Biodiversity Meets the Atmosphere: A Global View of Forest Canopies

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The forest canopy is the functional interface between 90% of Earth's terrestrial biomass and the atmosphere. Multidisciplinary research in the canopy has expanded concepts of global species richness, physiological processes, and the provision of ecosystem services. Trees respond in a species-specific manner to elevated carbon dioxide levels, while climate change threatens plant-animal interactions in the canopy and will likely alter the production of biogenic aerosols that affect cloud formation and atmospheric chemistry.

The forest canopy—defined as the aggregate of all crowns in a forest stand—plays a crucial role in the maintenance of biodiversity and the provision of local and global ecosystem services. Forest canopies support about 40% of extant species (*1–4*), of which 10% are predicted to be canopy specialists (*1*). Forest canopies also influence the hydrology of more than 45 million ha of land by controlling evapotransipration and intercepting up to 25% of precipitation, and their removal often decreases local rainfall substantially (*5*). Work at this challenging frontier only began in earnest in the early 1980s and has already changed substantially our understanding of key ecosystem processes.

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Biodiversity Patterns and Predictions

Forest canopies are among the most species-rich yet most highly threatened terrestrial habitats (*6*). Twenty-two of the 25 global "biodiversity hotspots" embrace forest habitat that combines high levels of endemism with the imminent threat of degradation. Knowing the number of species is fundamental to formulating questions about ecosystem function and evolution, as well as informing conservation priorities (*7*).

Global estimates of 30 million to 100 million species by Erwin (*8*), on the basis of work in tropical canopies, were a key driver in the formulation of species coexistence and habitat specialization models. Detailed studies of herbivorous forest insects that suggest much lower levels of host specificity have recently resulted in revised estimates of 2 million to 6 million (*4*, *9*), resolving previous discrepancies between field data, data from taxonomic collections, and biogeographic estimates. These studies, which constantly reveal new species, also challenge equilibrium models of species coexistence (*4*).

A relatively high proportion of invertebrates, about 20 to 25%, are proposed to be unique to the canopy (*10*), although this proportion varies with forest type, canopy structure, and microclimate and is probably greater than 25% for herbivorous invertebrates (*11*). Ten percent of all vascular plant species are epiphytic canopy dwellers. This diversity can be attributed in part to the complex three-dimensional structure of the canopy, which affords opportunities for niche diversification and vertical stratification.

Ecophysiology and Ecosystem Function

Integration from leaf to canopy. Increased use of large cranes to access the canopy has presented exciting opportunities for studying trees as whole, integrated organisms. Together with the international network of FLUXNET towers, which measure canopy fluxes of water vapor, CO_2, and energy, this approach has led to advances in understanding how transpiration and photosynthesis are regulated and integrated from the leaf to the whole canopy. Recent work on canopy leaves has highlighted the important role that tree size, architecture, and allometry play in governing physiological behavior.

Much of the variation in leaf area–based rates of transpiration and photosynthesis within tree crowns and among co-occurring canopy species can be ascribed to variation in leaf area–specific hydraulic conductance (LSC), a measure of liquid-water transport efficiency to the canopy evaporating surfaces (*12*, *13*). LSC varies with morphological traits such as the diameter and length of conducting elements and differences in tree hydraulic architecture that alter the balance between transpiring leaf area and xylem. It seems clear that stomata limit transpiration to maintain the balance with tree hydraulic capacity (*14*), but that coupling photosynthesis with hydraulic capacity may involve independent adjustments in photosynthetic biochemistry. Nevertheless, higher order traits such as tree hydraulic architecture play a dominant role in constraining the physiological behavior of canopy leaves. Reliance on water stored in stems and other organs is an important homeostatic mechanism that maintains photosynthetic gas exchange, particularly because hydraulic path length increases with canopy height (*14*, *15*).

