Tropical Ecology **50**(1): 125-136, 2009 ISSN 0564-3295
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Canopy research in the twenty-first century: a review of Arboreal Ecology

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Abstract: After thirty years of development, canopy science is still an emerging frontier of exploration promising not only adventure and scientific discovery but also solutions to global challenges. Important environmental issues such as climate change, biodiversity conservation, and whole forest interactions have inspired data collection within canopies as well as above and below canopies, and catalyzing large-scale ecological monitoring. But perhaps most importantly, canopy ecology may herald a new set of metrics in scientific achievement for the next generation of ecologists. As canopy science matures, the treetops have become scientific, economic, and social drivers for outreach in education and conservation. Rather than relying on technical scientific publications and data sets as the only measures for promotion and tenure, the next generation of ecologists increasingly prioritizes education outreach and applied conservation as additional metrics for success as a scientific professional. The integration of research, education outreach and conservation as the new tool kit for young ecologists may lead to better stewardship of ecosystems.

Resumen: Después de 30 años de desarrollo, la ciencia del dosel sigue siendo una frontera emergente de exploración que promete no solamente aventura y descubrimiento científico, sino también soluciones a los retos globales. Temas ambientales importantes como el cambio climático, la conservación de la biodiversidad, y la interacciones a nivel del bosque completo han inspirado la obtención de datos en los doseles, así como debajo y arriba de ellos, y han catalizado el monitoreo ecológico de gran escala. Pero quizá más importante aún, la ecología del dosel podría anunciar un nuevo conjunto de medidas de los logros científicos para la siguiente generación de ecólogos. Conforme madura la ciencia del dosel, las partes altas de los árboles se han convertido en directrices científicas, económicas y sociales para el ámbito educativo y la conservación. En lugar de confiar en las publicaciones científicas técnicas y en los conjuntos de datos como únicas medidas para la promoción y la definitividad laboral, la siguiente generación de ecólogos está dando cada vez más una mayor prioridad al área educativa y a la conservación aplicada como indicadores adicionales del éxito del profesionista científico. La integración de la investigación, la educación y la conservación son el nuevo juego de herramientas para los ecólogos jóvenes que puede conducir a una mejor administración de los ecosistemas.

Resumo: Depois de trinta anos de desenvolvimento, a ciência sobre o copado é ainda uma fronteira emergente de exploração promissora, não só de aventura e descoberta científica, mas também, de soluções para os desafios globais. Uma questão ambiental importante tal como a mudança climática, a conservação da biodiversidade, e as completas interacções florestais têm inspirado a recolha de dados no seio do copado bem como acima e abaixo do mesmo, bem como catalisado uma monitorização ecológica em grande escala. Mas, talvez mais importante, a ecologia do copado pode encabeçar um novo conjunto de métricas de alcance científico para a

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próxima geração de ecologistas. À medida que a ciência sobre os copados amadurece, os cimos das copas das árvores podem tornar-se os motores científicos, económicos e sociais para a extensão na educação e conservação. Em vez de depender das publicações técnico-científicas e conjuntos de dados como a medida única para a promoção e status permanente, a nova geração de ecologistas dá primazia, de forma crescente, à extensão da educação e conservação aplicada como uma métrica adicional para o sucesso como profissional científico. A integração da investigação, da extensão da educação e conservação como uma nova ferramenta para os jovens ecologistas pode conduzir a uma melhor guarda dos ecossistemas.

Key words: Canopy research, ecology education, global canopy program, tropical rain forests.

