynamic mechanisms used by wingless insects to direct their aerial descent.

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See article publication in *Nature*, February 2005:

Yanoviak, S.P., Dudley, R. and Kaspari, M. 2005. Directed aerial descent in canopy ants. *Nature*. 433:624-626.

A NEW BOOK FOR A NEW LOOK AT TROPICAL RAIN FORESTS

by authors Richard Primack and Richard Corlett

2005. *Tropical Rainforests: An Ecological and Biogeographical Comparison*. Blackwell Science, UK.

There are many books on tropical rain forests already: do we really need another one? In reality, the large number of books with “tropical rain forest” in the title is rather misleading. Most deal either with a single site, country, or continent, with a single taxonomic group or only with human impacts and conservation. Very few academic books have attempted a broad overview of tropical rain forest biology. Tim Whitmore’s *An Introduction to Tropical Rain Forests*, Paul Richards’ *The Tropical Rainforest: an Ecological Study*, and Marius Jacobs’ *The Tropical Rain Forest: a First Encounter*, are unashamedly biased towards the plants, while John Terborgh’s *Stimulating Diversity and the Tropical Rain Forest* was not intended to be comprehensive. You have to go back as far as the two-volume *Tropical Rain Forest Ecosystems*, published by Elsevier in 1983 and 1989, for an attempt to deal with both plants and animals on a global scale.

Our book grew out of a conversation on the sidelines of the annual meeting of the Ecological Society of America in Providence, Rhode Island, way back in 1996. We had both been struck by the way speakers in a symposium referred to “the tropical rain forest” as if it were a single, uniform entity, all over the tropics. Even more disturbing for two ecologists who had worked mostly in Southeast Asia, was the implication that the rain forests of the Neotropics were typical and that what was being learned in Panama, Costa Rica and Mexico could be extrapolated without much modification to the rest of the tropics. This “typical” rain forest had bromeliads, sloths, hummingbirds and leaf-cutter ants, but lacked the dipterocarp trees, apes, civets, hornbills and fungus-growing termites that we were familiar with in Asia. Rain forest ecologists working in Africa, Madagascar, New

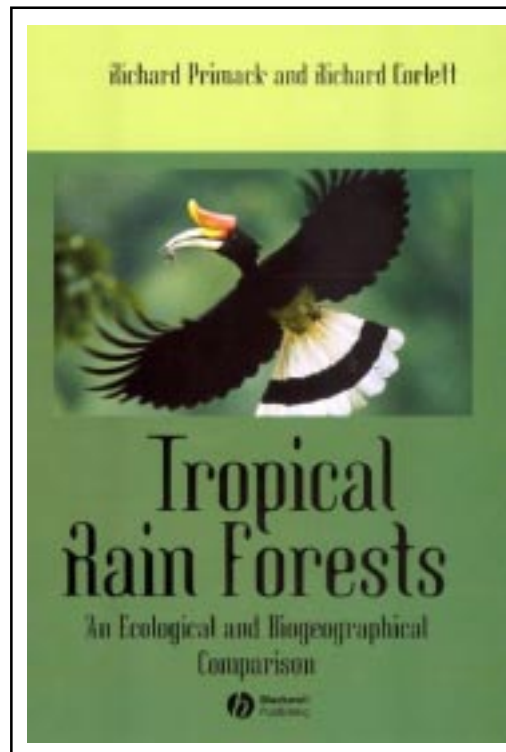
Guinea or Australia would have found this model equally unrecognizable.

We started with a shared conviction that tropical rain forests in different parts of the world differ in big and important ways. We initially envisaged a short paper pointing out this fact and giving a few examples of the differences we thought important. Over the next few years, however, the project took on a life of its own, partly in response to newly published research in a variety of fields.

Advances in molecular phylogeny, in particular, have helped put rain forest biogeography on a more solid footing. The paper eventually grew into a book. It was not until we saw the proofs that we realized exactly what we had taken on. The result, we hope, is a completely new view of tropical rain forests that emphasizes a cross-continental, comparative approach.