Canopy water and carbon fluxes are proposed to scale allometrically with tree size, as shown recently for 45 co-occurring tropical tree species (*16*, *17*), suggesting that photosynthesis may scale universally with tree size. This relation has also been documented for vascular epiphytes (*18*). If these allometric scaling models prove valid, analysis of the role of species composition in determining water and carbon fluxes in forest canopies will be greatly simplified, allowing better predictions of response to climate change.

Many ecophysiological processes of plants measured at a leaf or branch may also be integrated to the stand or regional level with the help of SVAT models (soil-vegetation-atmosphere-transport) (*19*), remote sensing, and surrounding technologies such as LIDAR (light detection and ranging), which may be used to investigate the three-dimensional nature of the canopy (*20*). The vegetation spectral properties fundamental to remote sensing are measured from above the surface, but their validation in forest ecosystems requires canopy access (Fig. 1). For example, canopy cranes at Lambir National Park, Malaysia, and in the Republic of Panama are being used to validate satellite-mounted sensors by making possible simultaneous measurements of the physiological status and structure of the upper canopy. With such validation, remote sensing, along with data collected from micrometeorological flux towers, will contribute to increased understanding of processes controlling the exchange of mass and energy at the canopy-atmosphere interface.

Plant reproductive biology. Climatic signals controlling phenology are well understood for the temperate zone, where flowering and animal migrations have been shown environmental controls of phenology in wet tropical forests and the implications of global change for plant reproduction.

Ecosystem processes and services. Canopy research is uncovering the mechanisms behind processes such as pollination, herbivory, and decomposition, which are critical for the long-term fate of many threatened forests and species supported in their crowns.

Pollination services have been valued at U.S.$12 billion per annum (*26*), and pollinator-plant relationships vary on a continuum from extreme specialization to extreme generalization (*27*). Extreme specialization, as in the case of agaonid fig-wasps or arboreal orchids, is associated with highly derived coevolutionary pollination syndromes such as the synconia of figs (*28*) and pseudocopulation in orchids (*29*). At the extreme of generalist pollination strategies, leaf beetles may switch from herbivory to pollination during mast flow- shown that ants in tropical-forest canopies are key herbivores (*34*). Levels of herbivory on vines, lianas, and epiphytes remain little studied and are ripe for further investigation (*9*).

Detritus-based food webs are ubiquitous: Within the canopy, trees grow roots from branches and inside trunks to access them (*35*). Dead and moribund branches have a rich associated fauna of saproxylic insects (*36*) (saprophages plus fungivores) and 40% or more of the canopy populations of Coleoptera (*37*). Perched litter, principally associated with the "baskets" of *Asplenium* ferns, are a prominent feature of most Old-World canopies (*2*), as is suspended litter and soil in temperate forests (*38*). These not only represent an additional, substantial biomass of detritus, but also have a rich fauna with many endemic species of groups such as Collembola (*2*) and Acari (*3*).

Fig. 1. Canopy-access techniques. (**Left**) Single-rope technique for sampling suspended soils [credit: N. N. Winchester]. (**Middle**) Construction of Sarawak canopy crane [credit: T. Nakashizuka]. (**Right**) Canopy bubble–helium-filled balloon for canopy access [credit: L. Pyot/Océan Vert].

to occur earlier as spring temperatures increase (*21*, *22*). In contrast, in the relatively aseasonal wet tropics, signals are uncertain, precluding predictions about the possible effects of global climate change.

Flower opening, or anthesis, responds to low-temperature events, threshold levels of drought, or the return of rains after drought (*23*). These signals are being altered by global climate change. Canopy experiments have shown that light levels limit the carbon budgets of mature trees (*24*) and that terminal branches are the primary site of carbohydrate storage for reproduction (*25*). Further canopy-based studies of the differentiation of reproductive buds, interannual variation in carbohydrate stores, and physiological responses to drought stress and low-temperature excursions, all of which may be influenced negatively by climate change, are now required to understand the

ering events in dipterocarps (*30*). Global climate change is likely to affect pollination success by altering synchrony between flowers and their pollinators (*21*, *31*).

