

A physiological basis for biosphere–atmosphere interactions in the boreal forest: an overview

HANK A. MARGOLIS^{1,2} and MICHAEL G. RYAN³

¹ Centre de Recherche en Biologie Forestière, Faculté de Foresterie et de Géomatique, Université Laval, Sainte-Foy, Québec G1K 7P4, Canada

² Biospheric Sciences Branch, Code 923, NASA Goddard Space Flight Center, Greenbelt, MD 20771, USA

³ USDA Forest Service, Rocky Mountain Research Station, 240 West Prospect Street, Fort Collins, CO 80526-2098, USA

Received April 30, 1997

Summary Interdisciplinary field experiments for global change research are large, intensive efforts that study the controls on fluxes of carbon, water, trace gases, and energy between terrestrial ecosystems and the atmosphere at a range of spatial scales. Forest ecophysiology can make significant contributions to such efforts by measuring, interpreting, and modeling these fluxes for the individual components of forest ecosystems and then integrating the results into holistic ecosystem process models. The Boreal Ecosystem–Atmosphere Study (BOREAS) was undertaken because of the importance of the boreal forest biome to various global change issues. The study was conducted from 1993 to 1996 at sites in Saskatchewan and Manitoba, Canada. Results have shown that physiological processes of plants in the boreal forest can have large-scale consequences. For example, the composition of tree species strongly influences flux rates, with deciduous species having much higher carbon and water fluxes than coniferous species. Additionally, physiological limitations to transpiration in boreal conifers, even when soil water is abundant, reduces latent heat flux and increases sensible heat flux over large regions. This physiological control of transpiration can increase the depth of the atmospheric boundary layer on warm spring days to a level similar to that found in desert biomes. This special issue features 10 articles that address various aspects of the physiological basis of biosphere–atmosphere interactions in the boreal forest. The articles emphasize the environmental controls on water flux, carbon flux, and ecosystem productivity.

Keywords: carbon flux, climate change, ecosystem productivity, energy flux, flux of trace gases, scaling, transpiration, water flux.

Role of tree physiology in interdisciplinary field experiments

Interdisciplinary field experiments for global change research are large, intensive efforts that attempt to understand the controls on the fluxes of carbon, water, trace gases, and energy between a particular biome and the atmosphere. The experiments focus on one or more study areas, defined either as a

transect or as a specific area of landscape. The individual disciplines involved can include boundary layer meteorology, land surface climatology, micrometeorology, trace gas biogeochemistry, atmospheric chemistry, hydrology, soil physics and chemistry, physiological ecology, landscape ecology, and remote sensing science.

A principal objective of these experiments is to develop techniques for extrapolating measurements of fluxes at small spatial scales to progressively larger scales. Consequently, the development and use of remote sensing for estimating the biophysical properties of various land surfaces is a key component of such endeavors. For example, remote sensing can produce maps of vegetation stratified by functional types, biomass density, and forest age as well as maps of structural characteristics such as leaf area and canopy height. However, the algorithms currently work better for some of these parameters (e.g., fraction of photosynthetically active radiation absorbed by the land surface) than others (e.g., forest age). These maps enable fluxes measured for a small portion of the landscape to be extrapolated to larger spatial scales. However, these kinds of extrapolations require a close coordination of the field measurement program with the development and testing of both climate models and ecosystem process models.

The first of a series of interdisciplinary field experiments over the last decade examined biosphere–atmosphere interactions in the Konza Prairie of Kansas in 1987 and 1989 (Sellers et al. 1988, Sellers et al. 1992b, Hall and Sellers 1995). The experiment was the First International Satellite Land Surface Climatology Project (ISLSCP) Field Experiment (FIFE). This was followed by several smaller experiments in other biomes (Levine et al. 1993, Glooschenko et al. 1994, Waring and Peterson 1994, Prince et al. 1995). In 1994 and 1996, the largest interdisciplinary field experiment to date, the Boreal Ecosystem–Atmosphere Study (BOREAS), was conducted in the boreal forest region of Canada (Sellers et al. 1995). In summer 1993, there was another field experiment conducted in the boreal forest of eastern Siberia that, like BOREAS, measured carbon, water and energy fluxes at a range of spatial scales (cf. Hollinger et al. 1995, Schulze et al. 1995, Arneth et al. 1996, Lloyd et al. 1996). Finally, a major field experiment is being planned for the Amazon basin of Brazil in

1998–2001 to examine biosphere–atmosphere interactions in this important tropical biome (LBA Science Planning Group 1996).

The study of biosphere–atmosphere interactions considers both the direct effects of climate on ecosystem function and the potential feedbacks of the land surface to the physical climate system. To understand these interactions at different scales requires a nested experimental design whereby measurements of fluxes from eddy covariance towers, small research plots, and individual components of ecosystems (e.g., leaves, branches and individual trees) are combined with regional flux measurements by aircraft-mounted eddy covariance systems, radiosonde measurements of atmospheric properties, and satellite measurements of vegetation structure, weather, and energy absorbed by the vegetation (Figure 1).

Tree physiology is one of the disciplines that can make a significant contribution to this important area of global change research. Forests occupy one-third of the terrestrial land surface (Schlesinger 1991). This vast surface area and the generally greater leaf areas of forests compared with other terrestrial ecosystems indicate why forests are responsible for a such a significant portion of the fluxes of carbon, water and energy between the land surface and the atmosphere on a global scale. Forest ecophysiology is concerned with the measurement, interpretation, and modeling of carbon and water fluxes to and from the different components of forest ecosystems such as leaves, branches, stems, roots, groundcover, and soil. Interpre-

tation of measurements often involves examining the environmental controls on these fluxes and this is critical to understanding how vegetation can in turn modify the physical environment.