The book focuses on the differences that have resulted from the long periods of geographical separation between the five major rain forest regions: tropical America, Africa, Southeast Asia, Madagascar and New Guinea, as well as the smaller, outlying areas in Australia, Sri Lanka and elsewhere. Tens of millions of years of independent evolution in environments that differ in important ways have produced many different rain forests, each with its own unique species

and interactions. After an introduction to the varied environments and biogeographic histories responsible for these differences, successive chapters are devoted to plants, primates, carnivores and plant-eaters, birds, fruit bats and gliding vertebrates and insects. Of particular interest to canopy biologists will be the sections on epiphytes, ant plants and climbers in the plant chapter, on canopy vertebrates in the primate, bird and bat chapters,



and butterflies, ants, wasps, bees and termites in the insect chapter. Many of the differences we highlight are well known, such as the contrast between primate communities in the Neotropics and the Old World Tropics. Others are probably pointed out for the first time.

Our book was intended as a scientific celebration of rain forest diversity, so we have tried to restrict the discouraging realities of the twenty-first century tropics to the final chapter. Here we have kept to the 'many rain forests' theme of the earlier chapters and show how the biological differences among regions interact with the differing threats and may, as a result, require different responses. We discuss which approaches to rain forest conservation are working, which are not and which still need to be tried. It is impossible to write optimistically about rain forest conservation as a whole, but there are some bright spots and examples of best practice. In particular we review the value and problems of establishing national parks and other protected areas, cooperating with local people in conservation projects and regulating trade in rain forest products.

Although we have taken a broader view than any recent book on rain forests, there are some very obvious omissions, such as reptiles, amphibians and freshwater fish. There is surely enough known for comparative overviews of all three groups, but the literature is generally inaccessible to the outsider and there were no recent cross-continental reviews to get us started. For most of the numerous invertebrate groups that we have omitted, by contrast, there probably isn't even enough known. But we issue a challenge to the readers of this newsletter: please prove us wrong! We would love to see ecological and biogeographical comparisons of the vertebrate groups mentioned above, in addition to rain forest snails, spiders, cockroaches, flies and earthworms.

Throughout the book we emphasize the need for comparative studies of rain forests in different parts of the world using standardized methods. At the end of each chapter we suggest specific questions that could form the basis for such cross-continental comparisons. An example of such a question requiring comparative studies would be: Why do Southeast Asian rain forests have far more species of gliding animals in the canopy than are found in rain forests elsewhere? Is it because everwet, dipterocarp rain forests in Asia have a lower density of insects and small vertebrates as a food source than more seasonal rain forests? Another would be: Do neotropical tank bromeliads, by providing sources of water in the canopy, alter the ecology of animal communities and ecosystem processes in a way that is fundamentally different

from the canopy biology of rain forests elsewhere? We hope that readers of this newsletter will come up with many other questions of your own. An organization such as ICAN, with its global focus, in collaboration with the Canopy Database Project <<www.canopy.evergreen.edu>>, can play a leading role in the initiation and coordination of these comparative studies. The simplest approach is for key elements of particularly successful studies to be replicated at other sites around the world. If you want to quantify bird abundance, or insect diversity, or rates of herbivory, try to find a method that has been used before elsewhere, rather than producing a unique data point that cannot be compared with existing information. The pantropical network of 50-hectare forest plots established by the Institute for Tropical Forest Science is by far the most ambitious example of the approach we advocate and it would be great to see more canopy studies done in these plots. Most researchers, however, are confined by time and money to single sites, so the comparative element can only come from the use of standardized methods and cross-continental cooperation.

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CORRECTION

ICAN would like to make a correction from the Fall 2004 edition of *What's Up?* (11:1). The article titled "Center for Canopy Ecology" included an announcement that the Selby Gardens had eliminated canopy ecology from its mission. Please be advised that although the Center for Canopy Ecology has moved to the Sarasota campus of New College of Florida as we printed, The Marie Selby Gardens continues to address issues of canopy ecology. The true mission of The Marie Selby Botanical Gardens is to understand and conserve tropical plants — with emphasis on epiphytes and their natural habitats — through programs of research, education and horticultural display that promote appreciation of plant life and provide enjoyment for all who visit the Gardens.

For more information go to <<www.selby.org>>



GLOBAL CANOPY PROGRAMME UPDATE

CANOPY TRAINING COURSE - SABAH, MALAYSIA

The GCP's first Sabah Canopy Training course took place last month in Danum Valley, Borneo. The course trained 18 scientists and technicians from Malaysia, the Philippines and China to carry out and support research in ASEAN (Association of southeast Asian nations) region countries.

