Access to the Upper Forest Canopy with a Large Tower Crane

Sampling the treetops in three dimensions

Geoffrey G. Parker, Alan P. Smith, and Kevin P. Hogan

he uppermost forest canopy is a frontier of scientific research (Erwin 1983). It is the primary interface between the atmosphere and the forest and is a reservoir of biological diversity. But understanding of this important portion of the forest is far from adequate because of the difficulties in gaining access to the tops of trees. Most techniques currently available to study canopies provide limited flexibility and maneuverability, little safety, and almost no access to the important outermost canopy zone.

The inability to study the functioning of the upper forest canopy in situ has stalled progress on a variety of critical research pursuits. For example, the examination of forest/atmosphere interactions (crucial to understanding global climate) and rigorous analyses of canopy biodiversity (an essential basis for conservation decisions) are both severely limited by the lack of controlled canopy access.

A tower crane with a long horizontal jib brings the previously unreachable portions of forests within the range of scientific scrutiny. It allows repeatable observations and experimental manipulations on individual

Geoffrey G. Parker is forest ecologist at the Smithsonian Environmental Research Center, Edgewater, MD 21037-0028. Alan P. Smith is assistant director for terrestrial research and Kevin P. Hogan is a postdoctoral associate at the Smithsonian Tropical Research Institute, Unit 0948, APO 34002-0948, Republic of Panama. © 1992 American Institute of Biological Sciences.

The upper forest canopy is viewed from an atmospheric perspective

canopy elements, measurements of whole-canopy organization and structure, and freedom to take spatially detailed measurements of environmental quality in forests.

With the tower crane, investigators approach the canopy from above, from an atmospheric perspective, rather than from the forest floor. A cage (or gondola) containing the investigator and equipment is lowered into the canopy from the jib. The jib angle as

well as the range and the height of the gondola may be precisely controlled. Thus, the gondola is completely maneuverable in three dimensions, limited only by the presence of trunks and branches.

There has been only one application of a tower crane to explore the canopy. It employed a small prototype crane installed in a forested park in Panama. In this article, we discuss the general background, rationale, and potential of this novel access system and describe some initial results of the ongoing study.

The upper forest canopy

The first layer of leaves and twigs at the top of the forest is the outermost

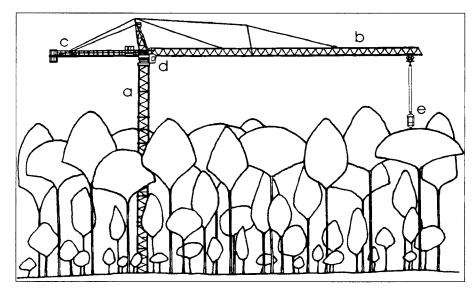


Figure 1. Sketch of the canopy crane operating in a forest showing the tower (a), jib (b), counterjib and counterweight (c), the operator's cab (d), and the gondola (e) attached to the hook. The radius and height of the jib are 82 and 52 m, respectively.

664 BioScience Vol. 42 No. 9

canopy. The surface of this zone is at variable heights from the ground, as it includes canopy gaps of various ages (depths) and extents, individual crowns, and spaces between crowns. This poorly explored zone may be thought of as a subsystem of the forest (Carroll 1980).

Environmental conditions in this zone differ strikingly from those at lower levels within the forest (Jones 1983, Oke 1987). The uppermost forest levels are more arid, windy, and bright, with greater daily and seasonal variation in temperature and humidity. Plant tissues and canopy fauna are exposed to more pollutants, much more ionizing radiation, and more desiccation. At this level, atmospheric conditions are relatively unaltered by the forest (Parker et al. 1989), whereas at all other layers of the forest these parameters are substantially moderated by the outermost layer (e.g., Lee 1983). The character and function of this outer layer is therefore of foremost importance in understanding the reciprocal effects of canopy and atmosphere.

The forest canopy is home to much biological diversity. The insect fauna of tropical tree crowns is exceedingly rich and host-tree specific (Erwin 1982). Furthermore, the diversity of arthropods appears to be particularly high in the upper canopy. However, little is known about the canopy communities of any forest (e.g., Schowalter et al. 1981). Information on these biotic interactions is essential for wise conservation decisions.

