and fertilization, seed development and maturation, seed predation, dispersal and germination, and seedling growth, many of which are mediated by mutualistic and antagonistic interactions with animals acting as pollinators, dispersers, seed predators, and leaf herbivores. These processes unfold in the context of the disturbance regime, which creates differential opportunities for propagules and seedlings. Quite different reproductive strategies exist among forest trees within and among communities. The most obvious is the overwhelming dependence of tropical trees on animal interactors for pollination and seed dispersal, compared to temperate species, for which abiotic agents are comparatively more important. Such differences in pollination and seed dispersal vectors are reflected in the efficiency of gene transfer and patterns of gene flow, and information about seed production and gene flow is critical for the design of forest management plans and strategies for the conservation of plant genetic resources.

Currently, there is little information about the pollinators and seed dispersers of many forest trees, or indeed about the importance of flower and fruit resources to animal communities. Even basic knowledge about factors that regulate seed production, viability, dormancy, and germination for many tree species remains to be discovered, and only recently have we begun to understand the importance of natural disturbance in shaping plant communities through differential reproductive success. Our ability to rehabilitate, conserve, and manage existing forests will continue to be improved by continued research on tree reproductive ecology within the context of the natural disturbance regime.

See also: **Ecology**: Biological Impacts of Deforestation and Fragmentation; Natural Disturbance in Forest Environments; Plant-Animal Interactions in Forest Ecosystems. **Sustainable Forest Management**: Causes of Deforestation and Forest Fragmentation. **Tree Physiology**: Physiology of Sexual Reproduction in Trees.

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Forest Canopies

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Importance

The word canopy is derived from the Latin *conopeum*, describing a mosquito net over a bed. For canopy researchers in many tropical and temperate forests, this derivation is all too fitting. Forest canopies are home to perhaps 50% of all living organisms, many of which are uniquely specialized for life in the treetops and seldom, if ever, venture to the ground below. The canopy is the photosynthetic powerhouse of forest productivity which fuels this spectacular diversity of species. Over 90% of photosynthesis occurs in just the upper 20% of tree crowns. Here, over 60% of the total organic carbon in forests is fixed and stored, forming an important buffer in the global carbon cycle. Other ecophysiological processes within tree crowns mediate the flow of nutrients through soil, regulate nutrient cycling processes that affect site productivity and the biomass distributions of plants and animals, as well as moderate the rates of transpiration and CO_2 exchange to the atmosphere that are crucial components of regional climatic circulation. In a very real sense, forest canopies form the substrate, the buffer, and the catalyst for interactions between the soil and the atmosphere. In this article, we highlight many aspects of forest ecosystem dynamics that are controlled directly by canopy processes. More importantly, however, detailed understanding of the structural and functional complexities of forest canopies has advantages beyond the scale of ecosystem functioning of local forest stands. Forest canopy dynamics are now incorporated as vital variables when modeling forest responses to the three most pressing issues in global change biology: the maintenance of biodiversity, the sustainability of forest production, and the stability of global climate.

Definition

For much of the early development of canopy biology, the nature and limits of forest canopies have been poorly defined. In a functional sense, the forest canopy includes all aboveground plant structures and the interstitial spaces between them, which collectively form the interface between the soil and the atmosphere. Historically, there was a tendency to use more subjective definitions of the canopy that only included arbitrary portions of the upper foliage of the tallest trees. In practice, however, it has always proven difficult to objectively define vertical substrata within forests, from either a structural or functional point of view. There is now clear recognition that most forest processes vary continuously from the soil to the atmosphere and there is little utility in considering the canopy out of context from forest dynamics as a whole. After all, tree crown physiology, resource allocation, growth and reproductive fitness are all critically dependent on belowground conditions experienced by tree roots, as much as they are on aboveground processes.

Discovery and Exploration

More than 85 years ago the naturalist and explorer William Beebe wrote that

> another continent of life remains to be discovered, not upon the earth, but one to two hundred feet above it.

It would be another decade before the first intrepid biologists ventured into the tropical forest canopy in Guyana, South America, using rudimentary line-throwing catapults and local Indian tribesmen as climbers. Scientific exploration did not really begin in earnest until the 1960s with a proliferation of simple observation towers built in various parts of the world, including the Democratic Republic of Congo, Malaysia, Panama, and Uganda, site of the famous Haddow Tower. Overwhelming numbers of new species, mostly insects, have since been discovered and critical observations made on the behavior and life history of rare birds, reptiles, amphibians, and mammals in their natural habitats. However, these descriptive accounts of canopy life amounted to no more than a drop in the ocean compared to the vast expanses of unexplored forest canopies in the world. Rigorous, comparative studies of canopy communities were set back for years by the logistical difficulties of conducting treetop investigations.

The scope and extent of canopy studies expanded greatly through the late 1970s and early 1980s, with a number of research groups working largely independently of each other. Without a doubt, this period of canopy science was more tool-driven (developing new techniques) than question-driven (developing new scientific hypotheses). As a result, even after intensive forest canopy studies became commonplace in the late 1980s, the wider scientific community still viewed the emerging discipline with mild disdain – a poorer anecdotal or descriptive cousin of terrestrial biology. Today, major new developments in canopy access systems, and a changing mind-set among canopy researchers, have all but allayed these criticisms. Forest canopy studies, today, address all manner of hypotheses using rigorous, replicated experimental designs that are the equal of any scientific investigation. Liberated from the constraints of three-dimensional movement within canopies, scientists are finally appreciating that answers to many of their questions about forest ecology and the interactions between the atmosphere and the soil can only be found by incorporating within-canopy processes. Once called the last great biotic frontier, forest canopies are now better understood than ever before and better appreciated and valued for the critical roles they play in forest ecosystem dynamics.

Modern Canopy Access Systems

Advances in canopy access systems have allowed canopy biologists to address an increasing diversity and complexity of issues. The advantages and limitations of each method for addressing differing ecological questions are outlined in **Table 1**.