Canopy research is changing our understanding of herbivory. The accepted view of tropical rainforests as bastions of specialization—the association of particular herbivore species with a restricted set of available plant species—appears to be a major oversimplification. Herbivores attacking species of rainforest trees are probably less specialized than had been supposed (*4*), and possibly less specialized than their temperate-forest counterparts. Herbivores can be nearly 20 times as abundant per unit of foliage in mature trees than in seedlings (*32*) and at times of leaf flush within mature canopy plants (*33*), indicating a greater complexity of function than previously supposed. Recent work has

Global Change

The forest canopy is the functional interface between a rich and complex biological habitat and the atmosphere across more than a quarter of the global land surface. It plays an interactive role in the carbon cycle and in local and regional hydrological patterns, and has an impact on atmospheric chemistry. It is a key habitat in which to monitor and investigate principal actors in global change such as CO_2 enrichment and habitat disturbance.

Canopy disturbance. Canopy organisms are highly susceptible to human disturbance (*39*). Malcolm and Ray (*40*) propose that damage to the high canopy is the most appropriate measure of anthropogenic disturbance to forests and that more specifically, the number of openings in the canopy is a key correlate of many of the resultant ecological changes.

Timber harvesting disrupts the complex vertical stratification of habitats and resource use in the canopy (*41*) and can substantially alter nutrient dynamics (*42*). Selective logging in tropical forests may not always reduce tree diversity, but it extensively modifies pollinator diversity and behavior, reducing the reproductive capabilities of logged and even neighboring unlogged species of forest tree (*31*). The impact is less severe in forests that have frequent natural-disturbance events such as hurricanes and associated fires (*43*). Canopy habitat specialists are affected more by timber harvesting than are generalists, and there is evidence that insectivorous birds, for example, suffer greater effects than do other guilds as a consequence of impacts on their prey (*44*), suggesting a cascade along links within canopy food webs.

Canopy animals use branches and flyways as primary access routes to food and mates. Logging roads and powerline corridors in forests have strong barrier effects upon these animals (*45*), causing high levels of mortality, and fragmenting and isolating populations. Artificial openings in the canopy influence microclimate, vegetation, and animal assemblages, resulting in varying penetration depths from a few to several hundred meters (*46*, *47*). For sensitive species, edge effects compound the impact of forest clearance.

Climate change and hydrology. What will be the response of the canopy system to an elevated CO_2 environment? Controversy remains about whether old-growth forests are CO_2 sinks (*48*) or sources (*49*), partly because the methodologies for assessing the carbon balance of forests are themselves the subject of debate (*50*, *51*). New canopy research may help to resolve this dispute. Rather than increasing carbon storage, forests could become more dynamic in elevated CO_2 environments. Greater vigor in the growth of lianas—when they reach the canopy—may enhance tree turnover (*52–54*) and the concomitant risk of carbon loss. Data from studies at the atmosphere-canopy interface indicate that any early increases in CO_2 uptake by forests under elevated CO_2 may not be sustained beyond an initial response phase (*55*). The uncertainty over how forests will respond to elevated CO_2 is partly due to oversimplification of the system in past experimental work. Adult trees are likely to respond very differently to changes in resource supply than will young trees, particularly when nested in a matrix of natural neighbors and microbial symbionts (*56*). Thus, confidence criteria developed on the basis of pots in a greenhouse or young trees in a plantation are no longer satisfactory; a major gap between precision and relevance has opened up (*57*). However, whole-forest manipulations can now been achieved with mid- to long-term canopy access systems.