Introduction

History of methodology to study forest canopies

Forest canopies have long eluded scientific research because of the logistical difficulties of reaching tree crowns and the subsequent challenges of sampling for researchers who manage to ascend above the forest floor (Lowman 2004a; Moffett & Lowman 1995). Original methods including slingshots, ropes, and simple hardware (Fig. 1) have advanced to include networks of cranes, towers and walkways that facilitate more rigorous experimental testing of hypotheses about canopy processes (Fig. 2). Only in the last two decades have scientists undertaken extensive exploration of this complex world of plants, insects, birds, mammals, and their interactions. Biologists in the nineteenth century traditionally based their ideas about forests on observations made at ground level. These forest floor-based perceptions are summarized in a comment by Alfred R. Wallace (1878):

"Overhead, at a height, perhaps, of a hundred feet, is an almost unbroken canopy of foliage formed by the meeting together of these great trees and their interlacing branches; and this canopy is usually so dense that but an indistinct glimmer of the sky is to be seen, and even the intense tropical sunlight only penetrates to the ground subdued and broken up into scattered fragments… it is a world in which man seems an intruder, and where he feels overwhelmed."

Ideas about forest canopies changed very little for almost one hundred years until biologists began applying technical climbing hardware to trees in the 1970s. This creative approach was undertaken independently at two locations around the world, at a time before the invention of internet, so the researchers were unaware of their common methodology. Don Perry (1986) adapted technical climbing hardware to ascend a *Ceiba pentandra* (kapok tree) at La Selva Biological Station in Costa Rica, while Lowman stumbled upon caving hardware as a means to explore leaf longevity in emergent trees of the Australian rain forests (Lowman 1985, 1999). At this time, communication of methods and findings from remote tropical jungles on the opposite sides of the globe was slow, and only via snail mail. Canopy access using ropes, although independently evolved across the globe, eventually appeared side-by-side in the journal *Biotropica*, when Perry's colleague published her Costa Rica work in the same issue as Lowman's first Australian data set (Lowman 1984; Nadkarni 1984). As two post-doctoral canopy women whose careers invariably shared commonality halfway around the world, subsequent communication has since led to many collaborative canopy programs.

The 1970s and early 1980s represented the era of single rope techniques (SRT). This portable, relatively inexpensive method of canopy study allowed canopy access even to graduate students with their modest budgets. Ropes and harnesses were not effective, however, to reach the leafy perimeters of tree crowns, since ropes were restricted to positions looped over sturdy branches close to the tree trunk; and SRT was not useful for emergent trees whose enormous canopies usually extended far away from the main trunk itself. To access foliage on the extremities, Peter Ashton and

Fig. 1. Single rope techniques provide canopy access to a *Ceiba pentandra* tree along the Amazon River, Peru.

colleagues invented the canopy boom, a horizontal bar with a bosun's chair at one end, that swung into the leafy canopy away from the main trunk (Appanah & Chan 1981). Scaffolds were trialed in eucalypt forests of Australia; and cherry pickers were also used to access the outer and upper perimeters of tree canopies for studies of eucalypt dieback (Lowman & Heatwole 1992).

In 1992, Alan Smith of Smithsonian Tropical Research Institute (STRI) set up the first construction crane to study forest canopies in Panama (Parker *et al.* 1992). Although relatively