Methods of Access

Ground-based methods It is not always necessary to climb into the forest canopy to complete a canopy study. For example, taking advantage of a ridge-top, hill, or bridge may provide a direct view into adjacent tree crowns. Technology such as radiotelemetry, hemispherical photography, telephoto lenses, and binoculars allow similar visual access to the canopy from the ground below. Most often, however, researchers want to collect samples or specimens from the canopy as well. One of the earliest methods for ground-based observers to retrieve samples from the canopy was the use of trained monkeys tethered to ropes. This method works extremely well for intensive botanical inventories of large areas over short periods of time. Other widely used methods for collecting plants include bending branches down, using a net or pole-pruner and 'harvesting' foliage with a shotgun or rifle. Canopy arthropods are frequently captured from the ground using insecticidal knockdown (canopy fogging or canopy misting), light traps, and a variety of baited interception traps. Canopy birds and bats are sampled using modified mist-net systems.

Ground-based methods are popular because of their ease of sampling targeted organisms, but the scope of such studies is limited because they do not incorporate *in situ* sampling in the canopy. Disregarding *in situ* canopy sampling can lead to biased results and hinder attempts to answer larger-scale questions in forest ecology. Some of the methods

Table 1 Modern canopy access systems and criteria for the selection of an appropriate method

Method of access	*Biology of organism*			*Spatial access*			*Replication and randomization*	*Long-term monitoring*	*Impact on ecosystem*	*Logistical constraints*				*Research applications*
	Sessile	*2-D mobility*	*3-D mobility*	*Horizontal extent*	*Vertical extent*	*Access to canopy–atmosphere interface*				*Cost*	*Ease of use*	*Major constraints*	*Major advantages*	
Ground-based methods														
Trained animals	X			Wide	Excellent	Not usually	Good replication and randomization	Difficult	Negligible	Moderate	Easy; one person	Locating and training	Rapid, high replication	Botanical surveys; plant phenology
Mechanical extension samplers (e.g., shotgun, nets)	X	X		Narrow	Narrow	No; unless SRT employed	Moderately good	Yes	Low–moderate; branch and foliage damage	Low	Easy; one person	Permits; skill; reach	Large sample area; flexible	Plant–insect interactions; leaf chemistry; vegetation dynamics
Intercept traps, mist-nets		X	X	Narrow	Wide	Not usually; can be attached to towers or poles above canopy	Good	Yes	Low; rope burn on branches	Low–moderate	Easy; one person	Activity-based	Standardized; quantitative	Arthropod, bird, and bat surveys; quantitative monitoring
Insecticide knockdown			X	Narrow	Moderate–wide	No	Low replication; good randomization	No	High; kills most arthropods	Moderate	Moderate; two people	Selective sampling difficult; wind	Comparative studies; surveys of large areas	Taxonomy; arthropod diversity; community composition
Climbing and mechanical methods														
Single rope technique (SRT)	X	X		Excellent; restricted to adjacent trees at each site though	Very good	Not usually; addition of mechanical extension samplers increases access	High level of replication and repeatability; limited full randomization	Difficult	Low; rope burn; snaps branches; damages epiphytes	Low–moderate	Easy; one person; stamina required	Branch availability; restricted reach; mobility	Flexible; lightweight; portable; versatile	Varied, e.g., phenology; canopy–soil interactions; arthropod community composition; herbivory
Ladders, booms, cherry-pickers	X	X		Moderate–very good	Moderate	Not usually; depends on canopy height	Moderate–good	No	Moderate; nails; vehicle access	Moderate–high	Easy; one or two people	Limited to sites near roads or on large trees	Stable platform; good horizontal reach	Herbivory; pollination; ecophysiology; vegetation dynamics

Towers and cranes														
Meteorological towers	X			Narrow	Excellent	Yes	Poor	Yes	Site construction	High	Difficult to build; easy use	Limited replication	Stable platform for instruments	Ecophysiology; photosynthesis; gas exchange; hydrology; canopy architecture; phenology; vertical stratification
Canopy crane	X	X		Moderate	Excellent	Yes	Low	Yes	Site construction; noise	High–very high	Difficult to build; easy use	Limited to fixed site; crane driver required	Long-term collaborative studies; stable platform	Varied, e.g., phenology; plant–insect interactions; vegetation dynamics; epiphyte communities; canopy architecture
Walkways, platforms, and cable cars														
Walkways, platforms	X		X	Narrow–moderate	Narrow–moderate	No	Moderate	Yes	Initial construction	Moderate–very high	Difficult to build; easy use	Limited to fixed site	Comfortable; useful for large groups; stable	Vertebrate behavior; monitoring forest dynamics
Cable cars, trams, ski lifts	X		X	Wide	Narrow; upper canopy	Yes	Moderate	Yes	Site construction; noise	High–very high	Difficult to build; easy use	Limited to fixed site	Long horizontal transects	Animal diversity; vertebrate behavior; seasonality
Balloons and rafts														
Canopy raft and sled	X	X	X	Excellent	Moderate–wide	Yes	Limited	No	Crushes foliage and branches	Very high	Moderate; climbing skills	Limited time at one site; wind	Stable platform above canopy	Varied, e.g., herbivory; arthropod community structure
Remote sensing														
Satellite data	X			Excellent	Narrow	Yes	Excellent	Yes	No	Very high	Access to data difficult	Available technology; computer processing	Landscape-level data	Landscape-level analyses of canopy architecture, leaf chemistry, productivity

mentioned above can be modified to collect samples directly in the canopy using line and pulley systems.

Climbing techniques and mechanical methods Brazilian Indians traditionally climbed tree trunks up to 40 cm in diameter using a loop of woven vines or cloth called a 'peconha', but this method is dangerous and cannot be used on trees of a larger diameter. Safety is a high priority for canopy biologists and modern climbing techniques incorporate rigorous safety measures. There are two climbing methods in practice today. The single rope technique (SRT) uses a relatively long (up to two times canopy height) fixed static rope, anchored to the ground at one end and climbed from the other end using mechanical 'jumar' ascendors. Alternatively, the arborist method involves the climber using a relatively short (e.g., 15 m) movable rope (lanyard pulley system) and is useful for climbing very tall trees or trees with few branches, and for transferring between adjacent trees within the canopy. Together, the two methods give almost total access to the canopy, including the outer foliage.

