Tree Physiology 22, 1035–1043

Canopy processes research

MICHAEL G. RYAN

US Department of Agriculture-Forest Service, Rocky Mountain Research Station, 240 West Prospect Street, Fort Collins, CO 80526, USA

Colorado State University, Department of Forest Sciences, Fort Collins, CO 80523, USA (mgryan@fs.fed.us)

Received April 10, 2002; accepted June 30, 2002; published online October 1, 2002

Summary The forest canopy regulates the exchange of carbon, water and energy between the ecosystem and the atmosphere, and provides a habitat for a wide variety of species. Understanding canopy processes is important for modeling forest production and carbon sequestration, and for predicting the effects of global changes in climate and atmospheric chemistry on the functioning of forest ecosystems. The Canopy Processes Working Group of the International Union of Forest Research Organizations has provided a forum for researchers working on forest canopies for nearly 20 years, principally through international meetings held every 2–3 years. In this paper, I review the history of the Canopy Processes Group, show how the research focus has changed and broadened, and provide a brief overview of some of the problems that remain to be solved. These include the topic of our 2001 meeting (Linking the Complexity of Forest Canopies to Ecosystem and Landscape Function), integration of canopy and respiratory processes, carbon allocation, physiological changes with tree age, predicting the response of forests to global change, understanding the genetic control of canopy structure and function, and scaling ecophysiological processes and modeling. Determining how forests will respond to global change and understanding the physiology of forest production will require increased attention to canopy processes and an increased focus on the interactions of canopy processes with other components of the ecosystem.

Keywords: carbon allocation, control of canopy structure and function, genetic, global change, modeling, photosynthesis, physiological changes with tree age, respiration, scaling ecophysiological processes.

Introduction

The International Union of Forest Research Organizations (IUFRO) Working Group on Canopy Processes (S2.01.12) aims to promote an international forum for interaction and collaborative research for scientists working in ecology, physiology, biophysics and genetics of forest canopies. The Canopy Processes Group has been in existence for nearly 20 years, and during that time, it has held seven international meetings and co-sponsored two workshops. Selected papers from most of these meetings and one of the workshops have been published as special issues of *Tree Physiology*. The objective of this paper is to introduce a new generation of canopy researchers to the history of the field and to highlight some of the problems that remain to be solved as well as some new techniques and advances that may help solve those problems.

History of the IUFRO Canopy Processes Working Group

The word canopy derives from the Greek *konops* (mosquito), and the Latin *conopeum* (mosquito net over a bed)—a connection familiar to many who measure gas exchange within the canopy. The term canopy is loosely defined for forests, but it usually refers to the upper layer of a forest (the leaves and branches). Our group generally views the canopy as a surface, rather than a composite of individuals.

The common interest uniting the diverse members of The IUFRO Canopy Processes Working Group is a desire to understand the physiological processes (particularly, but not exclusively, in the canopy) that regulate forest function (carbon, water, nutrient cycling and forest growth). A premise of the group is that robust predictions of function are possible only if the physiology and mechanisms are known (see Landsberg and Gower (1997) and Waring and Running (1998) for background and a general outline of the approach). This physiological approach is used almost exclusively to assess ecosystem response to global change (VEMAP Members 1995) and can successfully predict forest production (Landsberg and Waring 1997).

The Canopy Processes Group provides a forum where researchers interested in canopy structure and ecophysiology can meet with researchers interested in ecosystem-level questions. Ecosystem researchers gain insight from understanding the fine-scale structure and physiology behind ecosystem behavior. Researchers focusing on processes at the smaller scales can learn how their knowledge can be extrapolated, and gain an appreciation of the level of detail needed for understanding at the larger scales. These collaborations will become increasingly important as we attempt to interpret ecosystem flux measurements acquired from an increasing number of sites (Buchmann 2002).

The working group started with an interest in linking canopy structure to forest production—how the forest canopy intercepts radiation and the interaction between energy interception and growth. The first meeting was in 1985 in Tsukuba, Japan, and our working group was then called "Biological Productivity—Crown and Canopy Structure." The foreword to the proceedings (Fujimori and Whitehead 1986) aptly describes the issues: "Management urgently requires the application of research results for directing the manipulation of crown and canopy structure appropriate to produce forests which satisfy a wide variety of land use issues. While considerable effort is being directed towards canopy process studies and the calculation of budgets for energy, carbon, nutrients and water, there is increasing awareness that essential information describing the dynamics of crown and canopy structure, and their interaction with silviculture, is lacking."