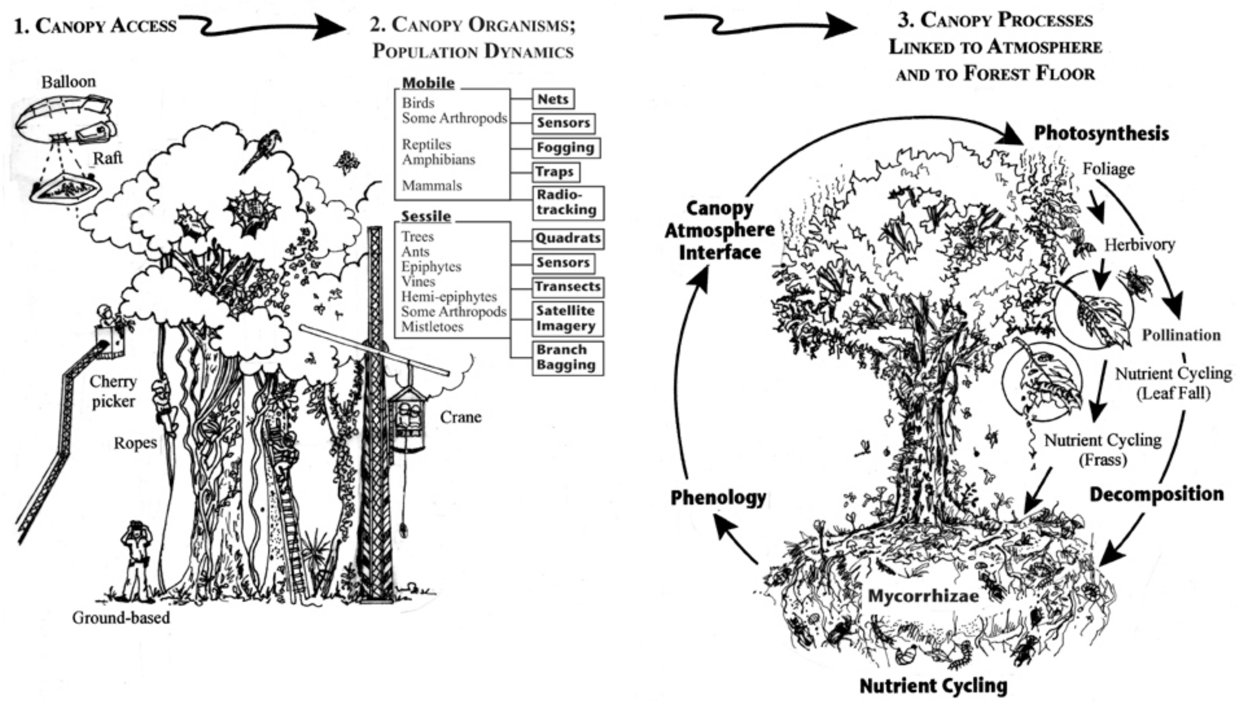

Fig. 2. Schematic drawing of the development of canopy biology, and of nutrient cycling from canopy to forest floor.

expensive, this device allowed access to any region of canopy beneath the crane arm without regard to the tree trunk. Specific protocols such as measuring herbivory (Shaw *et al*. 2006), carbon uptake (Korner *et al.* 2005), and even lizard exclusion (Dial & Roughgarden 2004), have facilitated more rigorous experimental approaches in the canopy, especially with the advent of cranes. Under the auspices of the Global Canopy Programme (GCP), four new whole-forest observatories are proposed that will expand the current crane network of nine to include tropical forest sites in Brazil, India, Madagascar, and Malaysia (Mitchell *et al*. 2002). In partnership with ATREE (Ashoka Trust for Research and Ecology and the Environment), India's crane will be cited in the Western Ghats.

Simultaneous with the launch of the cranes, French botanist Francis Hallé designed a colorful hot-air balloon and raft operation, called Radeau des Cimes (translation: raft on the rooftop of the world). Its inflatable raft is 27 m diameter and forms a base camp for researchers in the treetops. A dirigible, or hot air balloon, operates in conjunction with the raft, transporting researchers to new locations in the canopy to study biodiversity and the canopy-atmosphere interface. In 1991, the French expedition pioneered a new technique called the sled, or skimmer. This small (5 m) inflatable equilateral triangle is towed by the balloon so the scientists can trawl the uppermost canopy for biodiversity surveys. With the sled, rapid collection of canopy leaves, flowers, vines, or epiphytes as well as their pollinators or herbivores can be conducted offering spatial without the limitations of temporal variability (Mitchell *et al.* 2002; Lowman 2004a).