Arborist methods and SRT are often used to set up rigging lines in the canopy which enable a variety of instrumentation and collecting equipment to be hauled up and down from the ground. Line insertion techniques vary widely depending on the tools available. For example, ropes can be thrown by hand using throw bags, hand catapults, pole catapults, line-throwing guns, crossbows, or longbows (the best option for high canopies). Ropes, together with flexible ladders lashed to the tree, can allow rapid, repeated access into the canopy. Horizontal reach can be extended by using telescoping booms, consisting of lengths of aluminum piping that slide into one another, a steel cable, bosun's chair and manual lifting gear.

A more mechanized, but still highly mobile, access technique is the use of a hydraulic cherry-picker. Of course, roads are generally required in order to drive the cherry-picker to study sites, and trees along the forest edge tend to be the only ones accessible by this method. Booms and cherry-pickers provide stable working platforms and increased access to the outer foliage than climbing methods.

Towers and cranes Towers were first utilized to study vertical gradients in solar radiation, temperature, humidity, and wind speed in the late 1960s. Towers are costly to erect, but permit a range of investigations not possible from the ground. Towers can also be combined with horizontal access systems. The planned Canopy Operation Permanent Access System (COPAS) in French Guiana has multiple towers and a connecting cable system which will give access to 1.5 ha of forest canopy and will likely provide more detailed information than a single tower alone.

Canopy cranes provide even greater vertical and horizontal access than COPAS. The use of large construction cranes in forest canopies was pioneered in Panama at the Smithsonian Tropical Research Institute. Cranes provide permanent access to a finite number of trees, limited only by the length of the crane arm. Researchers are housed inside a gondola and maneuvered to specific sites within the canopy by ascending above the canopy and then descending back down into it. There are now 11 canopy cranes in place worldwide and an expanded network of cranes is planned as part of the Global Canopy Programme initiative.

Aerial walkways, platforms, and cable cars Aerial walkways and platforms have been used extensively to allow long-term observation within the canopy. They offer a good place to observe, educate, and study in large groups for long periods of time and they can become an integral part of the landscape, allowing researchers to study animal behavior or collect samples on a regular basis. Trams (or cable cars) supported by steel towers have also been suspended in or above the treetops in many parts of the world.

Balloons and rafts The canopy sky raft ('radeau des cimes') and sled were developed by Francis Hallé of Operation Canopéé in France. The large, inflatable raft is lowered onto the forest canopy surface by a dirigible balloon and is supported by several large canopy trees. The raft only remains in place for a few days or weeks to avoid permanent damage to trees or the risk of slipping. The sled is towed underneath the dirigible and can be flown just above the top of the canopy to sample many different tree crowns over a short period of time. Both the sled and raft have stable internal platforms from which to suspend climbing ropes, thereby increasing the vertical range of sampling. Another method of balloon access is a one-man helium balloon tethered to cables across the forest canopy, giving access to the outer edges of the canopy.

Remote sensing Forest canopy structure can be measured remotely using a wide range of sensors fitted to weather balloons, planes, or satellites. Three broad classes of sensors are available: (1) optical, (2) laser, and (3) radar. Aerial photographs can be taken that measure the outlines of individual tree crowns and the spatial extent of canopy gaps. Canopy height can be estimated crudely using stereo-pairs of airphotos. Optical satellite data (such as the LandSat multispectral scanner) can be used to estimate structural properties of canopies much more accurately, and even some aspects of leaf physiology and chemistry, including photosynthesis, transpiration, nitrogen, lignin, and pigment concentrations in leaves. Laser devices, particularly light detection and ranging (LIDAR) instruments, precisely measure vertical height from the ground to the canopy (in forests with fairly open structure). For dense forests, radar images (e.g., synthetic aperture radar (SAR)) provide an excellent means for penetrating foliage and estimating canopy structure. Both LIDAR and SAR can approximate vegetational biomass from signal reflection and scatter. Combinations of these methods have proven useful in monitoring forest responses to environmental change, such as in the use of the Scanning LIDAR Imager of Canopies by Echo Recovery (SLICER) to validate SAR data in North American forest ecosystems.

Selecting an Appropriate Method

Simply getting into the forest canopy is often the easy part – choosing the most *appropriate* method of access and deciding how to collect data once you are there is much more difficult. It relies on a clear evaluation of the research objectives and the tools and skills available to implement them. There are six major considerations when selecting an appropriate canopy access system (**Table 1**).

1. Life history and biology of the organism. A recurrent problem in forest canopy studies is how to sample efficiently and adequately document the life history of canopy inhabitants. The appropriateness of sampling techniques and methods of access will depend on the species or canopy properties under study. Some ground-based methods and towers, for instance, may be well suited to studying sessile organisms or organisms with limited mobility that perceive branches as two-dimensional planes, but are not as good for highly mobile organisms.
2. Spatial extent. From a research perspective, the most crucial attributes of a climbing method are the volume and shape of the space that can be accessed. Towers limit canopy access to a vertical transect line at one location, whereas walkways and trams permit good horizontal access at one vertical height. Other methods, such as canopy cranes, provide much better access to a fixed volume of canopy space, but suffer from limited ability to relocate to a new sampling location, as can easily be done with SRT, cherry-pickers, or other techniques.
3. Replication and randomization. Spatial and temporal replication are key considerations for any canopy study. There is a clear trade-off between ease of repeated access to a single point (e.g., towers, platforms, and so on) and access to multiple replicate locations in space (e.g., SRT, canopy raft, sled, and so on). Because of safety considerations for all canopy access techniques, true three-dimensional randomization is rarely achieved.
4. Long-term monitoring, in particular, is largely restricted to permanent structures such as towers, walkways, and cranes because of the need to have fixed, stable access over long periods of time, without the risk of cumulative damaging effects on the canopies under study.
5. Impact on the ecosystem is increasingly important when selecting a canopy access system. The technique used to access the canopy should avoid any damage that may affect the variables being measured, or the health of the tree being climbed. Regular checks on permanent structures and branches that are climbed on a regular basis are essential.
6. Lastly, logistical constraints play a central role in determining which method of access to choose. However, problems caused by the physical environment, costs, or available time should not be allowed to dictate the level of replication, randomization, or spatial access appropriate to the research question being addressed.