The tradition of canopy access

Ascending into the forest canopy is an old and lofty human enterprise; exploration of the treetops for scientific reasons is relatively recent (Bates 1960, Perry 1986). Mitchell (1982) described its history, particularly the methods used in tropical forests. The various techniques range from simple to complex, with a wide variation in safety and flexibility.

Although tree trunks are often climbed directly (e.g., Denison et al. 1972), climbing ropes attached to limbs high in the tree is the more common access method (e.g., Nadkarni 1988, Perry 1977). This approach uses the vertical rope technique developed for mountain climb-

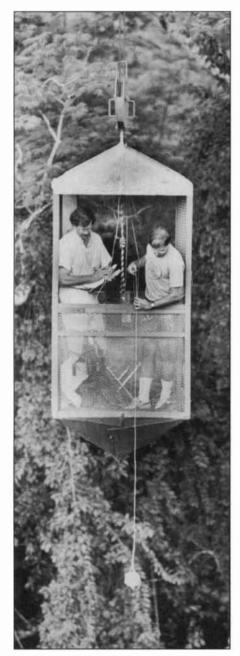


Figure 2. View of the gondola during microclimate measurements 25 m above the ground in a dry forest near Panama City, Panama. The gondola is a welded steel cage measuring approximately 1 x 1 x 2 m.

ing, caving, and rescue work (Padgett and Smith 1987). It is easily learned, and the danger and exertion can be reduced with practice. However, the availability of secure anchor points limits movement to the vicinity of supporting stems or limbs. Rope systems can be designed to provide some lateral freedom. For example, the rope web of Perry and Williams (1981) permitted a climber access to a large

volume of canopy space, but it was elaborate to install and arduous to use. Climbing is generally not suitable for the upper quarter of the height of the forest, where limbs are too small to safely support a person's weight.

Only a small portion of the outer canopy may be reached with fixed towers, masts, or scaffolding. Aerial walkways (Mull and Liat 1970), cable tramways (Perry 1986), and horizontally supported spars (Denison et al. 1972, Mitchell 1982) provide additional lateral movement, although usually at levels below the outer canopy. Ultimately, fixed structures are limited in spatial flexibility. Also, their installation may cause some modification of forest structure: for example, the position of a tower will always remain a gap in the canopy.

A large, semirigid platform constructed of inflated tubes in a hexagonal array supporting a strong mesh netting was placed on the top of overstory trees in French Guiana (Halle 1990). With this canopy raft, researchers moved and worked directly on 600 square meters of upper canopy surface, where animal and plant collections were readily made. The raft was deployed with a large hot-air dirigible, and it was easily moved from one location to another.

The raft must be installed in closed canopies of uniform height. Because the presence of the raft alters the exchange between atmosphere and canopy, it is not suitable for measurements of environment conditions or of plant physiological responses. Furthermore, the raft tends to depress the crowns of the support trees, settling slowly downward. Finally, several pilots and a large ground crew are necessary to support the raft operation while in position.

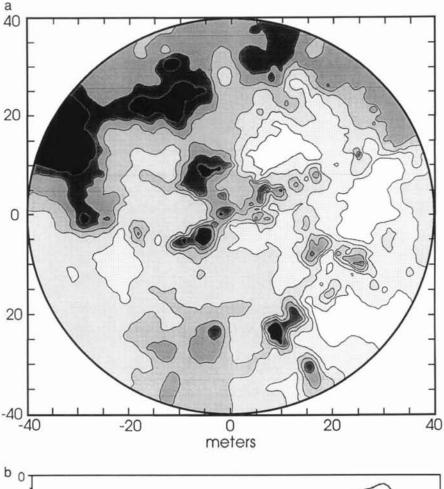
Cranes and rafts have unique and complementary potentials. Whereas the crane is employed for long-term measurements of many parameters at a given location, the raft is useful for some short-term sampling at numerous sites.