In recent years, canopy biologists have utilized innovative combinations of field tools many meters above the forest floor. Korner *et al.* (2005) measured canopy response to increased atmospheric carbon dioxide in Swiss temperate forests using a crane outfitted with portable analyzers. At another European crane site near Leipzig, Germany, Szarzynski & Shaw (2005) quantified canopy light with infra-red photography, called "thermal imaging" (Fig. 3). A third innovative field team uses towers, catwalks, and plastic panels above the canopy to facilitate manipulative experiments simulating drought in Amazonian lowland tropical rain forest (Cattânio *et al*. 2002). Using a combination of hot-air balloon,

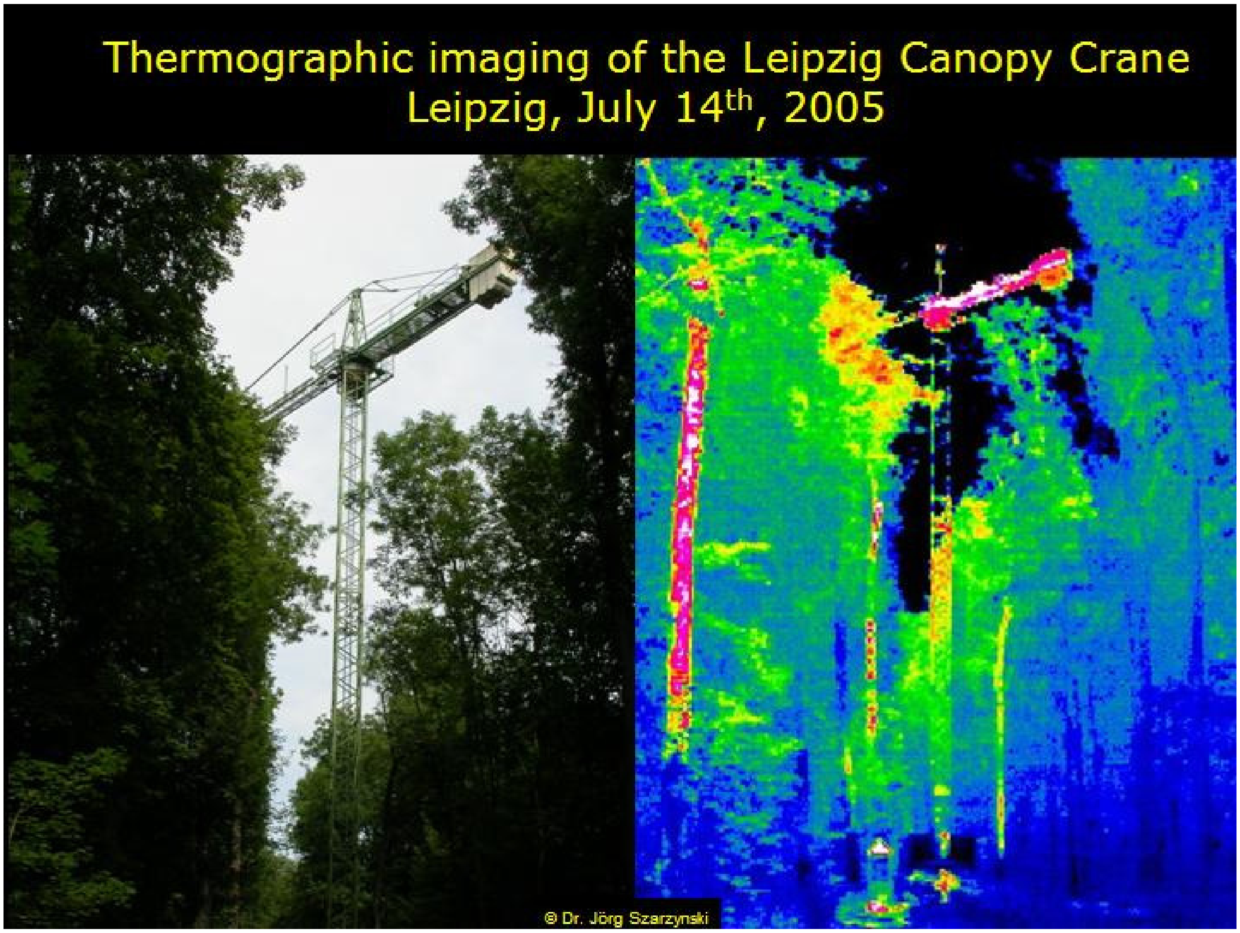

Fig. 3. Thermal imaging of the deciduous forest surrounding the Leipzig canopy crane in Germany (Photo by David Shaw).

inflatable raft, ropes and construction crane (Fig. 4), Yves Basset of the Smithsonian Tropical Research Institute coordinated the first comprehensive, collaborative survey of canopy arthropods through a vertical column of Panamanian tropical forest (Didham & Fagan 2003).