Within an interdisciplinary field experiment, the measurement and interpretation of fluxes from different ecosystem components allow us to understand the role of these components in the total ecosystem flux as measured by micrometeorological techniques such as eddy covariance or eddy accumulation (e.g., Baldocchi et al. 1988, Baldocchi and Vogel 1996, Black et al. 1996, Goulden et al. 1996, Baldocchi et al. 1997; Figure 2). These net ecosystem flux measurements are made continuously at the stand level (around 1 km² for mature forest vegetation) and periodically at the landscape level with aircraft-mounted eddy covariance systems. Ecophysiologicals are also involved in the measurement and interpretation of net primary productivity of aboveground and belowground ecosystem components as well as changes in soil carbon content. Such measurements are valuable when they are compared with ecosystem flux measurements summed over the growing season or with output from ecosystem process models. Physiological measurements, combined with optical or microwave

INTENSIVE FIELD CAMPAIGNS

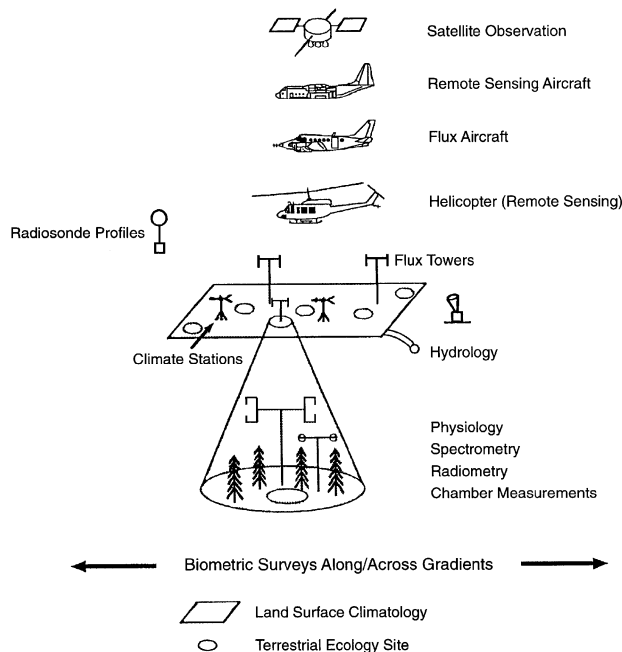


Figure 1. During interdisciplinary field experiments, coordinated measurements of ecosystem states, ecosystem processes, and atmospheric properties are taken at a wide range of spatial scales. Adapted from BOREAS Experiment Plan, Version 3.0. (Courtesy of Piers J. Sellers, NASA Goddard Space Flight Center, Greenbelt, MD.)

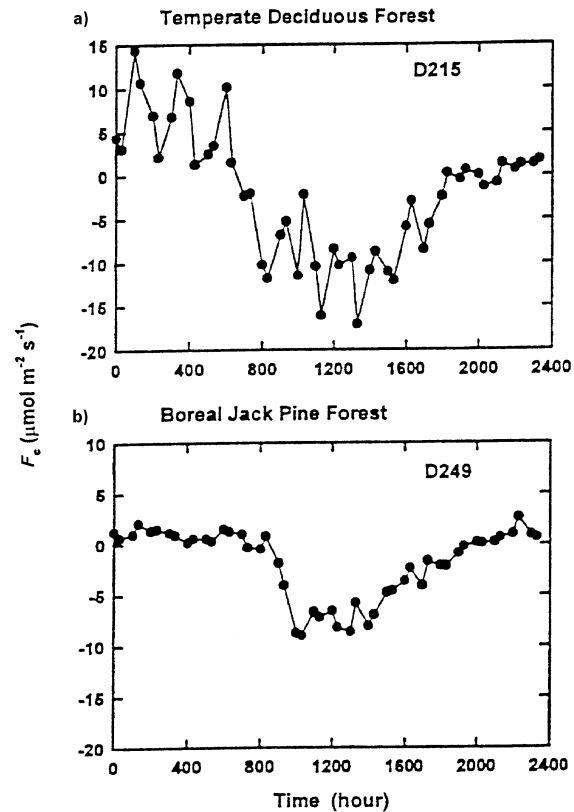


Figure 2. Typical diurnal patterns of eddy correlation CO₂ flux densities (F_c) (net ecosystem exchange) throughout the day over a temperate broad-leaved forest in Tennessee (Julian day 215) (a), and over the Old Jack Pine stand in the BOREAS Southern Study Area in Saskatchewan (Julian day 249) (b). Negative flux numbers indicate flux from the atmosphere to the vegetation. (From Baldocchi and Vogel (1996).)

reflectance measurements, can also help in the development and validation of remote sensing algorithms for estimating the biophysical characteristics of the land surface, e.g., leaf area (Goel 1988, Hall et al. 1995), total biomass (Hall et al. 1995, Ranson et al. 1995, Waring et al. 1995), and absorbed photosynthetically active radiation (Asrar et al. 1984, Baret and Guyot 1991, Goward and Huemmrich 1992, Sellers et al. 1992a).

This special issue of *Tree Physiology* features 10 articles that provide examples of how ecophysiological studies can contribute to understanding biosphere–atmosphere interactions within the context of the interdisciplinary field experiment conducted in the boreal forest biome of central Canada in 1994, the Boreal Ecosystem–Atmosphere Study (BOREAS). It is intended as a complement to a much larger special issue to be published in 1997 or 1998 in the *Journal of Geophysical Research (Atmospheres)* that will feature over 80 articles from the full range of disciplines involved in BOREAS.

Rationale for conducting a major field experiment in the boreal forest biome

The boreal forest biome is composed of upland forests, extensive wetlands, and many lakes. It is dominated by coniferous tree species and is one of the largest biomes on Earth, covering an area of around 14.7×10^6 km², approximately 11% of the planet's terrestrial surface (Bonan and Shugart 1989). Its soils are a major storehouse for organic carbon (Tans et al. 1990, Schlesinger 1991) and are thought to supply a significant proportion of the annual global emissions of methane (CH₄) (Asselman and Crutzen 1989, Fung et al. 1991). Furthermore, it is the biome that appears to account for up to half of the “missing sink” of CO₂, i.e., that portion of the CO₂ emitted by fossil fuel combustion that does not accumulate in the atmosphere (Slegenthaler and Sarmiento 1993, Ciais et al. 1995, Keeling et al. 1996b).

Because of the size of the biome and the large amount of carbon stored in the soil and biomass, boreal forests are critically important to the global carbon cycle. However, the sensitivity of this important biome to changes in the physical climate system is not well understood. Consequently, improving our understanding of the processes that control the storage and fluxes of carbon, water and energy between the boreal biome and the atmosphere would represent a significant advance in our understanding of biosphere–atmosphere interactions on a global basis. It would also enhance our ability to link the effects of a dynamic biosphere to the general circulation models (GCM) on which we rely so heavily for predicting the effects of climate change (Sellers et al. 1997).