Set within a temperate deciduous forest, the Swiss Canopy Crane, together with the new "web-FACE" or Free Air Carbon Enrichment system (*58*), yields insights into the response of deciduous forests to a CO_2-rich world (Fig. 2). Stable–carbon isotope tracers document immediate signals of canopy CO_2 enrichment in soil biota, with mycorrhizae as prime carbon acceptors. Changes in canopy leaf-tissue quality under elevated CO_2 levels have been demonstrated and exert major effects on insect feeding behavior. FACE experiments at this and other sites, together with laboratory-based studies, have found that leaf-chewing insects commonly show an increase in consumption of plant material resulting from the higher C:N ratios occurring in the affected plant tissue (*59*). Some insects do show a lowered reproductive rate in elevated CO_2 environments, but the sap-feeding Homoptera consistently show elevated fecundity (*59*). These insects are major pests in plantations and are vectors for a wide range of plant diseases, outbreaks of which may be affected by the impact of atmospheric change on canopy functioning. There is an urgent need to further replicate these experiments in both temperate and tropical forests in order to define the links that have been identified between forest biodiversity, CO_2, and hydrology and their implications for forest management.

Global environmental change may also involve changes in the photosynthetically active radiation (PAR) reaching the canopy. Decreases in PAR resulting from a rise in anthropogenically derived airborne particulates (*60*) and from recent redistributions of convective activity and cloud cover within the tropics (*61*) could limit carbon acquisition by canopy trees (*24*). However, where cloud-free skies predominate, higher amounts of diffuse radiation, caused by atmospheric particulates, enhance whole-canopy photosynthesis (*62*).

Evapotranspiration supplies most of the atmospheric water vapor above forest canopies, with estimates ranging from 3 to 5 mm/day for the eastern and central parts of the Amazon basin (*63*) to 1.6 mm/day for a semiarid temperate pine forest (*64*). Spatial variability in water-balance components reflects variation in the three-dimensional structure of forests. Forests over large portions of the Amazon Basin and the temperate zone are evergreen, despite periods of three to six nearly rainless months per year. These forests sustain high levels of evapotranspiration during the dry season by accessing water deep in the soil profile. Reductions in transpiration as a result of increased stomatal closure in elevated CO_2 environments or disturbances to the canopy profile will affect forest microclimate and local and regional hydrological patterns, including flood cycles.

The biogenic emission of aerosols from forests critically influences continental cloud structure. Continental clouds are typically much deeper and less efficient at producing rain droplets than are maritime clouds. Observation of cloud structure collected in the Amazon during the Wet Season Atmospheric Mesoscale Campaign (WETAMC) in Rondonia (southwest Amazon) has revealed the presence of highly efficient shallow clouds, termed "green ocean clouds," with a structure

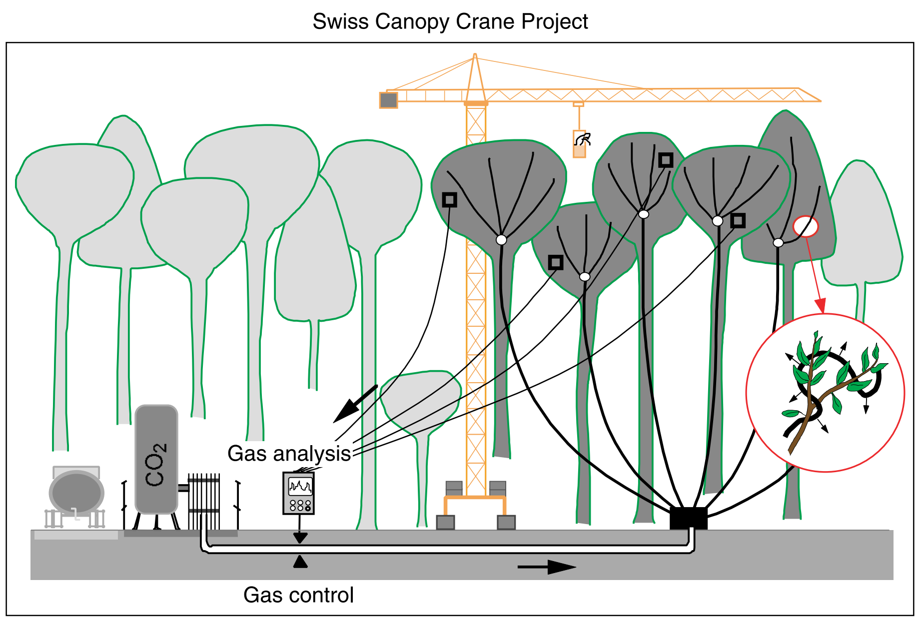

Fig. 2. Swiss canopy crane with FACE delivery system.