Canopy walkways have provided unprecedented access to bromeliads to survey biodiversity and other ecological phenomena (Burgess *et al.* 2002, 2003; Lowman *et al.* 2006). Towers combined with aerial imagery and sampling techniques have fostered a new era of forest canopy modeling, including studies of deforestation, gas exchange, and simulations of atmospheric gases (e.g. Keller & Lerdau 1999). Because the forest canopy represents a direct interface between earth and atmosphere, this layer of biodiversity plays a critical role in environmental monitoring of temperature changes, rainfall variability, eddy fluxes, pollution, and productivity (reviewed in Laurance & Peres 2006).

The new National Ecological Observatory Network (NEON) proposes to deploy a network of facilities including cranes, towers, sensor technologies, miniaturized analytical instruments, and remote cameras to document and forecast changes in ecosystems at regional and continental scales (Senkowsky 2005). In addition to research alone, NEON will enhance science education and outreach for citizens, students, and policy-makers. Canopy access, as part of the NEON toolkit, has the potential to inspire students and citizens with an enthusiasm for ecology as well as with sophisticated data sets.

At the fourth international canopy conference in Leipzig, Germany, in July 2005, 42 of 87 talks reported new findings on canopy biodiversity (and

Fig. 4. Methods of canopy access used in the project IBISCA. From top left, clockwise: canopy crane (gondola view), canopy bubble, canopy fogging, Ikos (tree platform), single rope techniques and canopy raft (photo IBISCA archives).

29 featured arthropods). Of note, the notion of regional knowledge transfer was introduced to canopy science through several reports. In one case, indigenous villagers were trained as

parataxonomists in New Guinea to contribute to a larger study on the effect of canopy openness on insect herbivores (Basset *et al*. 2004). While their scientific results suggested that conspecific mature trees and seedlings/saplings supported distinct herbivore fauna (contrary to the assumptions of the Janzen-Connell), what might be more important than their scientific findings was the fact that these researchers empowered the indigenous people to understand their extraordinary biodiversity. Such regional knowledge translates into forest conservation when locals gain a global perspective of their unique biodiversity. Their research results indicated that tropical arthropods may be less specialized than previously thought in terms of resource use, but more specialized in terms of habitat use (Basset *et al*. 2003). If insect-plant interactions in the tropics are not as highly specialized as previously thought, global estimates of species richness may be overestimated (Novotny *et al*. 2002). Their studies also serve as an important conservation example of regional knowledge transfer (www.antu.cas.cz/png/index.html).

Forest ecosystems are threatened globally by fragmentation and deforestation (Laurance & Peres 2006). The integrity of forest canopies is critical to maintaining regional and global productivity and climate conditions. Continued efforts to identify and map biodiversity in forest canopies, to quantify canopy-atmosphere and canopy-soil fluxes, and to educate the public about both economic and ecological aspects of forest conservation are critical as global pressures on ecosystem health intensify (Bawa *et al*. 2004). In the Western Ghats, canopy biologists study pollination of emergent trees and also the ecology of interactions between the canopy tree *Cullenia exarillata* seeds and primates including the lion-tailed macaques, *Macaca silenus* (Ganesh & Davidar 1999). The advent of a canopy crane in India will generate greater media attention leading to public education about the ecosystem services provided by India's few remaining tracts of tropical forest.