Many of the studies simulating the impact of increased atmospheric CO₂ on climate have predicted that the greatest temperature increases will be between latitudes 45° N and 65° N with the most marked effects in the continental interiors (e.g., Harrington 1987, Tans et al. 1990, Denning et al. 1995, Sellers et al. 1996). An appreciable warming and drying during the next 50 to 100 years suggests that soil water reserves may be reduced by as much as half. Thus the current southern limit

of the biome could be pushed north through changes in productivity and disturbance frequency, whereas northward migration could be restricted by available energy and edaphic regimes. The simulations of Rizzo and Wiken (1992) predicted a reduction in the ecoclimatic zone of the boreal forest in Canada from 28.9 to 14.9% of the potential land area in response to a doubling in atmospheric CO₂ concentration.

A climatic response to a doubling in atmospheric CO₂ concentration directed strongly toward the boreal forest region becomes highly significant when we consider the important role the biome also seems to play in the large-scale dynamics of atmospheric CO₂. D'Arrigo et al. (1987) demonstrated the importance of the boreal forest in atmospheric CO₂ dynamics when they showed that the seasonal growth of the total boreal forest biome accounted for around 50% of the annual variation in atmospheric CO₂ concentration measured in Alaska between 1971 and 1982, and about 30% of the more globally representative CO₂ variation measured in Hawaii during the same period. An analysis of both the patterns of atmospheric CO₂ (Keeling et al. 1996a) and a satellite-measured vegetation index at 9 km² resolution (Myneni et al. 1997) showed that the length of the growing season in the boreal forest zone and photosynthetic activity by the forest appear to have increased during the 1980–1991 period.

An information system, referred to as the Earth Observing System (EOS), is being designed and implemented to provide the geophysical, chemical and biological information necessary for intense study of the Earth as an integrated system. This international effort involves the launch of several sophisticated, space-based, measurement systems (i.e., satellite observatories) over the next 15 years. An interdisciplinary field experiment of the boreal forest, with its emphasis on linking measurements of physical and biological processes of the boreal biome to information available from remote sensing technology, will serve as one of the scientific foundations of EOS. Such a field experiment will help us understand how to interpret correctly data from the boreal forest obtained by the EOS observatories. It will also yield valuable information about which strategies to follow in the design and implementation of these sensor systems.

The Boreal Ecosystem–Atmosphere Study (BOREAS)

BOREAS is an interdisciplinary field experiment designed to elucidate the role of the boreal forest in global change. It is a collaborative effort between the United States of America and Canada, and also involves participation by scientists from the United Kingdom, France and Russia. BOREAS is led by the National Aeronautics and Space Administration (NASA) in the USA and by the Canada Centre for Remote Sensing (CCRS) in Canada. Additionally, five other Canadian agencies and three other U.S. agencies also contributed significantly to BOREAS: namely, the Natural Sciences and Engineering Research Council, the Atmospheric Environment Service, the Canadian Forestry Service and Agriculture and Agrifood Canada in Canada; and the National Oceanic and Atmospheric Administration, the Environmental Protection Agency, and the

National Science Foundation in the United States. Thus, BOREAS provides a useful example of how the interests of a wide range of government agencies can be brought together in a major global change field experiment.

BOREAS has two principal objectives: (1) to improve our understanding of the processes and states that govern the exchanges of energy, water, heat, carbon and trace gases between boreal forest ecosystems and the atmosphere with particular reference to those processes and states that may be sensitive to global climate change; and (2) to develop and validate remote sensing algorithms to transfer our understanding of the above processes from local to regional scales. The articles in this special issue focus primarily on the first objective. The second objective is addressed to a greater extent in the previously mentioned BOREAS special issue of the *Journal of Geophysical Research (Atmospheres)*.

BOREAS field measurements were made in two study areas in central Canada and along the ecological gradient that separates them (Figure 3). Each BOREAS study area was large enough to ensure an adequate resolution by satellite sensors while permitting reasonable logistics for researchers on the ground. The Southern Study Area (SSA), located in and around Prince Albert National Park near Prince Albert, Saskatchewan, is 11,170 km² in size (Figure 3). It lies near the southern edge of the boreal forest biome where ecosystem processes are likely to be water-limited during the summer. The Northern Study Area (NSA), about 500 km northeast of the SSA, lies about 40 km west of Thompson, Manitoba and is 8000 km² in size (Figure 3). It is representative of the northern portion of the boreal forest, where ecosystem processes are likely to be largely temperature-limited during much of the growing season. The two sites represent opposite ends of an ecological

gradient from warm-dry to cold-wet and serve as a spatial analog of how ecological processes might change in response to changes in climate.

Most of the BOREAS field measurements were made during the Intensive Field Campaigns (IFC), when the type of nested measurements illustrated in Figure 1 were taken concurrently. In 1994, there were three IFCs; one in early spring (IFC-1; May 23 to June 16), one in midsummer (IFC-2; July 19 to August 8); and one in late summer (IFC-3; August 29 to September 20). Two less intensive measurement campaigns were conducted during midwinter (February 1994) and the subsequent spring thaw concentrated on snow hydrology. Because initial results indicated that the timing of the spring thaw was critical to the annual carbon balance (e.g., Frolking et al. 1996, Frolking 1997) and because significant carbon fluxes occurred in the autumn (photosynthesis and respiration) and early winter (respiration), a smaller field effort was made during 1996 that focused on these periods. BOREAS also had a longer term measurement component (1993–1997) that included: (1) collecting climatic data across the region from 14 existing and 10 newly installed climate stations; (2) monitoring catchment hydrology; and (3) monitoring land cover from various satellite sensors (see Sellers et al. 1995 for further details).