Canopy access lags behind ocean access

Methods for studying canopies can be compared with those used in another

¹O. Pascal, 1992, personal communication.

October 1992 665



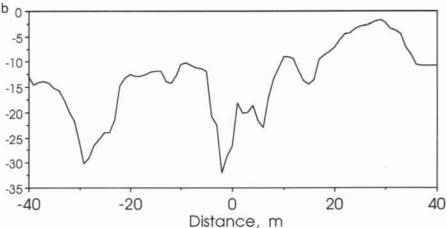


Figure 3. (a) Contour map of the upper canopy surface of a tropical dry forest in the Parque Metropolitana made in September 1990. North is to the right, and the crane tower sits at the center of the diagram. The contour interval is 5 m, referenced to the highest leaf. The lowest point on the ground is 35.9 m below. Deep regions (gaps) are shaded dark, whereas high levels (tall overstory crowns) are lightly shaded. (b) A north-south section through the center of the surface in Figure 3a. Note the exaggeration of the vertical axis.

inaccessible environment, the deep ocean. Researchers in both situations encounter depth/height and time limits. Equipment was devised in each case to increase range and maneuverability, for example, scuba equipment

and climbing spikes and grippers. To extend the duration of the stay, artificial habitats were constructed, for example, the underwater Sealab and platforms and walkways in the canopy environment.

In the water, means for remotely controlled sensing and sampling were developed, including drones and robot submersibles. Novel ecosystems (e.g., the sea floor vents) and archaeological sites (e.g., the wreckage of the Titanic) were first discovered using such tools. However, analogous devices for research in forest canopies, such as cameras and sensors mounted on balloons, are only now in development. Manned submersibles were long ago employed to allow people access to the deep-sea environment. Submersibles were first lowered into the depths from a surface vessel; independent and maneuverable submarines were devised subsequently. Comparable instruments for human access of the forest canopy (i. e., manned ascendibles) have not, until just recently, been available.

A top-down approach to canopy access

Designed for use under the congested conditions of narrow European streets, tower cranes are intended to be "quiet, relatively unobtrusive, and safe" (Shapiro and Shapiro 1988). In hammerhead-style cranes, the horizontal jib and counterweights, motors, and the operator's cab are supported atop the tower, which minimizes the crane's footprint on the ground. The components of such a canopy access system are illustrated in Figure 1. Powered by separate electrical motors for the jib azimuth (slewing motion), the range (trolley), and the height (hook) of the load, such cranes can rapidly hoist and transfer as much as 20 metric tons at a time. A crane operator controls the motion from a vantage above the load. The tower position may be fixed on a concrete foundation or on a moveable base mounted on a widegauge railroad track. Variously shaped areas may therefore be covered.

When the crane is employed for canopy access, the scientist and experimental apparatus are lowered into the forest within a frame cage (the gondola) attached to the crane hook. For measurements of environmental quality, a smaller instrument package (pod) may be deployed. The position of the gondola or pod is controlled by the crane operator; remote radio control is also possible. A positioning system can be provided to allow accu-

Figure 4. Diurnal changes in light intensity above (a) forest, in µmol m⁻² s⁻¹, leaf water potential in MPa (b), leaf fluorescence ratio (c), and initial fluorescence F₁ in relative units (d) in several species of canopy trees, from measurements taken on 13 April 1991. In all panels, the squares are Anacardium excelsum, circles are Didymopanax morototoni, and triangles are Luehea seemannii. Plotted points and bars are means and standard errors of 4-6 samples. Light was averaged over 5-minute intervals with a LI 190 quantum sensor and recorded with a LI-1000 data logger (LiCor, Lincoln, NE). Water potential was measured in the forest canopy by using a pressure bomb immediately after cutting twigs from the branch. Additional leaves were harvested and lowered to a mobile laboratory on the forest floor and maintained in the dark. Fluorescence was measured within 10-40 minutes with a chlorophyll fluorometer (PAM 101; H. Walz, Effletrich, Germany). When a dark-adapted leaf is stimulated by a low level of light (insufficient to induce photosynthesis), it fluoresces at a level designated F₂. In the presence of a high-intensity lamp flash (sufficient to saturate the light-harvesting system), it fluorescess at a maximal rate, F_m . The difference between these levels $(F_m - F_o)$ is called variable fluorescence, F_v . The fluorescence ratio (F_v/F_m) is a useful indicator of photoinhibitory damage (Demmig and Bjorkman 1987, Schreiber et al. 1986). The increases in F₀ in Didymopanax and Luehea suggest possible photodamage, but the decrease in Anacardium suggests that pigment systems have been produced that protect against photodamage.