Such progression from data sets to conservation solutions represent important next steps for canopy science, but will require scientists to communicate their information more effectively to the public sector (Lowman 2006). The next canopy conference, to be held in Bangalore, India, in 2009, will feature dedicated sessions on canopy education and outreach, climate change, and global forest conservation (www.canopy2009.org). In summary, canopy science is maturing beyond a methods-based, conventional-reporting focus to embrace cutting-edge global science questions using a sophisticated array of methods. This trajectory will have consequences not only for research, but also for education outreach and conservation.

Case studies where canopy research fosters conservation and ecology education through regional knowledge transfer

Our ancestors were tree dwellers. Throughout human history, people have taken to the trees as safe havens, sites of special spiritual connection, and as a cornucopia for food, medicines, materials, and productivity. In an evolutionary sense, humans descended from ancestors in the treetops. In Papua New Guinea, a tribe called the Korowai still lives in the treetops, erecting aerial houses accessible only by twig ladders. It is speculated that their unusual habit of community tree houses evolved as a mechanism to escape enemies on the forest floor, and provide a healthy environment above the dank, dark understory. Tree houses remain a recreational vestige of children and adults alike that inspire links between humans and the natural world.

Why do the treetops hold such a spiritual, as well as scientific importance for cultures throughout the world? And why have scientists overlooked canopy exploration in scientific discovery? Relatively few unknown frontiers of exploration remain in the 21st century, but the treetops are still considered a "black box" in science. Innovative partnerships between businesses, educators, and scientists linked by a common denominator of the treetops are emerging that positively impact science education, environmental justice, and local economies through efforts such as ecotourism.

(a) Fostering ecology education through canopy science

The Jason Expedition (www.jason.org), a distance learning program, annually engages over 3 million middle school students and teachers worldwide on remote field expeditions using satellite technology. In 1994, 1999, and 2004, the Jason Project featured canopy research, including the challenges of access and data collection in the treetops. During 2004, Jason XV studied the links between the brown (i.e. forest floor) and the green (i.e. canopy) food webs in the forest canopy of Barro Colorado Island, Panama (Lowman *et al.* 2006). Science curricula developed specifically for the canopies of Panama fostered student learning about the complex linkages among biodiversity, biogeochemical cycling, and global environmental conditions. Researchers conducted canopy studies that were broadcast live into classrooms throughout the world, providing a unique model that integrates research with ecology education. Middle school students even participated in data collection that led to scientific publications (e.g. Burgess *et al.* 2003).

(b) Promoting economic benefits from canopy access tools

Canopy research has also created local economic incentives for conservation of forests through ecotourism. With gadgets ranging from aerial trams to zip lines to canopy platforms connected by swaying bridges, canopy access tools provide recreational activities whereby the public can personally experience the treetops. While this may have slightly negative consequences to some wildlife, ecotourism does more good than harm by educating a new generation about the canopy (Lowman 2004b). Currently, over twenty-five canopy walkways exist worldwide, with missions of research and/or conservation education (Table 1).

Table 1. Current list of walkways and cranes that offer research and education programs, as collated at the Fourth International Canopy Conference (to submit additional sites, please contact: www.canopymeg.com).

Some Sites with Canopy / Cranes	
Australian Canopy Crane	Australia
Leipzig Canopy Crane	Germany
Kranzberg Canopy Crane	Germany
SollIing Research Crane	Germany
Tomakomai Crane	Japan
Panama City Crane	Panama
San Lorenzo Crane	Panama
Basel Canopy Crane	Switzerland
Wind River Crane	USA
Surumoni Crane	Venezuela

Contd…

Table 1. Continued.