The articles in this special issue focus primarily on the 1994 results of measurements from individual ecosystem components and small plots. Most of the studies were located at a subset of the sites where continuous net ecosystem fluxes were being measured by eddy covariance; five sites in the NSA and six in the SSA (Table 1, Figure 2). Most of these sites were at least 1 km² in size and had homogeneous vegetation cover. They are referred to frequently in the enclosed articles. In

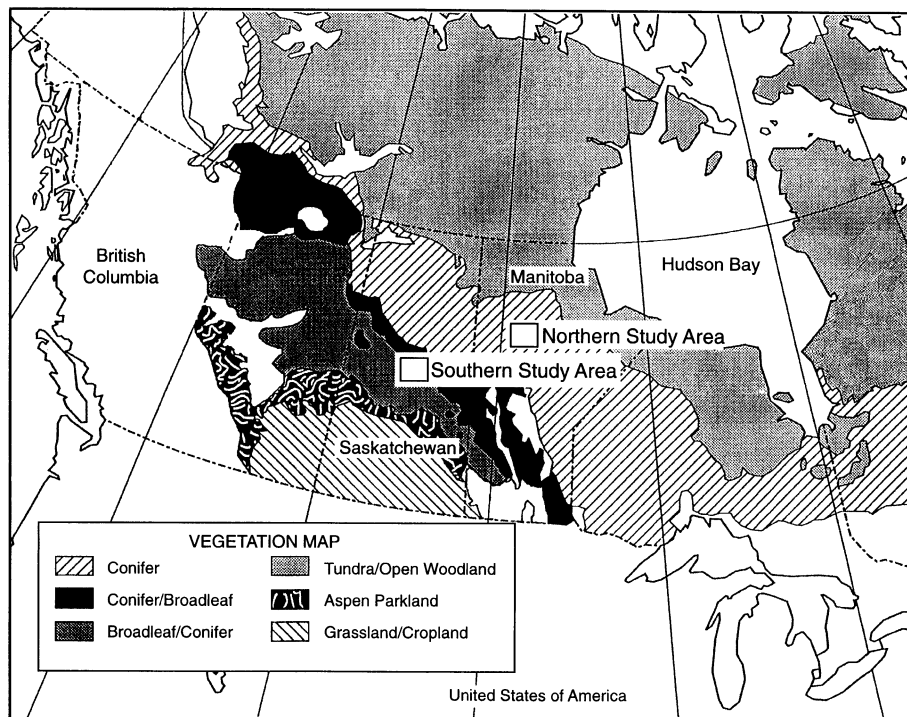


Figure 3. Location of the BOREAS Northern and Southern Study Areas in Canada and the surrounding vegetation types. Adapted from Sellers et al. (1995). Used with permission of the American Meteorological Society.

Table 1. BOREAS eddy covariance flux tower sites that were active during 1994. Unless otherwise indicated, fluxes of sensible heat, latent heat (water), and CO₂ were measured from May to September 1994. Commonly used abbreviations for the study areas and flux sites are indicated in parentheses.

Southern Study Area (SSA)	Northern Study Area (NSA)
Old Aspen (OAS)	Beaver Pond
Old Black Spruce (OBS) ¹	Old Black Spruce (OBS) ²
Fen	Fen
Old Jack Pine (OJP)	Old Jack Pine (OJP)
Young Jack Pine (YJP)	Young Jack Pine (YJP)
Young Aspen (YAS) ³	

¹ To differentiate between the same site type for different study areas, the study area abbreviation precedes the site abbreviation, e.g., SSA-OBS.

² NSA-OBS fluxes were measured continuously from 1993 through 1996 and are scheduled to continue for another three to five years.

³ No CO₂ fluxes were measured at SSA-YAS. Sensible and latent heat fluxes at SSA-YAS were measured during July and August 1994 only.

In addition to the flux tower measurements, a wide range of optical and microwave remote sensing aircraft and four different eddy covariance flux aircraft flew over the study areas during the IFCs (see Sellers et al. 1995 for details of aircraft missions). Finally, a network of 70 auxiliary sites was established in which basic measurements including net primary productivity (NPP), stand biomass, leaf area, and fraction of PAR absorbed by the land surface (fPAR) were taken to characterize better the range of sites present across the landscape. These auxiliary sites are particularly valuable for validating remote sensing algorithms of land surface biophysical properties as well as NPP models.

Small scale physiological processes can have large-scale consequences

An example of the effects of small-scale physiological processes on the properties of the atmosphere can be seen by comparing measurements of the atmospheric boundary layer from the BOREAS sites with those taken above other ecosystems. Figure 4 shows the relationship between height above the land surface and potential temperature (°K) for three biomes. Potential temperature is a variable that standardizes absolute temperature readings to a common atmospheric pressure and is calculated from radiosonde (weather balloon) measurements. Potential temperature eliminates the adiabatic cooling effect that occurs when atmospheric pressure decreases. To illustrate this idea, consider that it is adiabatic cooling that is largely responsible for the lower absolute temperatures on the top of a mountain relative to the bottom. Thus, if atmospheric pressure is the only variable influencing the absolute temperature on a mountain, the potential temperature at the bottom and the top of the mountain will be the same. Similarly, when the lower portion of the atmospheric boundary layer is highly

dynamic as a result of the convective movement of air on hot days, a portion of the lower atmosphere, referred to as the mixed layer, is created in which potential temperature stays relatively constant with height. The height of this mixed layer has a major impact on the dynamics of cloud formation, precipitation patterns and, over large areas, the formation of weather.

In the FIFE study of the Kansas prairie, boundary layer heights attained about 1.2 km at 1400 h on a warm summer day (33 °C at the land surface) (Gal-Chen et al. 1992, Figure 4). Similar measurements taken in spring in the Saudi Arabian desert showed boundary layer heights of around 3 km (37 °C at the land surface) (Blake et al. 1983, Figure 4). At the BOREAS Northern Study Area on a clear day in late spring (30 °C at the land surface), boundary layer heights also attained over 3 km in late afternoon (Betts et al. 1996, Figure 4). Thus, the boundary layer depth over this northern boreal forest was similar to that measured over one of the driest deserts on Earth. On the other hand, rapidly transpiring prairie vegetation had a much greater portion of its incoming energy used to evaporate water and thus the boundary layer heights were much lower. The explanation for why a boreal forest boundary layer in late spring so closely resembles that of a desert appears to reside in the physiological properties of the boreal vegetation.

Boreal forest soils are cold and roots are limited by either depth to permafrost or depth to the water table (Bonan and Shugart 1989). On June 10, 1994 (Figure 4), many of the organic soils in the BOREAS Northern Study Area were still frozen. Even when soils are not frozen, low soil temperatures offer a high resistance to the movement of water (Running and Reid 1980). Because much of the northern boreal forest is coniferous, tracheids are the dominant type of cells that transport water from roots to foliage. Because water must pass through a pit membrane to move from one tracheid to another, the resistance to water movement up the tree stem is much greater than for deciduous trees having wood comprised of vessels (Pothier et al. 1989). Stomatal conductance is also reduced when humidity is low. Finally, the stomatal conductance and photosynthetic capacities of boreal vegetation, particularly boreal conifers, are lower than those found in vegetation from most other biomes. Consequently, even though the boreal landscape is wet, the physiological properties of the vegetation are such that there is a high resistance to the movement of water between the biosphere and the atmosphere.