rate determination of the gondola's three-dimensional coordinates, so that a position may be revisited and individual canopy elements be resampled at will.

The gondola must be small for flexible access but large enough to accommodate the researchers and their equipment. An open gondola design allows the investigator to grasp a variety of upper canopy elements. The gondola body is shaped for easy penetration of and extraction from the canopy. A roof provides some protection from rains. Lights in the gondola would allow nocturnal operations.

Tower cranes have a good safety record in the construction industry (Allen 1985, Shapiro et al. 1980). Strict standards are in force for crane operation (ANSI 1984) and their use as personnel hoists (CIA 1989). Because the load requirements of canopy access are far less than those of construction applications, a canopy access system has a far greater margin of safety. A harness and lifeline secures the investigator within the gondola. A safety line and descending system provide a means for leaving a stranded gondola.

The canopy crane would yield access to an unprecedented region of canopy space. The longest reach available is approximately 80 meters (more than 2.0 hectares of coverage). In a 50-meter-tall forest, the accessible volume of a fixed crane of this size would exceed a million cubic meters. Cranes on tracked bases could potentially access much more area.

Installation of the crane in the

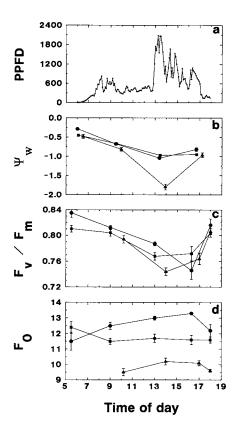
canopy can be achieved with little damage to the forest. Where roads are available, a second, mobile crane is used to raise the tower crane. Otherwise, installation by helicopter is an option. The footprint of the tower base can be relatively small: the foundation required for the largest available crane is less than 10 meters wide.

Novel research opportunities

The canopy access system opens a variety of new research opportunities. Initial efforts are intended to describe the details of the canopy components, the canopy environment, and varied interactions. Additional possibilities are expected to become evident once the system is in use.

Direct observation of canopy elements. Direct measurements and experimental manipulations within actual canopies are critical. Observations on plants or tissues in noncanopy environments or on young specimens of overstory species are not suitable proxies for direct measurements within the canopy (Boardman 1977, Cregg et al. 1989, Kramer and Kozlowski 1979, Leverenz and Jarvis 1979). The natural canopy environment is not comparable to that of large gaps or forest edges (Pearcy 1987), and it is not easily reproduced in the laboratory. The gondola of the canopy access system can help install and service experimental chambers and instruments to make the necessarv direct measurements.

Studies of individual canopy elements (e.g., branches, twigs, leaves,



epiphytes, lianas, and vines) can be conducted within the upper canopy environment with the canopy crane. For example, leaf physiological responses to experimental manipulations of atmospheric environment (e.g., temperature, ultraviolet light, carbon dioxide and ozone, and rainwater quality) can be studied where such conditions might occur. Measurements of gas exchange (e.g., nitrogen fixation, photosynthesis, and transpiration) may be conducted on leaves or whole branch systems with the canopy crane.