The course is a pioneering collaboration between the GCP, the Universiti Malaysia Sabah, Yayasan Sabah and the Royal Society South East Asian Rainforest Research Programme. Funding is supported for three years by the UK Government's Darwin Initiative. The aim of the project is to build capacity for studying the forest canopy in ASEAN region countries through training a new generation of climbing and science instructors. They can then train others to work in this complex but rewarding habitat. The course follows the great success of the GCP's Brazilian canopy training course which has been instrumental in building awareness and capacity for studying this rich and understudied habitat in South America.

The GCP course is the first in the world to be independently audited and to teach new access methods compliant with current British and European Safety Standards for work at height. The GCP hopes that institutions requiring their employees to undertake canopy research will in the future adopt these new techniques as part of their health and safety policy.

The 2005 course took place between 17th January and 5th February in a reserve of pristine, lowland Dipterocarp rainforest adjacent to Danum Valley Field Centre, Sabah. This is the tallest rainforest in the world with emergent trees rising to heights

of over 80m. The course included instruction in: rope access techniques, emergency procedures, casualty assessment and stabilization, ground-based and aerial rescue, line installation, hazard assessment, canopy rigging and work planning. All participants passed the strict assessment and attained the Basic Canopy Access Proficiency (BCAP) award.

In the first week, 8 research assistants from the Danum Valley Field Centre and the Universiti Malaysia, Sabah received instruction from Canopy Access Limited, a UK specialist rope-access company working in collaboration with the GCP.

In week two, 9 senior scientists and forest managers from the Universiti Malaysia Sabah, Yayasan Sabah, Xishuangbanna Tropical Gardens (Chinese Academy of Sciences), China, Griffith University, Australia and the ASEAN Regional Centre for Biodiversity Conservation (ARCBC) in the Philippines,

were also trained to BCAP level. They also received concurrent lectures on the state of canopy science from Professor Roger Kitching, a biodiversity specialist from Griffith University, Australia and Dr James Morison, an ecophysiologicalist from Essex University, U.K.

Initial training was carried out at low-levels on small trees adjacent to the Danum Valley Field Centre, but all participants also climbed high into the canopy, scaling epiphyte rich dipterocarps to heights of 45m. The training site was particularly rich in wildlife with frequent incidences of Orangutans and other primates watching the climbers from nearby branches.



Dr Xiaodong Yang from China checks a Malaise trap at 40m

Week three saw all participants learning and practicing the practical skills needed to carry out science in the canopy, placing traps high in the trees and discussing the possibilities for future canopy research in their respective countries.

This was the first of three courses to be run by the Global Canopy Programme and funded by the Darwin Initiative. In years two and three, this year's graduates will return to help train many more students to carry out work in the canopy of ASEAN countries. It is the belief of all involved that these courses



Alex Karolus from Danum Valley on his first canopy climb

will follow the success of the Brazilian model, generating excitement in and capacity to carry out high level research in the rainforest canopy.

If you would like to participate in or host a course please contact John Pike

jpik@globalcanopy.org

For further information please see our website

www.globalcanopy.org/training

CONTRIBUTE TO WHAT'S UP?

The International Canopy Network (ICAN) is currently seeking articles and information for the upcoming issue of What's Up?, set for publication in June, 2005. ICAN accepts articles, meeting, workshop and job announcements, relevant website addresses, and citations. Contributions can be sent via e-mail attachment, fax, or snail mail. Articles up to 1500 words are accepted (WORD format preferred) and graphics are welcomed. The deadline for submissions is May 15, 2005. For further information or to send contributions, please contact the ICAN office:

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BRAZILIAN GOVERNMENT OFFICIALLY ENDORSES THE OURO PRETO DECLARATION ON BRAZILIAN FOREST CANOPIES, BIODIVERSITY AND CLIMATE CHANGE

In June 2004, the International Workshop on Forest Canopy Research in Brazil: Training in Canopy Ecology and Biodiversity Conservation, was held in Ouro Preto, Brazil. The workshop body drafted the **The Ouro Preto Declaration on Brazilian Forest Canopies, Biodiversity and Climate Change**. It was signed by representatives from more than 30 Universities and forest and environment related institutions in Brazil. The declaration recognizes the importance of forest canopies and calls for further development of canopy research and training in Brazil.