Between 1985 and 2001, there were seven meetings (Table 1). Meetings were generally small (50–120 people), loosely focused on a particular topic, included visits to field research sites, often involving travel from site to site within a country, and were structured to foster interaction among participants. Between 1985 and 1989, the group's name changed to the shorter and more inclusive "Canopy Processes," and interests broadened to include more physiology, a focus on global change research (particularly the response of photosynthesis and growth to elevated concentrations of CO_2 and O_3), measurement of ecosystem fluxes and modeling to extend knowledge in space and time. Two past chairmen of the group, Jud Isebrands (1988–1993) and David Whitehead (1994–1999), particularly helped broaden the research interests of the group from forest production, and were active in focusing attention on global change issues, such as the responses to elevated concentrations of CO_2 and O_3.

The early focus on foliage and shoots has expanded so that many now consider the canopy to contain the entire ecosystem. This expansion has occurred because of advances in measurement technology and because of an increased understanding of the linkages between canopy processes and other ecosystem components (Waring and Running 1998). Just as the development of portable equipment for measuring carbon and water exchange spurred researchers into the field in the 1980s, the development of reliable sonic anemometers, fast-response open-path CO_2 and H_2O sensors, and computer processing and storage allowed routine measurements of carbon, water and energy exchange for the entire ecosystem by eddy covariance (Baldocchi et al. 1988). These ecosystem flux measurements have led to an increased understanding of the fine-scale (Goulden et al. 1998) and large-scale (Valentini et al. 2000) controls over carbon and water cycling in forest ecosystems. Because ecosystem fluxes can be partitioned to the canopy only by measuring fluxes for other components, many canopy researchers now work closely with scientists interested in belowground processes and nutrient cycling. Technological developments in mass spectrometry have also greatly decreased equipment costs and sample size, and increased op-

Table 1. Meetings and workshops of the Canopy Processes Working Group of IUFRO.

Meeting/Workshop title	Year, Location	Publication
Linking the Complexity of Forest Canopies to Ecosystem and Landscape Function	2001, Washington and Oregon, USA	Tree Physiology 22:1035–1200 (2002)
Canopy Dynamics and Forest Management: A Missing Link?	1999, Estonia, Finland, Sweden	Tree Physiology 21:777–1013 (2001)
Forests at the Limit: Environmental Constraints on Forest Function	1997, Kruger National Park, Africa	Tree Physiology 18:491–644 (1998)
Interactive Environmental Effects on Forest Stands	1995, New Zealand	Tree Physiology 16:1–318 (1996)
Ecophysiology and Genetics of Trees and Forests in a Changing Environment	1993, Viterbo, Italy	Tree Physiology 14:659–1407 (1994)
Dynamics of Ecophysiological Processes in Tree Crowns and Forest Canopies	1989, Rhinelander, Wisconsin, USA	Tree Physiology 7:1–367 (1990)
Crown and Canopy Structure in Relation to Productivity	1985, Tsukuba, Japan	Publication of the Forestry Research Institute of Japan. ISBN 4-990058-1-3 (1986)
Advancing Towards Closed Models of Forest Ecosystems (Workshop)	1990, Granby, Colorado, USA	Tree Physiology 9:1–324 (1991)
Techniques and Approaches in Forest Tree Physiology (Workshop)	1986, Ithaca, New York, USA	Portions of the workshop were published as Lassoie and Hinckley (1991)

portunities for studies based on the measurement of stable isotope ratios. Measurements such as the carbon isotopic composition of ecosystem respiration (Fessenden and Ehleringer 2002) also integrate carbon cycling for the entire ecosystem and further promote an ecosystem viewpoint.

Current questions in canopy physiology and techniques to help answer them

One of the most useful articles I read as a graduate student was a summary of a meeting held in Alisomar, California in 1985 that presented an overview of the current problems in plant ecophysiology (Ehleringer et al. 1986). At that point in my career, much of my knowledge was based on texts, not scientific articles, and texts generally stress what we know, gloss over inconvenient gaps in knowledge and present a monolithic front of knowledge. Therefore, it was refreshing to read an opinion of what was unknown and where the large cracks were in the monolith. I was inspired by presentations and discussions at the 2001 IUFRO Canopy Processes meeting to attempt a similar synthesis for canopy processes. Additionally, our meeting highlighted some of the techniques that promise to help address current problems in canopy science, and I discuss these as well.