Life history of canopy biota. The biology of canopy organisms, except for wide-ranging vertebrates and invertebrates, can be studied directly with the canopy access system. Repeated surveys of numerous individual leaves would yield rates of appearance, herbivory, and mortality. The identity, visitation rates, and success of overstory pollinators could be studied at close hand, as could the breeding systems of trees, the production of fruits, and frugivory. Flying insects could be sampled over a wide area with traps deployed from the gondola or jib. Foliage and stem arthropods could be collected from canopy elements di-

October 1992 667

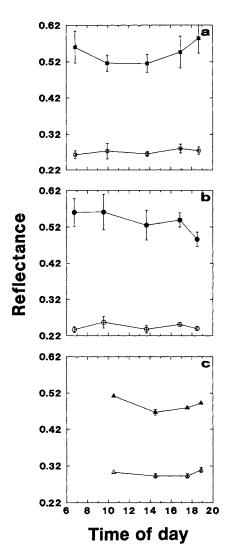


Figure 5. Leaf reflectance (fraction of incident light that is reflected) at both 531 nm (closed symbols) and 505 nm (open symbols) for leaves of Anacardium (a), Didymopanax (b), and Luehea (c). Reflectance was measured with a spectroradiometer with integrating sphere (LiCor, Lincoln, NE). The symbols for the species are as in Figure 4. Patterns of leaf reflectance for Anacardium and Luehea are consistent with possible production of protective pigments (c.f. Bilger et al. 1989, Gamon et al. 1990).

rectly or sampled by using insecticides. Other canopy animals, such as arboreal birds, herpetofauna, and mammals, could be studied above the forest from the vantage afforded by the crane.

Environmental measurements in three dimensions. The capacity to mount short-term sampling at any point in three-dimensional space allows accurate assessment of the spatial-tempo-

ral distribution of important environmental variables within a volume of forest. The lateral and vertical change of atmospheric parameters can be finely resolved at any desired location. The light environment of the upper part of canopy gaps may be assessed directly.

Long-term measurements of environmental characteristics or material fluxes (e.g., Baldocchi et al. 1988), in other studies usually made with instruments fixed on towers or masts, may be made wherever desired. Repeated sensor observations at predetermined positions within the canopy could be scheduled to run automatically: one could program the access system for unattended sampling.

A cooperative research facility

The access system provided by a tower crane could benefit scientists interested in all aspects of canopy science. Many investigators could cooperate in the use of the facility and the study of the focal canopy. Sharing of major scientific instruments is common, such as telescopes in astronomy, particle accelerators in high-energy physics, and deep-water vessels in oceanography.

The initial cost of the tower crane can range from \$250,000 to \$750,000, depending on the configuration. After installation, the operating expenses are relatively low: electrical power, the salary of a crane operator, and some routine maintenance. The initial cost of the canopy raft and dirigible is roughly comparable (approximately \$550,000). However, the expense of operating the raft is higher because it requires not only fuel for the dirigible but also the salaries of a large support crew (as many as ten people during intensive field studies).

Prototype trial

In September 1990, the Smithsonian Tropical Research Institute installed a small rented crane in a forested suburban park (the Parque Metropolitana) on the outskirts of Panama City. The stand is a diverse, dry Pacific forest, approximately 75 years old, that sits on the shoulder of a small hill. This venture is the first to study the upper forest canopy using a tower crane.

The prototype crane has an effective reach of almost 40 m, covering

approximately 0.5 ha of forest. This reach provides access to approximately 150,000 cubic meters of canopy space in the 30-meter-tall stand. To transport personnel and equipment, a small enclosed gondola was built and attached to the crane hook (Figure 2). The gondola has windows on all sides that open easily, with mesh screening to protect against stinging insects. The gondola position is controlled by a crane operator, who follows directions given from the gondola by hand, voice, or walkie-talkie.

The gondola provided a steady working platform when aloft; anchoring to adjacent branches was rarely necessary. Movement between sampling points was generally quite rapid and smooth. Although abrupt stops could cause the gondola to rock, the overall sensation was secure. Moreover, the presence of the crane appeared not to disturb animals: iguanas sunning in the upper canopy were not troubled when the gondola approached within 2 m (Anderson 1990).

Numerous observations and experiments have been initiated during this ongoing prototype study, including studies of leaf physiology (photosynthesis, transpiration, water relations and water use efficiency, and photoinhibition), the physical organization of the upper canopy, competitive interactions between lianas and their hosts, and the structure of communities of stingless bees and ants. Here we describe measurements on the structure of the upper canopy and observations on the physiology of overstory leaves.