The high surface resistance in the boreal forest results in high ratios of sensible to latent heat (energy used to evaporate water) and thus the development of a deep, dry atmospheric boundary layer. For example, the sensible heat (H) from the surface between 0800 and 1530 h for the FIFE site averaged 120 W m⁻², latent heat (LE) was 325 W m⁻², giving an evaporative fraction (LE/(H + LE)) of 0.73. For the BOREAS site, however, sensible heat flux averaged 280 W m⁻² from 0900 to 1500 h, and latent heat averaged 130 W m⁻², giving an evaporative fraction of 0.32 (Alan Betts, Atmospheric Research Inc., Pittsford, VT, personal communication).

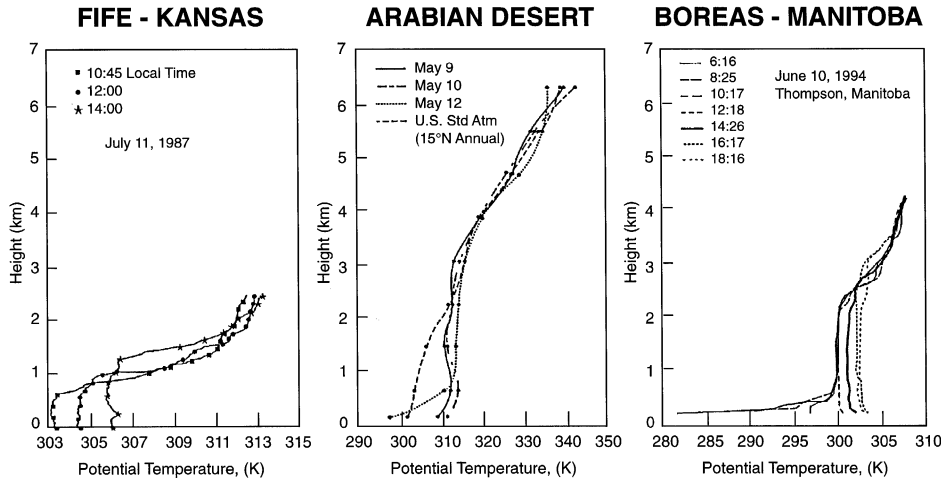


Figure 4. Height above the land surface versus potential temperature ($^{\circ}\text{K}$) over the Kansas prairie during the FIFE experiment (July 11, 1987), over the Saudi Arabian desert (May 9, 10 and 12, 1979), and over the BOREAS Northern Study Area (June 10, 1994). See text for further details. Adapted from Gal-Chen et al. (1992), Blake et al. (1983), and Betts et al. (1996), respectively. Used with permission of the American Geophysical Union, the American Meteorological Society, and the American Geophysical Union, respectively.

Because this strong limitation on latent heat production in the boreal forest is largely a result of the physiological properties of the vegetation, it is important to understand how the physiology of boreal forest vegetation responds to different environmental conditions. This is particularly critical for understanding the potential positive and negative feedbacks that might occur between the boreal forest and the atmosphere under different climate change scenarios. However, there may well be regional and temporal differences in how the boreal forest influences the atmospheric boundary layer. For example, Hollinger et al. (1995) reported that the boundary layer above the boreal forest in eastern Siberia in July was not as high as that found in BOREAS, but rather more similar to that reported for the Kansas prairie.

Issue contents

This special issue contains articles that examine various aspects of the physiological basis of biosphere-atmosphere interactions in the boreal forest. They emphasize how environmental conditions control water flux, carbon flux, and ecosystem productivity.

Water flux

We have seen in the previous section how important the portion of energy used to evaporate water from a vegetated surface can be in determining the properties of the atmospheric boundary layer. Hogg and Hurdle (this issue) used the heat pulse method to measure sap flow at two different trembling aspen stands in the Southern Study Area (SSA). Sap flow increased linearly with vapor pressure deficit (VPD) up to 1.0 kPa, then stayed constant as VPD increased. Constant transpiration at VPDs > 1.0 kPa indicates that aspen stomata strongly regulate transpiration, perhaps to maintain leaf water potential above a threshold that could damage the water conducting system.

Saugier et al. (this issue) report on the use of three different methods for measuring transpiration from the SSA Old Jack Pine stand. Transpiration rates estimated by branch bags, sap flow, and eddy correlation measurements from above and

below the canopy were comparable. Transpiration in this mature jack pine stand was very low, even when the soil was well supplied with water. The authors suggest that these low transpiration rates resulted from low leaf area and a reduction in stomatal conductance at high VPDs.

Dang et al. (this issue) examined the regulation of stomatal conductance and other leaf-level physiological variables by shoot water potential and VPD in mature black spruce, jack pine and aspen at the Northern Study Area (NSA). They defined the response of the three species to both factors under controlled environmental conditions in the laboratory, and then showed how these results were consistent with field measurements. Shoot water potential had little effect on gas exchange for these mature stands with well-developed root systems, even though 1994 was the driest year on record at the NSA. In all species, stomatal conductance decreased markedly as VPD increased; however, because VPD averaged only 1.0 kPa over the growing season, the overall stomatal limitation to CO_2 assimilation appeared to be minor.

Carbon flux

An important characteristic of the boreal forest biome is the widespread occurrence of mosses as a groundcover. The gas exchange characteristics of these plants, which possess no stomata, has rarely been studied. Goulden and Crill (this issue) used an automated gas exchange system at the NSA Old Black Spruce site to measure CO_2 flux for feathermoss growing under a black spruce canopy and for sphagnum moss growing in open sites too wet to support tree growth. Maximum photosynthesis occurred between 5 and 8 $^{\circ}\text{C}$. Moss photosynthesis accounted for 10 to 40% of whole ecosystem carbon uptake and 50 to 90% of whole ecosystem respiration measured simultaneously by flux tower eddy covariance.

Lavigne and Ryan (this issue) examined autotrophic respiration in stems of aspen, black spruce and jack pine at both BOREAS study areas. They report that both construction respiration and maintenance respiration rates varied with species and in the case of jack pine, with stand age. Construction respiration (carbon efflux per unit of carbon incorporated into

structural matter) was greatest for black spruce and least for jack pine. Maintenance respiration rates were highest for young jack pine and mature black spruce trees. They suggest that stand-specific respiratory parameters, rather than general parameters, should be used in ecosystem process models.