Influence of canopy structure on function

Canopy structure can vary greatly with species, forest age, environment and total leaf area. One of the most dramatic examples of differences in structure occurs with the development of even-aged stands (Parker 1995, Lefsky et al. 1999, Parker et al. 2002). As trees in a stand grow, the canopy structure changes from a very open and clumped organization (broadly spaced seedlings), to a uniform shallow canopy at canopy closure, and then to a complex, deep vertical structure as trees die, crowns abrade and new recruits display leaf area much lower in the canopy (Brown and Parker 1994, Parker 1995, Parker et al. 2002). The overall pattern of these structural changes occurs in widely different environments and applies to both broadleaf and evergreen tree species. Many other examples of differences in structure exist, such as savanna versus closed-canopy forest, shade-tolerant versus shade-intolerant conifers, and mesic versus dry forests.

The influence of canopy structure on radiation interception and carbon, water and energy exchange has been the focus of much research (e.g., Wang and Jarvis 1990, Law et al. 2001*a*, Baldocchi et al. 2002, Palmroth et al. 2002), but systematic study of the effect of differences in structure on fluxes has yet to be made and evaluated (but see Raulier et al. 2002 and Zweifel et al. 2002). Models have been developed that can treat three-dimensional structure in great detail (e.g., Wang and Jarvis 1990, Williams et al. 1996, Baldocchi 1997). However, most models of ecosystem fluxes treat the canopy as a simple surface (e.g., Raich et al. 1991, Running and Hunt 1993, Landsberg and Waring 1997), perhaps because no method currently exists to compensate for the effect of structural complexity in simple models of light penetration (Kull and Tulva 2002). Additionally, comparisons between complex and simple models of light penetration have shown that the simple models perform quite well (McMurtrie and Wang 1993); however, these comparisons have generally been made for simple canopies. Canopy structure may also influence the composition of stable isotopes of carbon through the influence of light flux density on photosynthesis, and by changing the isotopic composition of source air within the canopy by impeding mixing of respired CO_2 with the atmosphere (Brooks et al. 1997*a*, 1997*b*, Buchmann et al. 2002). Understanding fractionation via photosynthesis is important because stable isotopes are increasingly being used to infer ecosystem metabolism at the larger scale (Fung et al. 1997). Structural complexity is also important in creating habitat for a wide variety of canopy-dwelling plants, insects and animals, which in turn may affect carbon, water and energy exchange in yet undocumented ways (Warren et al. 2002).

Understanding the effect of canopy structure on canopy function is becoming increasingly important as we attempt to measure and model current fluxes, and their potential response to changes in climate. Land-use changes can drastically alter canopy structure (e.g., plantation forests are much simpler in structure than most natural forests), and have an important impact on the global carbon cycle.

Remote sensing from light detection and ranging (lidar), an emerging technology that uses an airborne or satellite-based laser to measure height from a surface, promises to provide detailed information on the distribution of plant canopies in three dimensions, as well as topography below the canopy (Lefsky et al. 2002). Lidar can provide high-resolution maps of tree height, cover and canopy structure, and can accurately estimate leaf area and aboveground biomass. Repeated lidar measurements should provide an excellent measure of net aboveground growth. Many types of lidar sensors exist, with differences in footprint sizes and resolution for use between the ground and canopy top. A satellite-based lidar, the Vegetation Canopy Lidar (VCL), is scheduled for launch in 2003 to inventory (with a 25-m footprint) 5% of the land surface between 68° N and 68° S (Lefsky et al. 2002).

The structural detail that lidar can provide greatly surpasses ground-based measurements. The combination of this detailed structural information and its variation in space with flux information from eddy covariance studies will provide an opportunity to advance greatly our understanding of the link between canopy structure and canopy function. The wealth of structural data soon to be available could also spur collaboration between scientists interested in structure as habitat, and those interested in relationships between structure and carbon, water and energy fluxes (one of the goals of the Global Canopy Program, http://www.globalcanopy.org).

Integration of canopy and belowground processes

Canopy processes are strongly dependent on other components of the ecosystem for water, nutrients and structure, and this insight appears to be guiding more holistic studies of canopy structure and function. For example, Brooks et al. (2002)

show that hydraulic redistribution by the root system can supply ~15% of daily sap flow in arid forests. We are also now discovering the influence of canopy function on nutrient cycling (Prescott 2002) and other belowground processes. One exciting recent innovation has been documentation of the large role of root respiration in soil respiration (Högberg et al. 2001), the rapid transfer and use of photosynthetic products below ground (Ekblad and Högberg 2001, Bowling et al. 2002), and the strong link between root processes and photosynthesis (Fitter et al. 1999). These studies show that aboveground processes should be considered when modeling soil respiration and when inferring ecosystem behavior from the $^{13}C/^{12}C$ composition of CO_2 respired from the ecosystem (Fessenden and Ehleringer 2002).