Soon after the workshop, the declaration was sent to the Ministry of Science and Technology in Brazil and also to the Secretariat of the Convention on Biological Diversity in Montreal. On 13th of December 2004 the Brazilian Ministry of Science and Technology responded by fully endorsing the declaration and will support canopy biodiversity research in Brazil. They included a three-page letter from the biodiversity section of the Ministry that further emphasized the importance of forest canopies and called for the Ministry to support these efforts. In particular they highlighted the importance of forest canopy research for studying regional and global hydrology, carbon dynamics and climate change. In addition, it emphasized the need for canopy data to improve the interpretation of satellite imagery that can then be used to examine the interactions between Amazonian forest cover, carbon storage and climate change. The GCP will post a copy of the letter on their website as soon as it has been translated into English.

The full text of the declaration can be viewed at

www.globalcanopy.org/news

MEETINGS AND SYMPOSIA



NORTHWEST SCIENCE ANNUAL MEETING

24-25 MARCH 2005

The Wind River Canopy Crane Research Facility (WRCCRF) will be presenting a symposium at the annual meeting of the Northwest Scientific Association this March 24 - 25, 2005 in Corvallis, Oregon. The symposium is titled "The Wind River Canopy Crane Research Facility: 10 years of research on the structure and function of an old-growth forest ecosystem." The symposium will include talks on the evolution of old-growth forest canopy structure, forest canopy biology, carbon dynamics of an old-growth forest, the physiologic consequences of being large and long-term measurements at WRCCRF. The WRCCRF Director, Professor Jerry Franklin will be the banquet speaker, discussing "Natural Resource Challenges in the 21st Century". In addition, there will be a workshop on NEON (Pacific Northwest Regional Planning for the National Ecological Observatory Network) facilitated by Mark Harmon and Jerry Franklin.

See the Northwest Scientific Association website for more details and registration information:

http://www.vetmed.wsu.edu/org_NWS/NWSci_Home.htm

Have you recently moved or changed your e-mail address? If so, please let us know so we can keep your records current. E-mail your new information to canopy@evergreen.edu

ECOLOGICAL SOCIETY OF AMERICA

7-12 AUGUST 2005

An organized oral session entitled **Casting Light on Nocturnal Stomatal and Canopy Conductance** will be held this August 7-12 at the Ecological Society of America annual meeting in Montreal, Quebec.

A central principle underlying research in plant physiological ecology is that stomata regulate water loss from leaves in relation to photosynthetic carbon fixation and water supply. This suggests that almost all land plants (excluding CAM) should close their stomata at night when there is no opportunity for carbon gain. However, there is increasing evidence that significant water loss occurs through stomata in the dark in many species from a range of environments. Recent work suggests that plants with inherently high daytime stomatal conductance tend to have high nocturnal stomatal conductance, and that stomata respond to air humidity variation in the dark. Is this a failure of the stomatal control system, or might it confer benefits, or even be necessary, in plants? Stomatal and canopy conductance have been measured so infrequently in the dark that mechanistic and ecological understanding is weak. Possible benefits of nocturnal stomatal conductance include improved nutrient acquisition, recovery from xylem cavitation, prevention of excess leaf turgor and continuation of oxygen delivery to xylem parenchyma. If nocturnal stomatal conductance is widespread, this phenomenon has wide implications for carbon and water budgets of plants and ecosystems, including (a) impacts on the oxygen isotope composition of carbon dioxide, which is increasingly being used to partition ecosystem respiration, and for which models are extremely sensitive to nocturnal stomatal conductance (b) the validity of assumptions made about zero night flow in sap flow methods and hydrological or land surface exchange models, and (c) possibly enhanced pollutant damage via stomatal uptake when photosynthetic electron transport is inactive. The occurrence and significance of nocturnal stomatal conductance spans multiple spatial scales from individual stomata to entire ecosystems, and disciplines from plant physiology to biogeochemistry.

For more information regarding this session, please contact Nathan Phillips at nathan@bu.edu.

RECENT CITATIONS IN CANOPY SCIENCE

Since there is no central journal on canopy science, it is useful to publish citations on canopy studies in the recent literature. Some of the papers listed below were obtained from ICAN subscribers sending in reprints; most were discovered through weekly literature searches on Current Contents on Diskette (CCOD).

CANOPY STRUCTURE

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FOREST MANAGEMENT

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