Sullivan et al. (this issue) examined the seasonal variation in photosynthetic characteristics in the laboratory and the field for branches from the Young Jack Pine, Old Jack Pine and Old Black Spruce stands in the BOREAS SSA. Assimilation rates under conditions of saturating light were highest in midsummer, especially for black spruce. Rates were reduced only slightly later in the growing season. The Young Jack Pine stand had higher needle photosynthesis and stomatal conductance than the Old Jack Pine stand.

An important, yet little studied, aspect of carbon flux from boreal ecosystems are the fluxes of monoterpenes. These compounds are important as defensive compounds against insects and, despite their low concentrations, as photochemically reactive compounds in the atmosphere. Lerdau et al. (this issue) showed for black spruce and jack pine that monoterpene emission rates were linearly related to monoterpene concentrations in the foliage and exponentially related to air temperature. As well, monoterpene fluxes were about three orders of magnitude less than CO₂ fluxes at these sites. Current theories predict an inverse relationship between foliar nitrogen and monoterpene concentration, but only some of the sites followed this pattern. The development of more accurate regional models of monoterpene emissions is complicated by the lack of an adequate theory of the ecological controls on monoterpene allocation by plants.

A technique permitting the nondestructive estimation of branch leaf area would be useful for photosynthetic studies that require repeated sampling of the same branch. Serrano et al. (this issue) examined the potential of obtaining nondestructive leaf area estimates from measurements of relative absorptance on intact branches made with an integrating sphere. They found that their nondestructive estimates agreed well with the more conventional destructive methods of estimating leaf area. However, they also found that it may be necessary to account for the variations in leaf absorptivity that sometimes occur because of differences in growing conditions, e.g., nutrient-deficient foliage.

In an earlier issue of *Tree Physiology*, Brooks et al. (1997) reported that aspen, jack pine, and black spruce at both BOREAS study areas had similar ratios of intercellular CO₂ to ambient CO₂, indicating a common balance between photosynthesis and stomatal conductance across the BOREAS region for these species. They also reported a pronounced gradient in atmospheric CO₂ concentrations along the canopy profile at night that became much less pronounced during the day. From these data, and from measurements of leaf photosynthetic gas exchange, they estimated that the jack pine and black spruce stands gained 5 to 6% of their carbon from respired CO₂.

Ecosystem productivity

The dynamics of fine roots is always the greatest unknown in understanding ecosystem carbon budgets and in estimating net primary productivity. This is particularly important in boreal forests because their soils contain 40% of the global terrestrial soil carbon. Steele et al. (this issue) showed that daily elongation of fine roots was highly correlated to soil temperature at a depth of 10 cm for the mature aspen, black spruce and jack pine stands at both the NSA and SSA. They also showed that annual fine root production exceeded annual mortality in all six stands and speculate that this imbalance may explain why so much soil carbon sequestration occurs in the boreal forest.

Ecosystem process models are one of the main tools available for estimating the response of boreal ecosystems to climate change. Kimball et al. (this issue) use the BIOME-BGC model to simulate gross primary production, respiration, net primary production (NPP) and net ecosystem exchange (NEE) at five BOREAS flux tower sites. Their simulations agree fairly well with aboveground NPP estimates obtained from allometric measurements and with the NEE measurements obtained from the flux towers. However, differences between the simulated and measured NEE on any given day were sometimes large. Their results show that all five sites were small net sinks of carbon, but that relatively minor climatic perturbations could change them to carbon sources.

Acknowledgments

The authors thank the many people involved with the management and science of BOREAS. However, we wish to make special mention of Piers Sellers, Forrest Hall, Josef Cihlar, Barry Goodison, and Diane Wickland for their devoted efforts to the project. We also thank Drs. Alan Betts, Lahouri Bounoua, and Jim Collatz for their useful input concerning atmospheric boundary layer dynamics. H. Margolis gratefully acknowledges the Natural Sciences and Engineering Research Council of Canada for its support of the efforts of all Canadian university scientists in BOREAS. He also thanks the U.S. National Research Council for their research associateship support in 1996 during which time a portion of this article was written.

References

- Arnth, A., F.M. Kelliher, G. Bauer, D.Y. Hollinger, J.N. Byers, J.E. Hunt, T.M. McSeveny, W. Ziegler, N.N. Vygodskaya, I. Milukova, A. Sogachov, A. Varlagin and E.-D. Schulze. 1996. Environmental regulation of xylem sap flow and total conductance of *Larix gmelinii* trees in eastern Siberia. *Tree Physiol.* 16:247–255.
- Asrar, G., M. Fuchs, E.T. Kanemasu and J.L. Hatfield. 1984. Estimating absorbed photosynthetic radiation and leaf area index from spectral reflectance in wheat. *Agron. J.* 76:300–306.
- Asselman, I. and P.J. Crutzen. 1989. Global distribution of natural freshwater wetlands and rice paddies, their net primary productivity, seasonality and possible methane emissions. *J. Atmos. Chem.* 8:307–358.
- Baldocchi, D.D. and C.A. Vogel. 1996. Energy and CO₂ flux densities above and below a temperate broad-leaved forest and a boreal pine forest. *Tree Physiol.* 16:5–16.
- Baldocchi, D.D., B.B. Hicks and T.P. Meyers. 1988. Measuring biosphere-atmosphere exchanges of biologically related gases using micrometeorological methods. *Ecology* 69:1331–1340.