Much global change research is focused on understanding the net ecosystem storage of carbon (net ecosystem production, NEP). Net ecosystem production represents the small balance between the two large fluxes of photosynthesis and respiration (Malhi et al. 1999). The regulation of autotrophic and heterotrophic respiration is poorly understood compared with photosynthesis (Malhi et al. 1999, Thornley and Cannell 2000). Additionally, there is evidence that respiration, not photosynthesis, controls the net carbon balance on larger scales (Valentini et al. 2000). Some of the challenges in understanding NEP and respiration include: (1) solving the technical difficulties in measuring respiration with eddy covariance and obtaining reliable estimates by other methods for comparison (Lavigne et al. 1997); (2) measuring and understanding the regulation of carbon in large, slowly responding pools (soil carbon, dead wood) in response to inputs and environmental changes (Malhi et al. 1999); (3) directly assessing foliar respiration during photosynthesis (photosynthesis is currently inferred by assuming respiration during the day equals that during the night, corrected for temperature); and (4) developing a new model for the control of autotrophic respiration (see section entitled "*Carbon allocation*"). Tools such as automatic chambers for measuring soil respiration (Goulden and Crill 1997), root periscopes, ground penetrating radar (Butnor et al. 2001) and techniques for assessing the isotopic composition of ecosystem respiration (Ehleringer and Cook 1998, Fessenden and Ehleringer 2002) and estimating total belowground carbon allocation (Giardina and Ryan 2002) promise to increase our understanding of respiratory processes and the strong links between above- and belowground processes in forest ecosystems.

Carbon allocation

Understanding the rules governing carbon allocation is an enduring problem in canopy and ecosystem studies (Landsberg et al. 1991). Although the transport–resistance model seems to capture the underlying processes well (Thornley 1998), our understanding of the mechanisms that control fluxes to different components (foliage, fruits, defense compounds, branches, stems, coarse and fine roots, mycorrhizae and root exudates) and the boundaries and coordination of these fluxes remain limited (Cannell and Dewar 1994, Sprugel 2002). Understanding has been constrained by the difficulty of measuring certain fluxes (particularly those below ground), a focus on measuring existing biomass rather than fluxes (production), imprecise terminology (allocation means both the flux and the ratio of the flux to total photosynthesis), and lack of model tests, particularly in forests. For example, a conceptual priority-based model of carbon allocation (Waring and Pitman 1985) has never been rigorously tested.

Allocation to autotrophic respiration (R) appears to be conservative in mature forests (0.4–0.6 of gross photosynthesis, P) (Ryan et al. 1994, Waring et al. 1998, Cannell and Thornley 2000), and is starting to be treated as a constant in ecosystem models (e.g., Landsberg and Waring 1997). However, allocation to respiration is not likely constant (Amthor 2000, Cannell and Thornley 2000), and even a shift as small as 0.1 in the R/P ratio could have a dramatic effect on forest growth because the wood production/P ratio is only 0.1–0.25 (Ryan et al. 1994, 1996). The standard model for estimating maintenance respiration as a strict, constant tax (the growth and maintenance model) is probably incorrect (Amthor 2000, Cannell and Thornley 2000, Thornley and Cannell 2000), but it is unclear what will replace it. A new paradigm will likely incorporate substrate supply rate, contributions to respiration demand from light reactions in photosynthesis (Tissue et al. 2002), ion uptake and variable maintenance costs linked with growth (Cannell and Thornley 2000) and recognition of the efficiency of respiration (Hansen et al. 1998).

Progress in understanding carbon allocation will come by placing component measurements in the context of the entire carbon budget, testing models of allocation, understanding the limits to the plasticity of allocation and understanding the rules that define material transport, scaling and allocation in plants (Enquist et al. 1999, Enquist 2002, Enquist and Niklas 2002). Measurements of rates and their response to the environment will yield little understanding without knowing how other components of the carbon budget vary in response to the same environmental change. The large number of sites measured for carbon flux with eddy covariance (> 150 worldwide, http://www-eosdis.ornl.gov/FLUXNET/) can provide an outstanding opportunity to improve our knowledge of the regulation of carbon allocation and respiration.