Some Sites with Canopy / Walkways	
Lamington National Park	Australia
Walpole Tree Top Walk	Australia
Tahune Airwalk	Australia
Mt. Equestrian Trails Lodge	Belize
Ecoparque de Una	Brazil
Ulu Temburong Walkway	Brunei
Vancouver Island Walkway	Canada
Halliburton Forest Walk	Canada
Xishuangbahnna Tropical Botanical Gardens	China
Caparu Station Walkway	Colombia
Paeque Nacional Natural	Colombia
Selvatura Park	Costa Rica
Drake Bay Walkway	Costa Rica
Tirimbina Rainforest Center	Costa Rica
Choco Canopy Walkway	Ecuador
Jatun Sacha Canopy Walkway	Ecuador
Tiputini Biodiversity Station	Ecuador
Nourages Field Station	French Guyana
Tree Trek Waldkletterpfad	Germany
National Park Hainich	Germany
Bioshere Houe	Germany
Kakum Forest Reserve	Ghana
Iwokrama Walkway	Guyana
Batuampar Walkway	Indonesia
Lambir Hills Walkway	Malaysia
Gunung Haliman Walkway	Malaysia
Taman Negra Walkway	Malaysia
Malaysian Walkway	Malaysia
Poring Hot Spring Canopy Walk	Malaysia
Otari-Wilton's Bush	New Zealand
ACTS Canopy Walkway	Peru
Canopy Inkaterra	Peru
Amazonia Expeditions	Peru
Momon River Lodge	Peru
HSBC TreeTop Walk	Singapore
Tsitsikamma Forest	South Africa
Sri Lanka Arial Walkway	Sri Lanka
Luguillo Exp. Forest (PR)	USA
Coweeta Hydrologic (NC)	USA
Ecotarium (MA)	USA
Hampshire College (MA)	USA
Hopkins Memorial Forest (MA)	USA
Marie Selby Bot. Gardens (FL)	USA
Millbrook School (NY)	USA
Myakka River State Park (FL)	USA
Oxbow Meadows (GA)	USA
Southeast Exp. Rainforest (AK)	USA
Cypress Valley (TX)	USA
University of the South (TN)	USA
Falealupo Walkway	Western Samoa
Borneo Canopy Crane	Malaysia

Fig. 5. The author teaches middle school children about canopy-forest floor interactions during the Jason Project, a distance learning broadcast that uses forest canopies as an effective driver for science education.

In Western Samoa, a canopy walkway was built to pay off a debt incurred to build a local school. Led by ethnobotanist Paul Cox, a team of American canopy builders (www.treefoundation. org) met with the fifteen village chiefs to discuss the risks of this ecotourism venture. After drinking copious amounts of *kava*, a local drink, the chiefs unanimously approved the construction of a walkway into an emergent *Ficus* tree. Profits from this successful venture paid for school construction without the more conventional "solution" of logging local forests (Lowman *et al.* 2006). The chiefs wisely recognized that logging would ultimately destroy their island ecosystems, and that ecotourism provided a more sustainable income stream.

Ecologists face increasing challenges to integrate sociological considerations with scientific research, and again, canopy biology can offer some innovative case studies. To conserve epiphytic mosses that are over-collected by zealous orchid growers as a potting substrate, Nalini Nadkarni engaged prisoners to cultivate threatened mosses of the Pacific Northwest forests (Fischer 2005). At present, growth rates of mosses are too slow for commercial production, but horticultural therapy offered both emotional and economic benefits for the inmates, as well as epiphyte conservation. In another example, Lowman engaged local communities to "own" real estate in the treetops and subsequently support the construction of treetop walks (Lowman *et al.* 2006). Visitors to walkways in Queensland, Australia and Sarasota, Florida, are encouraged to purchase a plank, which funds the maintenance of the walkway as well as a sense of ownership to heighten local forest conservation (www.treefoundation.org).

(c) Forest canopies as mediators of global environmental change

Canopy cover represents a key driver in social, economic and biological assessments of global change (e.g. Lamb *et al.* 2005). The growing number of options for safe, replicated canopy research has facilitated expanded studies of forest processes. Two relatively new areas of canopy exploration – nutrient cycling and decomposition from canopy to forest floor and back again, and experimental studies of climate change at the canopy-atmosphere interface – illustrate the overarching global significance of current canopy research.