Canopies as the Substrate, Buffer, and Catalyst for Forest Dynamics

Canopy Architecture

Canopies provide the dominant structural influence on the movement of organisms, the availability of habitat, and the interactions between species and their abiotic environment in forests. Although the importance of canopy structure is still not fully appreciated, there is a burgeoning interest in the quantitative measurement of canopy architecture – the sizes, shapes, angles, distribution, and development of tree crown elements, such as leaves, twigs, and branches, within a three-dimensional medium. The most comprehensive, qualitative system for describing the growth patterns of trees is the Hallé–Oldeman system. Architectural development of trees is viewed in terms of a genetically programmed model in which individual architectural units are reiterated throughout the growth and development of the tree (**Figure 1**). Architectural models differ in terms of the presence of vegetative branching, orientation of vegetative axes, continuous or rhythmic growth, and varying developmental patterns of terminal buds and sexual tissues. Although numerous combinations of these characteristics are theoretically possible, the growth forms of trees are remarkably restricted. It appears that only about 30 architectural models occur in plants. Even trees that are totally unrelated may share the same architectural models. The Hallé–Oldeman system provides an elegant conceptual model to unite the common features of plant growth form among species. However, variation in the expression of architectural units during development, or asymmetrical growth and damage, can cause large variation in the quantitative outcome of canopy morphology. No two trees are ever structurally identical. A more precise description of canopy structure would have to emphasize branch order, leaf arrangement, length and diameter, longevity, share in total photosynthetic activity, and reproductive output.

Most commonly, quantitative variation in canopy structure is measured using surrogate estimates of the vertical distribution of leaf area index (LAI, the ratio of the total one-sided leaf area to the projected ground surface area below, in $m^2 m^{-2}$) (**Figure 2**) or leaf area density (LAD, the mean one-sided leaf area per unit volume of canopy space, in $m^2 m^{-3}$). The utility of these measures is evident in the highly contentious issue of vertical stratification in forests. From simple observational studies, strong vertical layering of canopies was thought to be a characteristic of tropical forests, but in cases where LAI or LAD have actually been quantified, vertical stratification has been found to be indistinct or nonexistent. The problem remains, though, that a wide range of measures exists for quantifying canopy structure and each may give a different perspective on stratification. For example, silviculturists may focus on the distribution of tree heights, ecologists may focus on the distribution of tree species within the forest, and tree physiologists or atmospheric chemists may focus on the distribution of leaf surface area.

At least part of the difficulty in extrapolating forest function from forest structure is that different organisms and different abiotic variables respond to canopy architecture in differing ways. For example, LAI may be a good predictor of photosynthetic activity in the canopy, whereas leaf optical properties, leaf angles, and LAI may be required to understand light transmittance to the forest floor. Conversely, LAI may bear no relation to colonization and diversity of epiphytic plants within tree crowns, which are more dependent upon structural attributes of branches and twigs. More generally, some organisms 'perceive' the canopy as a true three-dimensional volume, whereas others may perceive the canopy as a set of highly convoluted, two-dimensional surfaces. For example, mites and other wingless arthropods may view canopies, for all intents and purposes, as flat surfaces, because dispersal through air is highly limited. Other organisms, such as birds or bats, clearly view the canopy as a volume. This can have important functional implications for the effect of canopy structure on the distribution and abundance of organisms (or nutrients or chemicals, for that matter). Recognition of this difference has led to some astounding developments in the quantification of canopy structure. Recent studies have reversed the

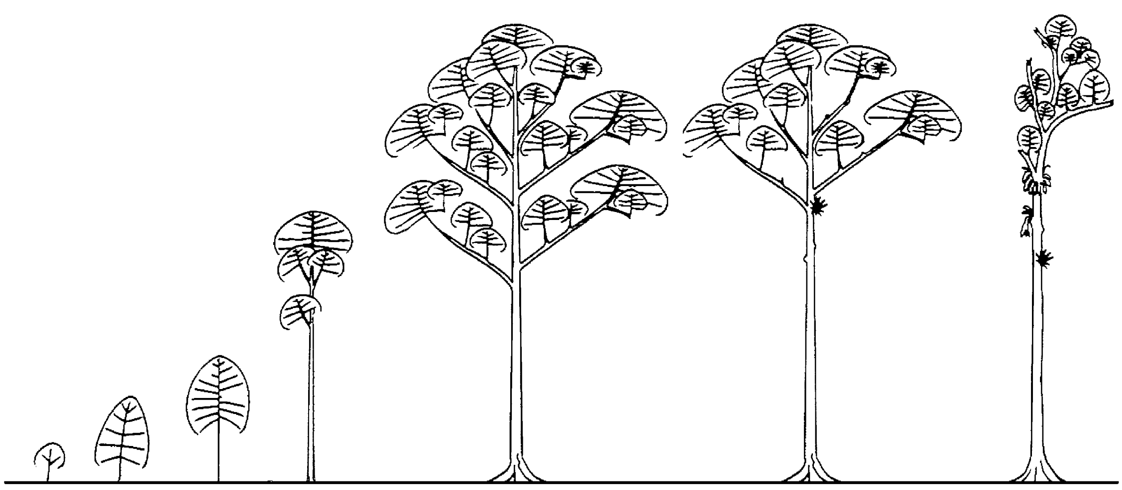

Figure 1 Schematic representation of the reiteration of architectural units during growth and development of a tropical tree. Although there are relatively few 'ground-plans' for crown architecture among species, every individual tree exhibits unique canopy structure due to asymmetrical growth and damage.