Physiological changes with tree size and age

Wherever we look, we find changes in physiology with tree size and age, and some of these changes have important consequences for carbon, water and energy fluxes, and for carbon storage in terrestrial ecosystems. For example, as trees become older and taller: (1) stomatal conductance and photosynthesis tend to decrease (Schoettle 1994, Hubbard et al. 1999, Day et al. 2001); (2) redundancy in the water-conducting xylem tends to increase relative to leaf area (McDowell et al. 2002*a*); (3) specific leaf area tends to decrease (Yoder et al. 1994, Thomas and Winner 2002); (4) minimum leaf water potential decreases in some species (McDowell et al. 2002*b*); (5) respiration tends to decrease as growth decreases (Ryan and Waring 1992, Anekonda et al. 2000, Pruyn et al. 2002); and (6) water stored in the sapwood contributes an increasing fraction of daily transpiration (Waring and Running 1978, Ryan et al.

2000, Phillips et al. 2002). Despite increasing interest in the topic (Bond 2000, Bond and Franklin 2002), most physiological studies on trees (including studies of responses to elevated concentrations of CO_2 and O_3) are made on rather small, young plants. Additionally, most tree species have never been examined for age-related changes in physiology.

Some of the interesting problems in this area include: (1) understanding coordination between the properties of the water conducting system (conductivity, resistance to cavitation, capacitance) and canopy gas exchange (Jackson et al. 2000, Sperry et al. 2002); (2) the role of capacitance for both water and carbohydrates in ameliorating the physiological problems imposed by large tree size, and also in buffering environmental variability; (3) the mechanistic basis of water capacitance: how water becomes available after embolism, how embolism repair works (Zwieniecki et al. 2001), and the environmental constraints on these processes; (4) the mechanistic basis for carbohydrate storage: the capacity, turnover rate and function; (5) the energetic cost of capacitance or other age-related structural changes; and (6) how changes in tree dominance with stand development alter resource use efficiency (Binkley et al. 2002). Access to large trees with canopy cranes and comparison of component and whole-ecosystem fluxes on different age classes of the same species (Law et al. 2001*b*; see also http://www.ierm.ed.ac.uk/CARBO-AGE/HOME.htm) will improve our understanding of these processes.

Global change

Predicting the response of forest growth and forest carbon, water and energy fluxes to changes in global climate (e.g., CO_2 concentration, temperature, precipitation, atmospheric deposition and O_3) remains at the forefront of research in forest canopies (Buchmann 2002). Short-term responses to elevated CO_2 concentration (Curtis 1996, Medlyn et al. 2001), elevated O_3 concentration (Pye 1988) and elevated temperature (Saxe et al. 2001) are well understood, but longer-term acclimation and interactive effects to changes in CO_2 concentration, temperature, water and nutrients are not. Key uncertainties are the interaction of increased atmospheric CO_2 concentration with nutrition (Oren et al. 2001, Maier et al. 2002), increased O_3 concentration (King et al. 2001), temperature (Saxe et al. 2001), ontogeny (Norby et al. 1999) and other multiple interactions. Most of the uncertainties involve complex feedbacks of canopy processes with the rest of the ecosystem, including processes such as decomposition, belowground allocation and nutrient cycling that have much longer time constants than canopy responses (Norby et al. 1999). Progress in understanding these longer-term interactions will come from large-scale ecosystem experiments in forests (FACE) and long-term, high-frequency estimates of ecosystem–atmosphere fluxes (Goulden et al. 1996, Hadley 2002), coupled with measurements of internal fluxes and changes in pools (Barford et al. 2001).

Linking canopy physiology and canopy structure with genetic information

Toby Bradshaw of the University of Washington gave a provocative talk at the 2001 IUFRO Canopy Processes meeting on the potential for increased wood and fiber yield from forests based on "domesticating" trees. Of all the crops grown for human use, trees are probably closest to their wild genotypes. In contrast, crops such as maize have been extensively modified from their wild ancestors to increase yields many thousands of times. Dr. Bradshaw challenged our group to use our expertise to imagine the structure and function of a model domesticated tree (for additional information and a discussion of some of the challenges of this approach, see Martin et al. 2001). Because natural selection favors reproductive success and longevity, trees invest much of their carbon into foliage and roots to acquire resources, to reproduce and to synthesize defensive compounds. Even trees selected for superior growth and supplied with ample water and nutrients allocate only 25–30% of annual net photosynthesis to aboveground wood production (J.L. Stape, University of São Paulo, Piracicaba, Brazil, personal communication). A model domesticated tree might have comparatively few roots and foliage and grow out instead of up so that crowns would not compete for light or prune branches by the mechanical action of wind. A short review of tree domestication and how it might be implemented is given in Mann (2002).