Canopy herbivores influence nutrient cycling – insect frass (feces) and defoliation directly remove leaf material that cascades to the forest floor and ultimately recycles (Fig. 2). At least seven mechanisms have been identified by which herbivores can influence soil nutrient dynamics (Hunter 2001) including the linkage between canopy defoliation and rates of nutrient cycling/export. At a watershed scale, important effects of canopy defoliation include changes in nutrient cycling and nutrient export (Eshleman *et al.* 1998). At the continental scale, insect outbreaks can wreak havoc on both the ecology of economy of entire regions (e.g. Lowman & Heatwole 1992).

"Through fall" can change in chemical composition as a result of folivory, primarily through increased rates of nutrient leaching from chewed leaves and dissolution of insect frass (Frost & Hunter 1994). Soil nutrient cycles can respond rapidly to inputs of frass and modified through fall because these inputs do not require the mineralization of complex organic matter. Simply put, they can speed up the rate of nutrient cycling. These effects are analogous to McNaughton *et al.*'s (1988) "fast cycle" or the "acceleration hypothesis" (Ritchie *et al.* 1998). In contrast, herbivore-mediated changes in the quality of leaf litter likely influence nutrient dynamics more slowly and are analogous to McNaughton *et al.*'s (1988) "slow cycle". In fact, depending upon the quality of litter fall, canopy herbivores might sometimes act to decelerate nutrient cycling. Both fast- and slow-cycle effects, and acceleration or deceleration of cycles, may occur in the same system but on different time scales. For example, herbivore activity may increase rates of nitrogen cycling and primary production in the short-term (e.g. through frass inputs) while causing both to decline in the long-term (e.g. through selection of chemically-defended plant parts that decompose slowly) (Uriarte 2000). Such detailed analyses of interactions cascading through the canopy to forest floor, and cycling back again, will facilitate better management of forest ecosystems, and also help to quantify global cycles essential to life on earth.

Both insect epidemics and humans reduce the forest canopy through defoliation and deforestation. Loss of forest cover is linked to climate change, and the subject of global investigations (Feddema *et al.* 2005). Canopy removal reduces evapotranspirative cooling, offsetting the effect of increased albedo, thereby increasing soil surface temperatures and reducing precipitation and relative humidity (Anhuf 2005; Foley *et al.* 2003). They calculated a net warming of 1-2 °C in tropical regions as a result of deforestation, an effect that would exacerbate the warming due to increased atmospheric CO_2. Surface warming and drying can stress and kill adjacent vegetation, leading to destabilizing positive feedback and an advancing front of declining forest. Using the Swiss canopy crane, Korner *et al.* (2005) exposed a deciduous stand to elevated carbon dioxide, simulating potential conditions of climate change. After only one season, nearly half of the emitted soil carbon dioxide originated from new carbon, and nearly all mycorrhizal fungi biomass was comprised of new carbon, indicating a very rapid canopy-soil linkage. Korner *et al.* (2005) studying the links between deforestation and precipitation predict that deforestation in Amazon region will lead to drier conditions. Reduced canopy cover and subsequent landscape degradation in turn affects the economics and social structure of many regions, in addition to the loss of ecological integrity (Lamb *et al.* 2005). Recent predictions abound as to the global consequences of tropical deforestation and climatic shifts (reviewed in Laurance & Peres 2006).

The relatively young, emerging science of canopy ecology inspires new and innovative research to solve global environmental challenges. Even more important, the "charisma" of treetop exploration can serve as a catalyst for ecology education and effective local conservation initiatives.

Acknowledgement

The author thanks Drs. Mark Hunter an Timothy Schowalter for collaboration on National Science Foundation grant DEB-9815133 that inspired some of this dialogue. In addition, National Science Foundation Informal Science Education grant "Out on a Limb – Forest Canopies" facilitated some of the ecology education outreach activities. In addition, the organizers of the Tropical Ecology Congress in Dehra Dun, India (December 2-5, 2007) provided the venue for our session on "Biodiversity Conservation in the Tropics: Issues, Concerns and Strategies" that included this paper.

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