LAI	Boreal: Deciduous broadleaf	Boreal: Evergreen needle-leaf	Temperate: Deciduous broadleaf	Temperate: Evergreen needle-leaf	Temperate: Evergreen broadleaf	Tropical evergreen broadleaf	Plantation forests
World average	2.6	2.7	5.1	5.5	5.7	4.8	8.7
SE	0.09	0.13	0.12	0.32	0.23	0.22	0.49
Maximum	4.0	6.2	8.8	11.6	15.0	8.0	18.0

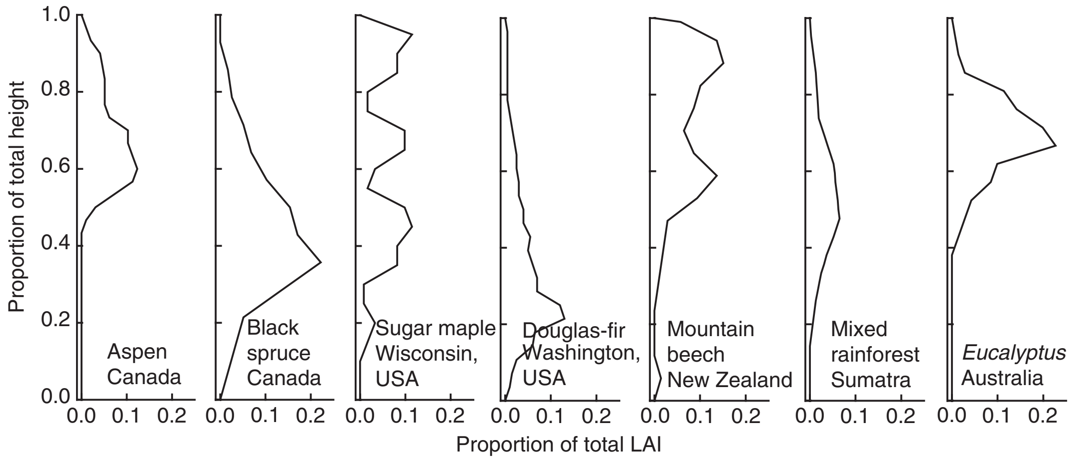

Figure 2 Summary of leaf area index (LAI) for major forest types of the world, showing the global average (in $m^2 m^{-2}$), standard error of the mean of multiple studies (SE) and maximum recorded value for each forest type. One example of vertical variation in canopy architecture is presented for each forest type. Aspen forest, Canada: canopy height (H_{max}) = 30 m, total LAI = 2.02. Black spruce forest, Canada: H_{max} = 14 m, LAI = 2.35. Sugar maple forest, Wisconsin, USA: H_{max} = 16 m, LAI = 6.10. Douglas-fir/western hemlock forest, Washington, USA: H_{max} = 56 m, LAI = 6.28. Mountain beech forest, New Zealand: H_{max} = 17 m, LAI = 6.95. Mixed broadleaf tropical rainforest, central Sumatra: H_{max} = 42 m, LAI = 7.50. *Eucalyptus nitens* plantation forest, Tasmania, Australia: H_{max} = 21 m, LAI = 7.00.

emphasis on quantitative structural elements in the canopy and measured the vertical distribution of empty space (gap size and frequency) in forests. Measurements produce a characteristic S-shaped distribution of open space with increasing height from the ground to the atmosphere above the forest.

Opportunities to integrate differing perspectives on canopy structure are expanding with the advent of remote sensing tools to more rapidly and accurately measure forest structure across large areas, and sophisticated computer software that can manipulate complex three-dimensional spatial models. The recent development of the Vertical Canopy LIDAR (VCL) has created new opportunities to remotely characterize the three-dimensional structure of the earth's surface by satellite and measure the vertical and horizontal distributions of plant structures across vast swathes of the planet. The VCL uses near-infrared wavelength laser pulses fired at regular intervals at the earth's surface. The time displacement of the reflected laser signal to the VCL determines the height above ground, with an incredible 30 cm vertical resolution, while the magnitude of signal scatter determines the absolute volume of canopy biomass intercepted by the laser. Already the VCL has produced revolutionary new views of forest canopies that would have taken several lifetimes of ground-based measurements to compile.

The measurement of canopy architecture has direct applications in a wide range of disciplines. For example, variation in forest canopy structure exerts strong regulation of radiation transfer to the ground surface, altering the extent of snow cover in forested regions of the boreal zone. Canopy removal by clear-cut harvesting slows snowmelt and markedly alters local climate compared to regions with intact canopy structure. In coniferous forests in Chile, forest canopy structure is also an important determinant of precipitation infiltration into soils, with dense canopies decreasing erosion and increasing the return time for landslide-forming events by over 20%. In other fields, quantitative models of three-dimensional canopy structures are being utilized to predict (and optimize) the dispersal pattern of pheromones released in forests to control insect pests, and drag coefficients and turbulence around canopy elements are being utilized to parameterize within-canopy atmospheric exchange models. The structural detail now being provided by high-resolution VCL remote sensing of forest canopies promises a revolution in our understanding of the relationships between (1) canopy architecture and habitat for plants and animals, (2) architecture and ecosystem functioning, and (3) architecture and carbon, water, and energy exchange.

Aboveground–Belowground Dynamics

Aboveground and belowground ecosystem processes are integrally linked by material transport between roots and crowns of individual plants and the plasticity of resource allocation among components of foliage, reproductive structures, branches, stems, defensive chemicals, roots, mycorrhizae, and root exudates. Although a full understanding of resource allocation in plants is limited by difficulties in measuring belowground processes, there is growing awareness that soil and root dynamics are critically dependent on forest canopy dynamics. Tree roots represent a major pool of stored nutrients and contribute a significant amount to total soil surface respiration in forests. For example, studies in pine forest in Oregon, USA, have shown that 18% of annual ecosystem respiration typically originates from foliage, 6% from woody debris and the remaining 76% from soil, with root respiration accounting for a massive 53% of total soil respiration. Most early studies concluded that root growth and respiration were limited by abiotic factors such as soil water content or soil temperatures, leading to concern over the effect of global warming on carbon balance within soils and possible atmospheric CO_2 emissions. However, new data suggest that root production is regulated instead by concurrent radiation interception and photosynthetic production in the canopy. Photosynthetic products are transferred below ground much more rapidly than ever previously imagined. In a remarkable experimental test of the importance of current photosynthesis to belowground respiration, researchers in northern Sweden girdled (stripped the bark from) mature pine trees over a large area to inhibit carbon allocation to the roots. Inhibition of root respiration virtually eliminated mycorrhizal fungi and reduced overall soil surface respiration by 54%, in striking concordance with findings on the importance of root respiration in Oregon.