Structure of the dry forest upper canopy

Knowledge of forest structure has commonly been obtained from observations taken at the ground. However, many of the details of the treetops are hidden from view. The bathymetry of the outer canopy was assessed by measuring the depth from a fixed height to the upper canopy surface. We lowered a weighted measuring tape from the gondola at 672 locations more or less evenly distributed throughout the area covered by the jib (mean interpoint distance 3.1 m). The species of tree leaf and the coverage by lianas or vines was noted at each contact point.

Of the canopy trees, the leaves of Enterolobium cyclocarpum (Corotú) cover 29.8% of the projected surface of the upper canopy in this stand; Anacardium excelsum (Espavé) covers nearly as much (28.5%). At least 25 other species constitute the outer canopy, including species of Luehea (Guácimo; 7.44%), Cecropia obtusifolia (Guarumo; 2.7%), and Didymopanax morototoni (Mangabe; 1.6%). Additionally, leaves of lianas or vines covered 35.6% of the upper canopy surface and were occasionally so dense it was difficult to distinguish the species of the host tree.

The uneven surface of this canopy had a mean depth of 13.9 m (standard deviation 7.95 m) relative to a plane defined by the highest leaf. The outer canopy has a very convoluted shape: we estimate the total area of this rumpled upper surface to be more than 2.5 times the projected area. A contour map of the upper surface (Figure 3a) details that structure. Three large crowns are apparent at the right of the figure; another is to the left. Gaps of various sizes are evident, including several that do not penetrate to ground level and may not be visible to a ground-based observer.

Figure 3b gives a central section through the canopy, illustrating some of the hills and valleys in this complex surface. The forest floor was rarely glimpsed (only 3.7% of the points) from the vantage of the outer canopy. This initial observation is being continued with studies of the dynamics of canopy structure at several spatial scales and the interactions between leaves of lianas and their host trees.

Physiological observations on canopy leaves

Most research on forest plant ecophysiology has been concentrated in the understory and has emphasized responses of plants to low and fluctuating light. However, uppermost-canopy leaves are subject to prolonged exposure to full sun, which may damage photosynthetic systems. This damage, referred to as photoinhibition, causes reduction in efficiency of photosynthetic utilization of light (Powles 1984). Water stress and high temperature can increase this sort of damage (Powles 1984).

Photoinhibition can be analyzed

through measurements of leaf fluorescence (Figure 4). Some plants may avoid damage from intense solar radiation by producing carotenoid pigments that dissipate excess solar energy as heat, protecting photosynthetic systems (Anderson and Osmond 1987, Demmig and Bjorkman 1987). Changes in reflection of light from leaves can indicate altered levels of these pigments. Changes in leaf fluorescence can also suggest production of protective pigments (Kitajima and Butler 1975).

Photoinhibition in leaves of Anacardium excelsum, Didymopanax morototoni, and Luehea seemannii was measured directly in the upper canopy (20–25 m above the ground). The experimental canopy crane allowed measurements of incident light in the environment of the experimental leaves, the direct assessment of foliar water stress, and the sampling of selected leaves for additional analyses.

As light increased in the canopy over the day (Figure 4a), so did the water stress (Figure 4b) and the extent of photoinhibition (Figure 4c,d) for all three species. There are differences between species of canopy trees in water stress and in the potential mechanisms of protection from photoinhibition. Anacardium and perhaps Luehea leaves appear to respond to stress with production of accessory pigments (Figure 5). Didymopanax and Luehea appear to sustain some damage to photosynthetic systems; Luehea was the most water stressed of the three. Regardless of the degree of photoinhibition and extent of photoprotection through pigment production, all three species showed recovery from stress by early evening (Figure 5b).

These preliminary results provided the basis for much more detailed studies now in progress on the response of canopy trees to high light stress. They suggest that tropical forest trees sharing the same environmental may use a variety of responses to stress. Such research is likely to reveal diverse physiological mechanisms paralleling the great species diversity of tropical forests.