similar to that of tropical oceanic clouds (*65*). It remains uncertain what is responsible for the rain efficiency of these clouds, but it seems likely that volatile organic compounds (VOCs) released from the forest canopy, acting in a similar way to biogenic compounds released by marine species, may well be the driving force for their development. VOCs also increase the reflectance of rain droplets, potentially screening out solar radiation (*66*).

The production and emission of VOCs by plants is highly dependent upon species composition (*67*). Understanding the species-level emissions of VOCs requires canopy access for both scientists and their instruments. Species changes resulting from disease, invasions, or climatic change can have extensive regional effects on VOC emissions and air quality. For example, the chestnut blight that hit the United States in the early 20th century led to oak dominance in many southeastern U.S. forests and has doubled the regional emission of isoprene, the most abundant biogenic hydrocarbon. This area is currently a global hotspot for emission of isoprene, the most abundant biogenic hydrocarbon (*67*). Although broad global patterns of emissions are recognized (*68*), refinement of our knowledge of the species-level controls on VOCs is critical to development of robust models of emissions under changing conditions (*69*).

Future Challenges

Despite 20 years of effort, the forest canopy remains one of the world's least-known habitats. Considerable advances in our understanding of diversity, ecosystem processes, and gas fluxes within and across the canopy-atmosphere boundary have been made. There is much more, however, that can be learnt regarding the impact of global change on mature, diverse forests. The Convention on Biological Diversity (CBD) Workplan on Forests and the Cairns Declaration on Forest Canopy Research now call on governments to support research into "endangered habitats and species including forest canopies" and to investigate "the interface between forest components and the atmosphere." In order to achieve these aims, a more integrated approach from soil to canopy to atmosphere is urgently needed.

Integration is required on a global scale across gradients from temperate to tropical regions and from managed to unmanaged forests, coordinating the efforts of ecologists, physiologists, and meteorologists. The infrastructure for implementing such research can be provided by expanding the existing network of whole-forest access sites and canopy-scale experiments as proposed by the Global Canopy Programme (*70*) and by sharing data in the manner begun by the International Canopy Network (*71*). The results of this approach should transform our knowledge of forest canopies before many are lost and reduce uncertainties in current predictive models of global change.