Forest canopies also affect belowground processes by storing nutrients in foliage and regulating the input of available carbon, nitrogen, and other elements to the soil through litter fall. Despite the long-standing belief that nutrient availability in forests depends on species-specific characteristics of the chemistry and decay rates of litter on the ground, recent studies show that soil nutrient cycling is better predicted simply by the total mass of litter produced from the canopy and total nutrient content of leaves. Given that 90% of net primary productivity is channeled directly into the detrital pathway (largely via litter fall), belowground nutrient recycling, site fertility, and soil surface respiration are primarily regulated by within-canopy processes that affect foliar litter production.

Much of forest ecosystem research and global change biology is focused on understanding net ecosystem productivity – the balance between photosynthesis and ecosystem respiration – and it appears that canopy processes are not only the critical drivers of photosynthetic production in forests, but they are also important catalysts for soil surface respiration rates.

The Canopy–Atmosphere Interface

Forest canopies form an important buffer between the soil and the atmosphere, regulating the exchange of carbon, water, and energy that affects atmospheric chemistry. Forest canopies interact with the atmosphere in two important ways. First, through structural interference of airflow that creates turbulence. Second, through the interception of solar radiation and exchange of CO_2 and water vapor during photosynthesis, respiration, and transpiration.

Boundary-layer dynamics around leaves and branches are crucial to understanding atmospheric processes. This is not surprising when a single tree crown spanning just 20 m across can have 10 000 m^2 of foliage surface area. As a result, canopy leaves can filter 20–30% of bulk precipitation and intercept and concentrate even greater amounts of airborne nutrients and pollutants from the atmosphere. Lowered air velocity around canopy elements partially isolates the upper canopy from airflow in the surrounding understorey and atmosphere, creating a zone of contrasting internal dynamics. This buffering effect is explicitly recognized in the measurement of atmospheric gas exchange. Partitioning net ecosystem CO_2 exchange (NEE) between the soil, canopy, and atmosphere is a major objective for scientists studying gas exchange using the eddy covariance technique (measurement of the turbulent fluctuations of vertical air movement in conjunction with temperature, water vapor, CO_2, and other gases, calculating flux rates as the covariance of wind and one of the other variables). This has been achieved in a number of ways, including simple comparisons of below-canopy and above-canopy eddy systems, or the compartmentalized measurement of gas exchange from individual ecosystem components, such as soil, roots, wood, and foliage, using experimental chamber techniques. Results from chamber measurements are then scaled up to the ecosystem level to calculate NEE from days to several years. Another method to partition and integrate the role of forest canopies in NEE at the ecosystem level is to analyze the stable isotope ratios of carbon and oxygen in CO_2, as these vary according to the source of CO_2 exchange from different ecosystem compartments (for example, autotrophic versus heterotrophic respiration). However, canopy structure can influence the composition of stable isotopes in belowground and above-canopy compartments by modifying radiation interception and photosynthetic activity of ground vegetation, and by reducing turbulent upwelling of air from the ground and thus inhibiting the mixing of respired CO_2 from the soil. These processes make modeling and prediction of NEE heavily dependent on measurement of the characteristics of canopy structure and an understanding of within-canopy dynamics.

The Functional Importance of Forest Canopies in Global Change

Globally, forests cover over 25% of the land surface and store almost 50% of terrestrial carbon. Conversion and management of forests are altering global stability on three central fronts: (1) the ability of forest ecosystems to support a large proportion of global biodiversity, (2) the global sustainability of fiber production from forests and the maintenance of site productivity, and (3) the stability of global carbon balance, atmospheric chemistry, and atmospheric circulation patterns. Forest canopy processes are central to understanding the importance of forests in all three aspects of global change (**Figure 3**).

Maintenance of Biodiversity

Individual tree crowns often harbor rich microcosms of epiphytic life, complete with fully functioning aerial soil communities and complex food web dynamics analogous to the more extensive soil communities below ground. Over 10% of all vascular plants in the world are canopy epiphytes, often with a restricted resident fauna of vertebrates and invertebrates associated with them. The