Scaling ecophysiological processes and modeling

Much research on canopy processes is focused on predicting behavior at scales larger than the shoot, and for long time periods. Predicting how forests will grow and respond to global change, and how vegetation affects local and regional weather are problems that require information at the canopy, ecosystem, landscape, regional and global scales for time periods of years to centuries. Yet most measurements occur at small scales in space and time, and extrapolating knowledge gained at such scales remains a formidable challenge (Ehleringer and Field 1993).

Much progress in scaling has been made in the past two decades. Within the canopy, the short-term environmental regulation of photosynthesis, evapotranspiration and energy balance is relatively well understood at the leaf level and for simple canopies (Landsberg and Gower 1997). For scaling from the canopy to the landscape, leaf area and leaf area index are useful measures because leaf area regulates and controls many ecosystem fluxes that can be assessed at the landscape scale by remote sensing (Waring and Running 1998). Leaf area estimates derived from remote sensing and linked with climate data have been used to generate many useful regional and global estimates, e.g., regional drought assessments, global patterns of net primary production, and regional water balance (Waring and Running 1998).

Increased understanding of the scaling of canopy processes has been brought about by: (1) the proliferation of sites measuring carbon, water and energy exchanges with eddy covariance, e.g., Euroflux (http://www.unitus.it/dipartimenti/disafri/progetti/eflux/euro.html), Ameriflux (http://public.ornl.gov/ameriflux/) and Fluxnet (Baldocchi et al. 2001); (2) measurements made at multiple scales (e.g., Rayment et al. 2002); (3) two large interdisciplinary studies focused on scaling canopy measurements in forests to landscapes, BOREAS (Margolis and Ryan 1997, Sellers et al. 1997, Hall 1999, Hall 2001) and LBA (http://lba-ecology.gsfc.nasa.gov/lbaeco/); and (4) the development, validation and expansion in the use of models (Ågren et al. 1991, VEMAP Members 1995, Waring and Running 1998, Amthor et al. 2001). Models, often validated with eddy covariance data (e.g., Kramer et al. 2002), are now being used to make canopy, regional and global estimates of carbon, water and energy fluxes (e.g., DeFries et al. 1999, Nemani et al. 2002).

Many challenges remain before reliable, long-term large-scale predictions of ecosystem fluxes are a reality including: (1) assessing current conditions through landscape inventories of species or functional groups, and carbon and nutrient stocks in biomass, soil dead wood and litter; (2) understanding how disturbance and changes in land use alter species or functional groups, processes and stocks across a landscape, and simulating fluxes for the resulting mixed forests of different ages and species; (3) understanding what regulates ecosystem fluxes at longer time scales; and (4) integrating more detailed understanding of processes into models, particularly the distribution of nutrients, photosynthetic capacity, and light within the canopy, age and height and autotrophic and heterotrophic respiration.

Concluding remarks

This brief overview of past and current research in canopy science shows that much progress has been made over the past 20 years, but many fundamental problems remain to be solved. Important processes have been identified, and models and measurements are converging for short-term, homogeneous canopies and forest ecosystems. However, determining the appropriate complexity for non-ideal ecosystems, and reliably predicting fluxes across space and time remain challenges.

Interest in forest canopies will likely continue to expand because of their importance in the global carbon cycle and their role in fiber production. Future research in canopy processes will increasingly integrate other components of the ecosystem, and will make use of highly sophisticated tools for experimentation, measurement and modeling. Future canopy scientists will need to continue to develop an interdisciplinary mindset to recognize and explore important linkages, continue to use advances in other fields and continue to promote the development of new techniques and equipment to elucidate the complexities of canopy science.

Acknowledgments

The 2001 IUFRO Canopy Processes conference organizing committee deserves many thanks for their ideas and help (Barbara Bond, Renée Brooks, Tom Hinckley, Beverly Law, Rick Meinzer, Al Mitchell, Doug Sprugel, and Richard Waring), as do Mike Cloughesy and his staff for logistical support. The conference thanks our meeting sponsors (Oregon State University, USDA Forest Service Rocky Mountain Research Station, NASA, NCASI, and IUFRO) for their generous support. I am also grateful to Jud Isebrands, David Whitehead, and Sune Linder for their tremendous support for the Working Group on Canopy Processes over the past 20 years, and I thank *Tree Physiology* for their long-term relationship with our group. I appreciate helpful suggestions on this manuscript from David Whitehead, Renée Brooks, Barbara Bond, Anna Schoettle, and Richard Waring.