Conclusions

Lack of a flexible access system has impeded fundamental research on the upper forest canopy. A large tower crane installed in a forest can provide the centerpiece of such an access system, allowing repeatable sampling in three dimensions, unprecedented control for observations, and experimentation within the canopy space of the forest. The technology necessary to implement this technique is readily available and is being used successfully in a trial configuration in a tropical forest. Observations made from the canopy crane suggest a wide diversity of functional behaviors of overstory leaves and a complex upper canopy structure. The access system reveals the canopy from an atmospheric perspective, in contrast with the common standpoint on the forest floor.

Acknowledgments

We thank José Herrera, crane operator, for his skilled collaboration on this project. The crane was funded by the Smithsonian Tropical Research Institute and by the Government of Finland, through the United Nations Environmental Program. Additional support for the work reported here came from the Smithsonian Environmental Research Center. We thank José Luis Machado, Jorge Illueca, and Mikko Pyhala (UNEP) for their assistance. Alan Smith thanks Michael C. Smith for first suggesting the use of cranes for forest research in 1986.

References cited

Allen, H. 1985. There'll be some changes in the city when the cranes come soaring in. *Smithsonian* 16: 44-53.

American National Standards Institute (ANSI). 1984. *Hammerhead Tower Cranes*. ANSI/ ASME B30.3-1984. American Society of Mechanical Engineers, New York.

Anderson, A. 1990. The view from the top. *Nature* 347: 5.

Anderson, J. M., and C. B. Osmond. 1987. Shade-sun response: compromises and photoinhibition. In D. J. Kyle and C. J. Arntzen, eds. *Photoinhibition*. Elsevier, New York

Baldocchi, D. D., B. B. Hicks, and T. P. Meyers. 1988. Measuring biosphere-atmosphere exchange of biologically related gases with micrometeorological methods. *Ecology* 69: 1331–1340.

Bates, M. 1960. The Forest and the Sea. Random House, New York.

Bilger, W., O. Bjorkman, and S. Thayer. 1989. Light-induced spectral absorbance changes in relation to photosynthesis and the epoxidation state of xanthophyll cycle components in cotton leaves. *Plant Physiol.* 91:

October 1992 669



At last we can see the earth as it really is. This small, pale ball floating in the vastness of space. Clearly with limits. Vulnerable, fragile.

For almost 100 years the Sierra Club has been fighting to protect the earth's fragile systems. We have successfully lobbied for laws to limit air and water pollution and to regulate poisonous toxic chemicals. We have won protection for swamps and meadows, rivers and mountains, deserts and prairies...those natural places which permit the earth to heal and renew itself. We have consistently been an effective voice for a world healthful for all its inhabitants.

The unique power of the Sierra Club springs from our active grass roots membership...volunteers who give freely of their time and expertise. If you want to participate in this work, or share in the satisfaction of it through a supporting membership, contact the Sierra Club, 730 Polk Street, San Francisco, CA 94109, (415) 776-2211.



542-551.

Boardman, N. K. 1977. Comparative physiology of sun and shade plants. Annu. Rev. Plant Physiol. 28: 355-377.

Carroll, G. L. 1980. Forest canopies: complex and independent subsystems. Pages 87–107 in R. H. Waring, ed. Forests: Fresh Perspectives from Ecosystem Analysis. Oregon State University Press, Corvallis.

Crane Institute of America (CIA). 1989. OSHA limits use of construction cranes and derricks as personnel hoists. *Indicator* 2: 1-2.

Cregg, B. M., J. E. Halpin, P. M. Dougherty, and R. O. Teskey. 1989. Comparative physiology and morphology of seedling and mature trees. Pages 111-118 in R. D. Noble, J. L. Martin, and K. F. Jensen, eds. Air Pollution Effects on Vegetation, Including Forest Ecosystems. Proceedings of the second US-USSR symposium.

Demmig, B., and O. Bjorkman. 1987. Comparison of the effects of excessive light on chlorophyll fluorescence (77 K) and photon yield of O, evolution in leaves of higher

plants. Planta 171: 489-504.