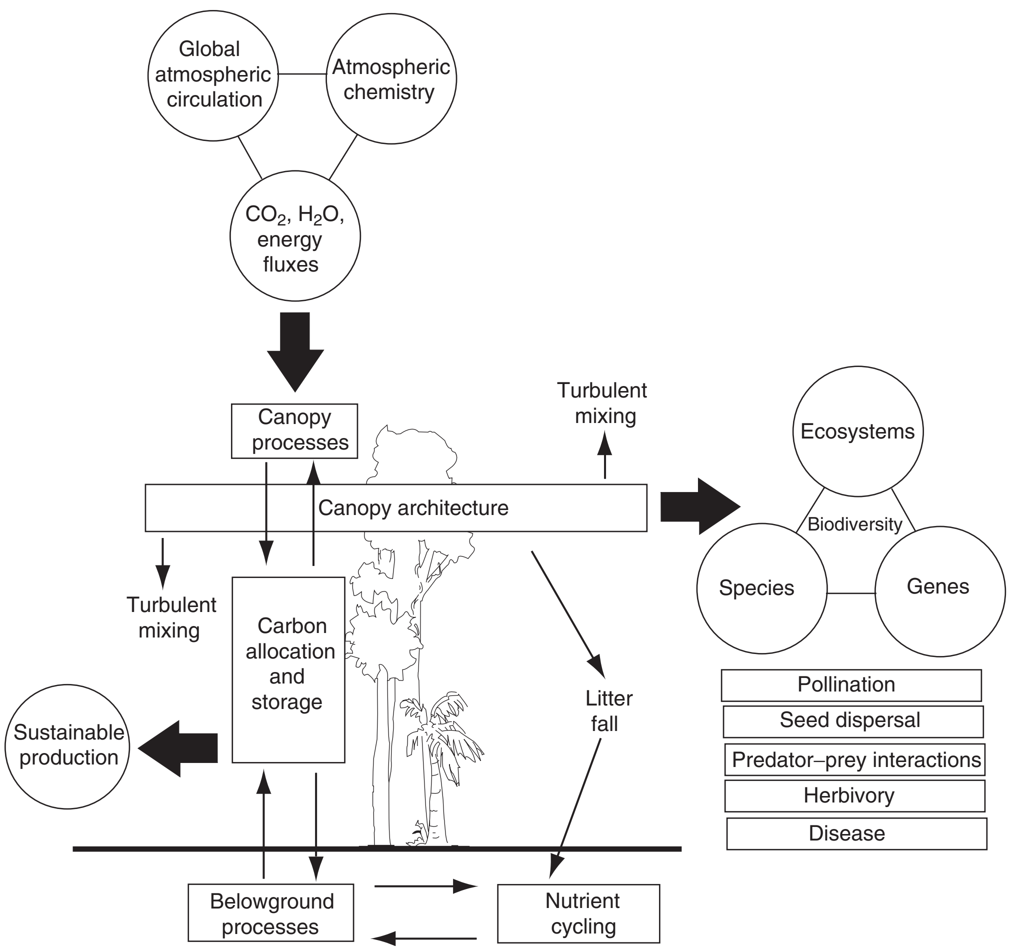

Figure 3 Conceptual diagram showing the key roles of forest canopies as the substrate, buffer, and catalyst for forest dynamics. The structural and functional attributes of forest canopies are central to the maintenance of global biodiversity, the sustainability of forest production, and the stability of global climate.

importance of canopy epiphyte communities is not trivial in terms of forest dynamics. Epiphyte biomass in some wet tropical forests is four times greater than that of host tree foliage, stored nutrients within epiphyte leaves may represent 50% of total canopy foliar nutrients, and dead leaves decay almost twice as fast in canopy soils than in ground soils. Incredibly, canopy soil biomass can be equivalent to the total biomass and available nutrient pools of terrestrial leaf litter in many forests. As a consequence, canopy epiphyte communities can have a large effect on primary production and nutrient cycling rates in forests.

The surface area, biomass, and productivity of tree crowns and associated epiphytic plants provide a diverse range of niches that are exploited by canopy organisms. Notable, in terms of their diversity and contribution to total global biodiversity, are the arthropods of tropical forest canopies. Large numbers of undescribed species in forest canopies have spurred intense speculation on the magnitude of total global biodiversity, with estimates ranging as high as 30–80 million species. With the availability of better data on species turnover rates between geographic regions, host specificity, species coexistence, and coevolutionary relationships among animals and plants in tropical forests, estimates have been revised downwards to 3–5 million species. This still represents a threefold increase in the total number of recognized species in the world – most of them thought to be in the canopies of tropical forests. However, there has been no rigorous assessment of whether a large proportion (42–66%) or a relatively small proportion (10–20%) of forest species are canopy specialists. It may well be that many forest canopy species utilize belowground habitats, or nonforest ecosystems, during larval life history stages of which we are not yet aware.

Nevertheless, it is the overwhelming superabundance and diversity of canopy organisms that perhaps best exemplifies the structural complexities of forest canopies, and is a cause for concern in the face of habitat modification. Variation in canopy architecture, changes in resource availability, and an increase in microclimatic extremes due to changing land use management all influence biodiversity in forest canopies. It is precisely the accelerating rates of forest loss and conversion since the 1950s, combined with recognition of the magnitude of forest canopy diversity in the 1980s, which have prompted fears of an extinction crisis. If even 10% of species in the world are solely restricted to forest canopies, and a further 50% of all forest species depend critically on the canopy for some aspect of their resource requirements, then preservation of intact forest canopy structure and function is clearly key to the long-term maintenance of global biodiversity.

Sustainability of Forest Production

Management of forests for fiber production uses conventional empirical, or statistical, approaches to estimating growth and yield based on accumulated experience of site quality, stand structure, or tree species traits in the area being harvested. However, the future of sustainable forest production lies in the application of process-based models for ecosystem management – models that define the actual mechanisms of net photosynthate assimilation, carbon allocation, and storage in aboveground structures, tree respiration, and long-term stand viability that is affected by processes such as nutrient recycling and maintenance of predator–prey interactions, pollination, and seed dispersal services. Forest canopies play a central role in all of these ecological and physiological processes and in the maintenance of ecosystem services in forests.

Process-based models have only recently begun to be implemented at an operational level in forest management. Not surprisingly, the initial focus has been on improving predictions of growth rates and enhancing total yield at the stand level. Several carbon balance models have been developed for this purpose, which treat the acquisition and distribution of photosynthetic products as central to understanding forest production. Gross primary productivity in this sense is driven almost entirely by canopy processes. Canopy architecture also affects the distribution of organisms and flux of abiotic variables that influence tree respiration. The dynamic balance between these effects of the canopy on assimilation and respiration of carbon determine the total amount and distribution of new growth. For example, Norway spruce trees with narrower geometrical crown shapes have a higher LAI, greater stemwood production per unit crown area and higher harvest index due to greater allocation of carbon to stems, rather than roots or foliage. This variation in allocation is determined both genetically and environmentally, but a radical new perspective on the importance of canopy architecture to forest production is that trees could be more intensively selected and 'domesticated' for improved carbon allocation performance. It should be recognized, however, that predictions of overall stand performance must incorporate not only the net carbon balance of individual trees, but also aboveground and belowground competition for resources between trees (whether of the same or different species) and the dynamics of stand structure in response to biotic and abiotic disturbances. For example, herbivory directly affects the amount of leaf material available for photosynthesis, carbon allocation to defensive chemicals, new foliage growth and stem increment, and ultimately forest production.