References

Ågren, G.I., R.E. McMurtrie, W.J. Parton, J. Pastor and H.H. Shugart. 1991. State-of-the-art of models of production–decomposition linkages in conifer and grassland ecosystems. Ecol. Appl. 1:118–138.

Amthor, J.S. 2000. The McCree–de Wit–Penning de Vries–Thornley respiration paradigms: 30 years later. Ann. Bot. 86:1–20.

Amthor, J.S., J.M. Chen, J.S. Cleiny et al. 2001. Boreal forest CO_2 exchange and evapotranspiration predicted by nine ecosystem process models: intermodel comparisons and relationships to field measurements. J. Geophys. Res. Atmos. 106:33,623–33,648.

Anekonda, T.S., R.S. Criddle, M.J. Bacca and L.D. Hansen. 2000. Influence of age on dark respiration in eucalypts. Therm. Acta 343:11–17.

Baldocchi, D. 1997. Measuring and modelling carbon dioxide and water vapour exchange over a temperate broad-leaved forest during the 1995 summer drought. Plant Cell Environ. 20:1108–1122.

Baldocchi, D., E. Falge, L.H. Gu et al. 2001. FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. Bull. Am. Meteorol. Soc. 82:2415–2434.

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

Baldocchi, D.D., K.B. Wilson and L. Gu. 2002. How the environment, canopy structure and canopy physiological functioning influence carbon, water and energy fluxes of a temperate broad-leaved deciduous forest—an assessment with the biophysical model CANOAK. Tree Physiol. 22:1065–1077.

Barford, C.C., S.C. Wofsy, M.L. Goulden, J.W. Munger, E.H. Pyle, S.P. Urbanski, L. Hutyra, S.R. Saleska, D. Fitzjarrald and K. Moore. 2001. Factors controlling long- and short-term sequestration of atmospheric CO_2 in a mid-latitude forest. Science 294: 1688–1691.

Binkley, D., J.L. Stape, M.G. Ryan, H.R. Barnard and J.H. Fownes. 2002. Age-related decline in forest ecosystem growth: an individual-tree, stand-structure hypothesis. Ecosystems 5:58–67.

Bond, B.J. 2000. Age-related changes in photosynthesis of woody plants. Trends Plant Sci. 5:349–353.

Bond, B.J. and J.F. Franklin. 2002. Aging in Pacific Northwest forests: a selection of recent research. Tree Physiol. 22:73–76.

Bowling, D.R., N.G. McDowell, B.J. Bond, B.E. Law and J.R. Ehleringer. 2002. ^{13}C content of ecosystem respiration is linked to precipitation and vapor pressure deficit. Oecologia 131:113–124.

Brooks, J.R., L.B. Flanagan, N. Buchmann and J.R. Ehleringer. 1997*a*. Carbon isotope composition of boreal plants: functional grouping of life forms. Oecologia 110:301–311.

Brooks, J.R., L.B. Flanagan, G.T. Varney and J.R. Ehleringer. 1997*b*. Vertical gradients in photosynthetic gas exchange characteristics and refixation of respired CO_2 within boreal forest canopies. Tree Physiol. 17:1–12.

Brooks, J.R., F.C. Meinzer, R. Coulombe and J. Gregg. 2002. Hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests. Tree Physiol. 22: 1107–1117.

Brown, M.J. and G.G. Parker. 1994. Canopy light transmittance in a chronosequence of mixed-species deciduous forests. Can. J. For. Res. 24:1694–1703.

Buchmann, N. 2002. Plant ecophysiology and forest response to global change. Tree Physiol. 22:1177–1184.

Buchmann, N., J.R. Brooks and J.R. Ehleringer. 2002. Predicting daytime carbon isotope ratios of atmospheric CO_2 within forest canopies. Funct. Ecol. 16:49–57.

Butnor, J.R., J.A. Doolittle, L. Kress, S. Cohen and K.H. Johnsen. 2001. Use of ground-penetrating radar to study tree roots in the southeastern United States. Tree Physiol. 21:1269–1278.

Cannell, M.G.R. and R.C. Dewar. 1994. Carbon allocation in trees: a review of concepts for modelling. Adv. Ecol. Res. 25:59–104.

Cannell, M.G.R. and J.H.M. Thornley. 2000. Modelling the components of plant respiration: some guiding principles. Ann. Bot. 85:45–54.