Denison, W. C., D. M. Tracey, F. M. Rhoades, and M. Sherwood. 1972. Direct, non-destructive measurements of biomass and structure in living, old-growth Douglas-fir. Pages 147-158 in J. F. Franklin, L. J. Dempster, and R. H. Waring, eds. Research on Coniferous Forest Ecosystems. Pacific Northwest and Range Experiment Station, Portland, OR.

Erwin, T. L. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. Coleopt. Bull. 35: 53-68.

_____. 1983. Tropical forest canopies: the last biotic frontier. Bull. Ent. Soc. Am. 29: 14-19.

Gamon, J. A., C. B. Field, W. Bilger, O. Bjorkman, A. L. Fredeen, and J. Penuelas. 1990. Remote sensing of the xanthophyll cycle and chlorophyll fluorescence in sunflower leaves and canopies. *Oecologia* 85: 1–7.

Halle, F. 1990. A raft atop the rain forest. *Natl. Geogr.* 178: 128-138.

Jones, H. G. 1983. Plants and Microclimate. Cambridge University Press, New York.

Kitajima, M., and W. L. Butler. 1975. Quenching of chlorophyll fluorescence and primary photochemistry in chloroplasts by dibromothymoquinone. Biochim. Biophys. Acta 376: 105-115.

Kramer, P. J., and T. T. Kozlowski. 1979. Physiology of Woody Plants. Academic Press, San Diego, CA.

Lee, R. 1983. Forest Microclimatology. Co-

lumbia University Press, New York.

Leverentz, J. W., and P. G. Jarvis. 1979. Photosynthesis in Sitka spruce. VIII. The effect of light flux density and direction on the rate of net photosynthesis and the stomatal conductance of needles. J. Appl. Ecol. 16: 919-923.

Mitchell, A. W. 1982. Reaching the Rainforest Roof: A Handbook of Techniques of Access and Study in the Canopy. Leeds Philosophical and Literary Society, Leeds, UK.

Mull, I., and L. B. Liat. 1970. Vertical zonation in a tropical rainforest in Malaysia. Science

196: 788-789.

Nadkarni, N. M. 1988. Tropical rainforest ecology from a canopy perspective. Pages 189-208 in F. Alameda and C. M. Pringle, eds. Tropical Rainforest: Diversity and Conservation. California Academy of Sciences, San Francisco.

Oke, T. R. 1987. Boundary Layer Climates. Methuen, London.

Padgett, A., and B. Smith. 1987. On Rope. National Speleological Society, Hunstville, AL.

Parker, G. G., J. P. O'Neill, and D. Higman. 1989. Vertical profile and canopy organization of a mixed deciduous forest. Vegetatio 89: 1-12.

Pearcy, R. W. 1987. Photosynthetic gas exchange responses of Australian tropical forest trees in canopy, gap and understory micro-environments. Funct. Ecol. 1: 169-178.

Perry, D. R. 1977. A method of access into the crown of emergent and canopy trees. *Biotropica* 10: 155-157.

_____. 1986. Life Above the Jungle Floor. Simon and Schuster, New York.

Perry, D. R., and J. D. Williams. 1981. The rainforest canopy: a method providing total access. *Biotropica* 13: 283-285.

Powles, S. B. 1984. Photoinhibition of photosynthesis induced by visible light. Annu. Rev. Plant Physiol. 35: 15-44.

Schowalter, T. D., J. W. Webb, and D. A. Crossley Jr. 1981. Community structure and nutrient content of canopy arthropods in clearcut and uncut forest ecosystems. Ecology 62: 1010-1019.

Schreiber, U., U. Schliwa, and W. Bilger. 1986. Continuous recording of photochemical and non-photochemical chlorophyll fluorescence quenching with a new type of modulation fluorometer. *Photosyn. Res.* 10: 51-62.

Shapiro, H. J., J. P. Shapiro, and L. K. Shapiro. 1980. Cranes and Derricks. McGraw-Hill, New York.

Shapiro, L. K., and H. J. Shapiro. 1988. Construction cranes. Sci. Am. 258: 72-79.