References and Notes

1. P. M. Hammond, N. E. Stork, M. J. D. Brendell, in *Canopy Arthropods*, N. E. Stork, J. Adis, R. Didham, Eds. (Chapman & Hall, London, 1997), pp. 184–223.
2. D. J. Rodgers, R. L. Kitching, *Ecography* **21**, 392 (1998).
3. D. E. Walter, O. Seeman, D. Rodgers, R. L. Kitching, *Aust. J. Ecol*. **23**, 501 (1998).
4. V. Novotny *et al*., *Nature* **416**, 841 (2002).
5. I. R. Calder, *Ecology* **153**, 203 (2001).
6. N. E. Stork, *Biol. J. Linn. Soc*. **35**, 321 (1988).
7. R. M. May, in *Nature and Human Society: The Quest for a Sustainable World*, P. H. Raven, T. Williams, Eds. (National Academy Press, Washington, DC, 2000), pp. 30–45.
8. T. L. Erwin, *Coleopt. Bull*. **36**, 74 (1982).
9. F. Ødegaard, *J. Biogeogr*. **27**, 283 (2000).
10. L. L. Sørensen, in *Arthropods of Tropical Forests: Spatio-Temporal Dynamics and Resource Use in the Canopy*, Y. Basset, V. Novotny, S. E. Miller, R. L. Kitching, Eds. (Cambridge Univ. Press, Cambridge, 2003), pp. 92–101.
11. Y. Basset *et al*., in *Arthropods of Tropical Forests: Spatio-Temporal Dynamics and Resource Use in the Canopy*, Y. Basset, V. Novotny, S. E. Miller, R. L. Kitching, Eds. (Cambridge Univ. Press, Cambridge, 2003), pp. 17–27.
12. P. J. Franks, G. D. Farquhar, *Plant Cell Environ*. **22**, 1337 (1999).
13. M. T. Tyree, F. W. Ewers, *New Phytol*. **119**, 345 (1991).
14. F. C. Meinzer, *Plant Cell Environ*. **25**, 265 (2002).
15. G. Goldstein, J. L. Andrade, F. C. Meinzer, *Plant Cell Environ*. **21**, 397 (1998)
16. F. C. Meinzer, G. Goldstein, J. L. Andrade, *Tree Physiol*. **21**, 19 (2001).
17. B. J. Enquist, G. B. West, E. L. Charnov, J. H. Brown, *Nature* **401**, 907 (1999).
18. G. Schmidt, S. Stuntz, G. Zotz, *Plant Ecol*. **153**, 65 (2001).
19. A. Oltchev, J. Constantin, G. Gravenhorst, A. Ibrom, *J. Hydrol. Hydromech*. **45**, 5 (1997).
20. C. V. M. Barton, P. R. J. North, *Remote Sens. Environ*. **78**, 264 (2001).
21. G. R. Walther *et al*., *Nature* **416**, 389 (2002).
22. A. H. Fitter, R. S. R. Fitter, *Science* **296** 1689, (2002).
23. S. J. Wright, in *Tropical Forest Plant Ecophysiology*, S. S. Mulkey, R. L. Chazdon, A. P. Smith, Eds. (Chapman & Hall, New York, 1996), pp. 440–460.
24. E. A. Graham, S. S. Mulkey, K. Kitajima, N. G. Phillips, S. J. Wright, *Proc. Natl. Acad. Sci. U.S.A*. **100**, 572 (2003).
25. E. Newell, S. S. Mulkey, S. J. Wright, *Oecologia* **131**, 333 (2002).
26. R. Costanza *et al*., *Nature* **387**, 253 (1997).
27. K. Faegri, L. van der Pijl, *The Principles of Pollination Ecology* (Pergamon, Oxford, ed. 3, 1979).
28. G. Michaloud, S. Carriére, M. Kobbi, *J. Biogeogr*. **23**, 513 (1996).
29. R. Peakall, A. J. Beattie, *Evolution* **50**, 2207 (1996).
30. S. Sakai, K. Momose, M. Yumoto, M. Kato, T. Inoue, *Am. J. Bot*. **86**, 62 (1999).
31. J. Ghazoul, M. McLeish, *Plant Ecol*. **153**, 335 (2001).
32. H. Barrios, in *Arthropods of Tropical Forests*, Y. Basset, V. Novotny, S. E. Miller, R. L. Kitching, Eds. (Cambridge Univ. Press, Cambridge, 2002), pp. 282–290.
33. Y. Basset, *Oecologia* **88**, 211 (1991).
34. D. W. Davidson, S. C. Cook, R. R. Snelling, T. H. Chua, *Science* **300**, 969 (2003).