- Baldocchi, D.D., C.A. Vogel and B. Hall. 1997. Seasonal variation of carbon dioxide exchange rates above and below a boreal jack pine forest. *Agric. For. Meteorol.* 83:147–170.
- Baret, F. and G. Guyot. 1991. Potentials and limits of vegetation indexes for LAI and APAR assessment. *Remote Sens. Environ.* 35:161–174.
- Betts, A.K., J.H. Ball, A.C.M. Beljaars, M.J. Miller and P.A. Viterbo. 1996. The land surface–atmosphere interaction: a review based on observational and global modeling perspectives. *J. Geophys. Res.* 101(D3):7209–7225.
- Black, T.A., G. den Hartog, H. Neumann, P. Blanken, P. Yang, Z. Nestic, S. Chen, C. Russell, P. Voroney and R. Stabeler. 1996. Annual cycles of CO₂ and water vapor fluxes above and within a boreal aspen stand. *Global Change Biol.* 2:219–229.
- Blake, D.W., T.N. Krishnamurti, S.V. Low-Nam and J.S. Fein. 1983. Heat low over the Saudi Arabian desert during May 1979 (Summer MONEX). *Monthly Weather Rev.* 111:1759–1775.
- Bonan, G.B. and H.H. Shugart. 1989. Environmental factors and ecological process in boreal forests. *Annu. Rev. Ecol. Syst.* 20:1–28.
- Brooks, J.R., L.B. Flanagan, G.T. Varney and J.R. Ehleringer. 1997. Vertical gradients in photosynthetic gas exchange characteristics and refixation of respired CO₂ within boreal forest canopies. *Tree Physiol.* 17:1–12.
- Ciais, P., P.P. Tans, M. Trolier, J.W.C. White and J.R. Francey. 1995. A large northern hemisphere CO₂ sink indicated by ¹³C/¹²C of atmospheric CO₂. *Science* 269:1098–1102.
- Dang, Q.-L., H.A. Margolis, M.R. Coyea, M. Sy and G.J. Collatz. 1997. Regulation of branch-level gas exchange of boreal trees: roles of shoot water potential and vapor pressure difference. *Tree Physiol.* 17:521–535.
- D'Arrigo, R.D., G.C. Jacoby and I.Y. Fung. 1987. Boreal forests and atmosphere–biosphere exchange of carbon dioxide. *Nature* 329:321–323.
- Denning, A.S., I.Y. Fung and D.A. Randall. 1995. Latitudinal gradient of atmospheric CO₂ due to seasonal change with land biota. *Nature* 376:240–243.
- Frolking, S. 1997. Sensitivity of spruce/moss boreal forest net ecosystem exchange of carbon to seasonal anomalies in weather. *J. Geophys. Res. (Atmos.) (D)*. In press.
- Frolking, S., M.L. Goulden, S.C. Wofsy, S.-M. Fan, D.J. Sutton, J.W. Munger, A.M. Bazzaz, B.C. Daube, P.M. Crill, J.D. Aber, L.E. Band, X. Wang, K. Savage, T. Moore and R.C. Harriss. 1996. Modeling temporal variability in the carbon balance of a spruce/moss boreal forest. *Global Change Biol.* 4:343–366.
- Fung, I.Y., J. John, E. Lerner, E. Matthews, M. Prather, L.P. Steele and P.J. Fraser. 1991. Three dimensional model synthesis of the global methane cycle. *J. Geophys. Res. (Atmos.)* 96(D7):13,033–13,065.
- Gal-Chen, T., M. Xu and W.L. Eberhard. 1992. Estimations of atmospheric boundary layer fluxes and other turbulence parameters from Doppler lidar data. *J. Geophys. Res. (Atmos.)* 97(D17):18,409–18,423.
- Glooschenko, W.A., N.T. Roulet, L.A. Barrie, H.I. Schiff and H.G. McAdie. 1994. The Northern Wetlands Study (NOWES): an overview. *J. Geophys. Res. (Atmos.)* 99(D1):1423–1428.
- Goel, N.S. 1988. Models of vegetation canopy reflectance and their use in estimation of biophysical parameters from reflectance data. *Remote Sens. Rev.* 4:1–121.
- Goulden, M.L. and P.M. Crill. 1997. Automated measurements of CO₂ exchange at the moss surface of a black spruce forest. *Tree Physiol.* 17:537–542.
- Goulden, M.L., J.W. Munger, S.-M. Fan, B.C. Daube and S.C. Wofsy. 1996. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. *Science* 271:1576–1578.
- Goward, S.N. and F.K. Huemmrich. 1992. Vegetation canopy PAR absorptance and the normalized difference vegetation index: an assessment using the SAIL model. *Remote Sens. Environ.* 39:110–140.
- Hall, F.G. and P.J. Sellers. 1995. First international satellite land surface climatology project (ISLSCP) field experiment (FIFE) in 1995. *J. Geophys. Res.* 100(D12):25,383–25,395.
- Hall, F.G., Y.E. Shimabukuro and K.F. Huemmrich. 1995. Remote sensing of forest biophysical structure in boreal stands of *Picea mariana* using mixture decomposition and geometric reflectance models. *Ecol. Appl.* 5:993–1013.
- Harrington, J.B. 1987. Climatic change: a review of causes. *Can. J. For. Res.* 17:1313–1339.
- Hogg, E.H. and P.A. Hurdle. 1997. Sap flow in trembling aspen: implications for stomatal responses to vapor pressure deficit. *Tree Physiol.* 17:501–509.
- Hollinger, D.Y., F.M. Kelliher, E.-D. Schulze, N.N. Vygodskaya, A. Varlagin, I. Milukova, J.N. Byers, A. Sogachov, J.E. Hunt, T.M. McSeveny, K.I. Kobak, G. Bauer and A. Arneeth. 1995. Initial assessment of multi-scale measurements of CO₂ and H₂O flux in the Siberian taiga. *J. Biogeogr.* 22:425–431.
- Keeling, C.D., J.F.S. Chin and T.P. Whorf. 1996a. Increased activity of northern vegetation inferred from atmospheric CO₂ measurements. *Nature* 382:146–149.
- Keeling, R.F., S.C. Piper and M. Heimann. 1996b. Global and hemispheric CO₂ sinks deduced from changes in atmospheric O₂ concentration. *Nature* 381:218–221.
- Kimball, J.S., P.E. Thornton, M.A. White and S.W. Running. 1997. Simulating forest productivity and surface–atmosphere carbon exchange in the BOREAS study region. *Tree Physiol.* 17:589–599.
- Lavigne, M.B. and M.G. Ryan. 1997. Growth and maintenance respiration rates of aspen, black spruce and jack pine stems at northern and southern BOREAS sites. *Tree Physiol.* 17:543–551.
- LBA Science Planning Group. 1996. The large-scale biosphere–atmosphere experiment in Amazonia (LBA): Concise experimental plan. LBA Project Office, NASA Goddard Space Flight Center, Greenbelt, MD, 44 p.
- Lerdau, M., M. Litvak, P. Palmer and R. Monson. 1997. Controls over monoterpene emissions from boreal forest conifers. *Tree Physiol.* 17:563–569.
- Levine, E.R., K.J. Ranson, J.A. Smith, D.L. Williams, R. Knox, H.H. Shugart, D.L. Urban and W.T. Lawrence. 1993. Forest ecosystem dynamics: linking forest succession, soil processes, and radiometric models. *Ecol. Model.* 65:199–219.
- Lloyd, J., B. Kruijt, D.Y. Hollinger, J. Grace, R.J. Francey, S.C. Wong, F.M. Kelliher, A.C. Miranda, G.D. Farquhar, J.H.C. Gash, N.N. Vygodskaya, I.R. Wright, H.S. Miranda and E.-D. Schulze. 1996. Vegetation effects on the isotopic composition of atmospheric CO₂ at local and regional scales—theoretical aspects and a comparison between a rain-forest in Amazonia and a boreal forest in Siberia. *Aust. J. Plant Physiol.* 23:371–399.
- Myneni, R.B., C.D. Keeling, C.J. Tucker, G. Asrar and R.R. Nemani. 1997. Increased growth in the northern high latitudes due to enhanced spring time warming. *Nature* 386:698–702.
- Pothier, D., H.A. Margolis, J. Poliquin and R.H. Waring. 1989. Relation between the anatomy and the permeability of jack pine sapwood with stand development. *Can. J. For. Res.* 19:1564–1570.
- Prince, S.D., Y.H. Kerr, J.-P. Goutourbe, T. Lebel, A. Tinga, P. Bessemoulin, J. Brouwer, A.J. Dolman, E.T. Engman, J.H.C. Gash, M. Hoepffner, P. Kabat, B. Montney, F. Said, P. Sellers and J. Wallace. 1995. Geographical, biological and remote sensing aspects of the Hydrologic Atmospheric Pilot Experiment in the Sahel (HAPEX-Sahel). *Remote Sens. Environ.* 51:215–234.