Other tree physiological processes, such as water balance or nutrient cycling, have received considerably less attention than carbon balance, but are nonetheless critical to forest production. For example, tree canopies on more fertile sites produce greater leaf biomass, which increases foliar litter inputs to the soil, reinforcing differences in site fertility, nutrient availability to roots and overall soil heterogeneity. This can be exacerbated in harvesting situations because forest removal eliminates the buffering influence of the forest canopy on soil microclimate and removes litter inputs. Without foliar litter inputs, it is thought that microbes become carbon-limited (instead of nitrogen-limited), leading to reduced assimilation rates of nitrates and contributing to a pulse of nitrogen availability in clearcut areas. This change in nutrient cycling even occurs in small gaps of just a few trees and in natural windfall gaps, but not following single-tree removals in which canopy cover is not greatly compromised.

Beyond physiological models of growth and yield, production can be limited by biological factors that limit growth (such as herbivory), increase mortality (such as disease), and reduce seed or seedling establishment (such as pollination limitation or seed predation). Many animals that live in forest canopies play important functional roles in the provision of ecosystem services, like pollination and predation, in forests. Maintenance of intact structure and functioning of forest canopies is likely to facilitate preservation of species that may have beneficial roles in the sustainability of future forest production. These roles may be as simple as pollinating flowers that ensure a continued seed supply for reforestation, or as important as dampening the oscillatory dynamics of pest insect populations.

Stability of Global Climate

Forest canopies account for at least 50% of global CO_2 exchange between terrestrial ecosystems and the atmosphere, as well as a significant proportion of global net primary productivity. Compelling evidence suggests that tropical forest canopies may be net carbon sinks, mitigating the rate of increase in atmospheric CO_2 concentration from anthropogenic sources. Increased deforestation and burning threatens to alter this balance by directly liberating vast amounts of carbon (and other elements) into the atmosphere, and indirectly limiting the net assimilation rate of carbon by disturbance to the remaining forest canopies. Synergistic interactions between deforestation, increased fire frequency, and drought in the Amazon Basin, the world's largest remaining expanse of tropical forest, are enhancing a positive feedback cycle in altered climatic circulation patterns and increased forest degradation. Experimental exclusion of rainfall from large areas of undisturbed tropical forest in eastern Amazonia has simulated the effects of increasing drought. A 40% reduction in precipitation throughfall to the soil significantly reduced tree growth and reproductive output, lowered net primary productivity and increased leaf loss and tree mortality, all of which resulted in the forest becoming a net source of CO_2 to the atmosphere rather than a net sink. Correlated drought and tree mortality effects have been detected at distances of up to 2–3 km inside 'intact' nature reserves, leading to concern over receding edges and the long-term viability of fragmented forest remnants. Because of the magnitude of change in disturbance regimes and climatic conditions in the wet tropics, vegetation dynamics in some areas are shifting away from high-diversity rainforest to low-diversity, fire-adapted sclerophyll vegetation.

The study of ecophysiological processes in forest canopies is not only critical for predicting forest responses to global change, but also for modeling how canopy structure and functioning mitigates future atmospheric CO_2 increase and climate change. Through diverse roles in carbon, water, and energy cycling, structural integrity of forest communities, nutrient cycling dynamics, and maintenance of forest productivity and biodiversity, forest canopies will shape the direction and magnitude of global change that human populations experience over the next millennium. We can either use this knowledge to advantage in conserving forests, or face a more extreme and more uncertain future.

See also: **Biodiversity**: Biodiversity in Forests. **Environment**: Carbon Cycle. **Hydrology**: Hydrological Cycle; Impacts of Forest Plantations on Streamflow. **Soil Development and Properties**: Nutrient Cycling. **Tree Physiology**: Canopy Processes; Forests, Tree Physiology and Climate; Shoot Growth and Canopy Development.

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Natural Disturbance in Forest Environments

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Introduction

Disturbance in plant communities has been defined as consisting of 'the mechanisms which limit the plant biomass by causing its partial or total destruction.' In forests, disturbance arises from the agencies of tree damage or death. At small spatial scales, individual trees die standing or fall over, but in both cases a gap in the canopy is created and this initiates a successional process known as the forest growth cycle. The agencies of natural disturbance at larger spatial scales include windstorms, fire, and landslides and these factors vary in their impacts on forests and the ensuing mechanisms of forest recovery. Natural disturbance regimes in forests are important because they impact on tree population dynamics, the relative abundance of different species and functional groups, the biomass and carbon content of vegetation, and interactions with other components of the biotic community. Community ecologists have highlighted the importance of disturbance among mechanisms proposed for the maintenance of tree species richness, particularly in species-rich tropical forest communities.

Small-Scale Disturbance: Gap Phase Dynamics

Small-scale natural disturbances are an inherent component of all plant communities because plants have a finite lifespan. In forests, the size of the individual tree at the time of its death and the mode of death determine the scale of the disturbance created. The death of individual small understory trees and shrubs that live their entire life in the shade, and of the suppressed juveniles of canopy trees, may have limited impact on forest stand structure. However, the death of canopy-level or emergent trees has significant potential for localized modifications of canopy structure, resource availability, and microclimates. Some large trees die standing, perhaps following lightning strike or the synergistic effects of old age and wood decay fungi. Many trees lose large branches or parts of their crown long before the entire tree has died, and these events may lead to partial opening of the canopy and to some damage of surrounding smaller trees and other plants. However, the threshold for a natural disturbance event is usually regarded as the death of an individual large canopy or emergent tree, which results in the creation of a hole through all layers of the forest down to 2 m above the ground surface (a canopy gap). The size of a canopy gap varies according to the height of the tree that died, its architecture (height : canopy width), and its neighborhood. The fall of a large tree will inevitably lead to damage or death of surrounding trees, particularly if their crowns are connected by lianas. Thus canopy gaps arising from small-scale tree death can vary from a lower limit of 25–50 m^2 up to about 1000 m^2 for a large multiple tree-fall gap. Gaps can be further divided into zones influenced by the fallen crown (crown zone), the bole (bole zone), and the site where the fallen tree had been rooted (root zone). In addition, when trees fall over, particularly during severe windstorms, they frequently create an elevated mound of consolidated soil and roots known as a tip-up mound and an associated pit with exposed subsoil on its base and sides. Microclimatic conditions and availability of