35. N. Nadkarni, *Science* **213**, 1024 (1981).
36. S. Grove, *Annu. Rev. Ecol. Syst*. **33**, 1 (2002).
37. P. M. Hammond, R. L. Kitching, N. E. Stork, *Ecotropica* **2**, 99 (1996).
38. N. N. Winchester, V. Behan-Pelletier, R. A. Ring, *Pedobiologia* **43**, 391 (1999).
39. M. Castelletta, N. S. Sohi, R. Subaraj, *Conserv. Biol*. **14**, 1870 (2000).
40. J. R. Malcolm, J. C. Ray, *Conserv. Biol*. **14**, 1623 (2000).
41. A. J. Davis, S. E. Sutton, *Divers. Distrib*. **4**, 167 (1998).
42. T. D. Schowalter, J. W. Webb, D. A. Crossley, *Ecology* **62**, 1010 (1981).
43. O. T. Lewis, *Conserv. Biol*. **15**, 389 (2001).
44. J. M. Thiollay, *Conserv. Biol*. **9**, 335 (1992).
45. M. Goosem, in *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*, W. F. Laurance, R. O. Bierregaard Jr., Eds. (Univ. of Chicago Press, Chicago, IL, 1997), pp. 241–255.
46. A. Foggo, C. M. P. Ozanne, C. Hambler, M. R. Speight, *Plant Ecol*. **153**, 347 (2001).
47. C. M. P. Ozanne, A. Foggo, C. Hambler, M. R. Speight, in *Canopy Arthropods*, N. E. Stork, J. Adis, R. Didham, Eds. (Chapman & Hall, London, 1997), pp. 534–550.
48. J. Q. Chambers, N. Higuchi, E. S. Tribuzy, S. E. Trumbore, *Nature* **410**, 429 (2000).
49. J. E. Richey, J. M. Melack, A. K. Aufdenkampe, V. M. Ballester, L. L. Hess, *Nature* **416**, 617 (2002).
50. Y. Mahli, J. Grace, *Trends Ecol. Evol*. **15**, 332 (2000).
51. C. Körner, *Science* **300**, 1242 (2003).
52. O. L. Phillips *et al*., *Nature* **418**, 70 (2002).
53. J. Granados, C. Körner, *Global Change Biol*. **8,** 1109 (2002).
54. S. A. Schnitzer, F. Bongers, *Trends Ecol. Evol*. **17**, 223 (2002).
55. S. Hättenschwiler, F. Miglietta, A. Raschi, C. Körner, *Global Change Biol*. **3**, 463 (1997).
56. C. Körner, *Plant Cell Environ*. **18**, 1101 (1995).
57. C. Körner, in *Ecology: Achievement and Challenge*, M. C. Press, N. J. Huntly, S. Levin, Eds. (Blackwell Science, Oxford, 2001), pp. 227–247.
58. S. Pepin, C. Körner, *Oecologia* **133**, 1 (2002).
59. J. B. Whittaker, *Eur. J. Entomol*. **96**, 149 (1999).
60. G. Stanhill, S. Cohen, *Agric. For. Meteorol*. **10**, 255 (2001).
61. J. Chen, B. I. Carlson, A. D. Genio, *Science* **295**, 838 (2002).
62. L. Gu *et al*., *Science* **299**, 2035 (2003).
63. E. Salati, P. B. Vose, *Science* **225**, 129 (1984).
64. P. M. Anthoni, B. E. Law, M. H. Unsworth, *Agric. For. Meteorol*. **95**, 151 (1999).
65. M. A. F. Silva Dias *et al*., *J. Geophys. Res*. **107**, 461(2002).
66. M. C. Facchini, M. Mircea, S. Fuzzi, R. J. Charlson, *Nature* **401**, 257 (1999).
67. M. Lerdau, A. Guenther, R. Monson, *BioSicence* **47**, 373 (1997).
68. A. Guenther *et al*., *J. Geophys. Res*. **100**, 8873 (1995).
69. M. Keller, M. Lerdau, *Global Biogeochem. Cycles* **13**, 19 (1999).
70. A. Mitchell, K. Secoy, T. Jackson, Eds., *The Global Canopy Handbook* (Global Canopy Programme, Oxford, UK, 2002).
71. Y. Basset, V. Horlyck, S. J. Wright, Eds., *Studying Forest Canopies from Above: The International Canopy Crane Network* (United Nations Environment Programme, Panamerica Editorial, Bogota, Colombia, 2003).

72. We thank S. Pimm, R. Southwood, W. Wint, and three anonymous referees for comments on the manuscript.