- Ranson, K.J., S. Saatchi and G. Sun. 1995. Boreal forest ecosystem characterization with SIR-C/XSAR. *IEEE Trans. Geosci. Remote Sens.* 33:867–876.
- Rizzo, B. and E. Wiken. 1992. Assessing the sensitivity of Canada's ecosystems to climatic change. *Clim. Change* 21:37–55.
- Running, S.W. and C.P. Reid. 1980. Soil temperature influences root resistance of *Pinus contorta* seedlings. *Plant Physiol.* 65:635–640.
- Saugier, B., A. Granier, J.-Y. Pontailier, E. Dufrêne and D.D. Baldocchi. 1997. Transpiration of a boreal pine forest measured by branch bag, sap flow and micrometeorological methods. *Tree Physiol.* 17:511–519.
- Schlesinger, W.H. 1991. *Biogeochemistry: An analysis of global change*. Academic Press Inc., San Diego, 443 p.
- Schulze, E.-D., W. Schultze, F.M. Kelliher, N.N. Vygodskaya, W. Ziegler, K.I. Kobak, H. Koch, A. Arneith, W.A. Kusnetsova, A. Sogatchev, A. Issajev, G. Bauer and D.Y. Hollinger. 1995. Aboveground biomass and nitrogen nutrition in a chronosequence of pristine Dahurian *Larix* stands in eastern Siberia. *Can. J. For. Res.* 25:943–960.
- Sellers, P.J., F.G. Hall, G. Asrar, D.E. Strebel and R.E. Murphy. 1988. The first ISLSCP field experiment (FIFE). *Bull. Am. Meteorol. Soc.* 69:22–27.
- Sellers, P.J., J.A. Berry, G.J. Collatz, C.B. Field and F.G. Hall. 1992a. Canopy reflectance, photosynthesis and transpiration, III. A reanalysis using improved leaf models and a new canopy integration scheme. *Remote Sens. Environ.* 42:187–216.
- Sellers, P.J., F.G. Hall, G. Asrar, D.E. Strebel and R.E. Murphy. 1992b. An overview of the first international satellite land surface climatology project (ISLSCP) field experiment (FIFE). *J. Geophys. Res. (Atmos.)* 97(D17):18,345–18,371.
- Sellers, P.J., F.G. Hall, H.A. Margolis, R. Kelly, D. Baldocchi, J. den Hartog, J. Cihlar, M. Ryan, B. Goodison, P. Crill, J. Ranson, D. Lettenmaier and D. Wickland. 1995. Boreal ecosystem-atmosphere study (BOREAS): an overview and early results from the 1994 field year. *Bull. Am. Meteorol. Soc.* 76:1549–1577.
- Sellers, P.J., L. Bounoua, G.J. Collatz, D.A. Randall, D.A. Dazlich, S. Los, J.A. Berry, I.Y. Fung, C.J. Tucker, C.B. Field and T.G. Jensen. 1996. A comparison of radiative and physiological effects of doubled CO₂ on the global climate. *Science* 271:1402–1406.
- Sellers, P.J., R.E. Dickinson, D.A. Randall, A.K. Betts, F.G. Hall, J.A. Berry, G.J. Collatz, A.S. Denning, H.A. Mooney, C.A. Nobre, N. Sato, C.B. Field and A. Henderson-Sellers. 1997. Modeling the exchanges of energy, water, and carbon between continents and the atmosphere. *Science* 275:502–509.
- Serrano, L., J.A. Gamon and J. Berry. 1997. Estimation of leaf area with an integrating sphere. *Tree Physiol.* 17:571–576.
- Slegenthaler, U. and J.L. Sarmiento. 1993. Atmospheric carbon dioxide and the ocean. *Nature* 365:119–125.
- Steele, S.J., S.T. Gower, J.G. Vogel and J.M. Norman. 1997. Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. *Tree Physiol.* 17:577–587.
- Sullivan, J.H., B.D. Bovard and E.M. Middleton. 1997. Variability in leaf-level CO₂ and water fluxes in *Pinus banksiana* and *Picea mariana* in Saskatchewan. *Tree Physiol.* 17:553–561.
- Tans, P.P., I.Y. Fung and T. Takahashi. 1990. Observational constraints on the global atmospheric CO₂ budget. *Science* 247:1431–1438.
- Waring, R.H. and D.L. Peterson. 1994. Overview of the Oregon Transect Ecosystem Research (OTTER) project. *Ecol. Appl.* 4:211–225.
- Waring, R.H., J. Way, E.R. Hunt, L. Morrisey, K.J. Ranson, J.F. Weishampel, R. Oren and S.E. Franklin. 1995. Imaging radar for ecosystem studies. *Bioscience* 45:715–723.