Curtis, P.S. 1996. A meta-analysis of leaf gas exchange and nitrogen in trees grown under elevated carbon dioxide. Plant Cell Environ. 19:127–137.

Day, M.E., M.S. Greenwood and A.S. White. 2001. Age-related changes in foliar morphology and physiology in red spruce and their influence on declining photosynthetic rates and productivity with tree age. Tree Physiol. 21:1195–1204.

DeFries, R.S., C.B. Field, I. Fung, G.J. Collatz and L. Bounoua. 1999. Combining satellite data and biogeochemical models to estimate global effects of human-induced land cover change on carbon emissions and primary productivity. Global Biogeochem. Cycle 13:803–815.

Ehleringer, J.R. and C.S. Cook. 1998. Carbon and oxygen isotope ratios of ecosystem respiration along an Oregon conifer transect: preliminary observations based on small-flask sampling. Tree Physiol. 18:513–519.

Ehleringer, J.R. and C.B. Field. 1993. Scaling ecophysiological processes: leaf to globe. Academic Press, San Diego, 388 p.

Ehleringer, J., R.W. Pearcy and H.A. Mooney. 1986. Recommendations of the workshop on the future development of plant physiological ecology. Bull. Ecol. Soc. Am. 67:48–58.

Ekblad, A. and P. Högberg. 2001. Natural abundance of ^{13}C in CO_2 respired from forest soils reveals speed of link between tree photosynthesis and root respiration. Oecologia 127:305–308.

Enquist, B.J., G.B. West, E.L. Charnov and J.H. Brown. 1999. Allometric scaling of production and life-history variation in vascular plants. Nature 401:907–911.

Enquist, B.J. 2002. Universal scaling in tree and vascular plant allometry: toward a general quantitative theory of linking plant form and function from cells to ecosystems. Tree Physiol. 22: 1045–1064.

Enquist, B.J. and K.J. Niklas. 2002. Global allocation rules for patterns of biomass partitioning in seed plants. Science 295: 1517–1520.

Fessenden, J.E. and J.R. Ehleringer. 2002. Age-related variations in $\delta^{13}C$ of ecosystem respiration across a coniferous forest chronosequence in the Pacific Northwest. Tree Physiol. 22:159–167.

Fitter, A.H., G.K. Self, T.K. Brown, D.S. Bogie, J.D. Graves, D. Benham and P. Ineson. 1999. Root production and turnover in an upland grassland subjected to artificial soil warming respond to radiation flux and nutrients, not temperature. Oecologia 120:575–581.

Fujimori, T. and D. Whitehead. 1986. Crown and canopy structure in relation to productivity. Forestry and Forest Products Research Institute, Ibaraki, Japan, 448 p.

Fung, I., C.B. Field, J.A. Berry et al. 1997. Carbon 13 exchanges between the atmosphere and biosphere. Global Biogeochem. Cycles 11:507–533.

Giardina, C.P. and M.G. Ryan. 2002. Total belowground carbon allocation in a fast growing *Eucalyptus* plantation estimated using a carbon balance approach. Ecosystems 5:487–499.

Goulden, M.L. and P.M. Crill. 1997. Automated measurements of CO_2 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.

Goulden, M.L., S.C. Wofsy, J.W. Harden et al. 1998. Sensitivity of boreal forest carbon balance to soil thaw. Science 279:214–217.

Hadley, J.L. and J.L. Schedlbauer. 2002. Carbon exchange of an old-growth eastern hemlock (*Tsuga canadensis*) forest in central New England. Tree Physiol. 22:1079–1092.

Hall, F.G. 1999. Introduction to special section: BOREAS in 1999: experiment and science overview. J. Geophys. Res. Atmos. 104: 27,627–27,639.

Hall, F.G. 2001. Introduction to special section: BOREAS III. J. Geophys. Res. Atmos. 106:33,511–33,516.

Hansen, L.D., R.W. Breidenbach, B.N. Smith, J.R. Hansen and R.S. Criddle. 1998. Misconceptions about the relation between plant growth and respiration. Bot. Acta 111:255–260.

Högberg, P., A. Nordgren, N. Buchmann, A.F.S. Taylor, A. Ekblad, M.N. Hogberg, G. Nyberg, M. Ottosson-Lofvenius and D.J. Read. 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411:789–792.

Hubbard, R.M., B.J. Bond and M.G. Ryan. 1999. Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. Tree Physiol. 19:165–172.

Jackson, R.B., J.S. Sperry and T.E. Dawson. 2000. Root water uptake and transport: using physiological processes in global predictions. Trends Plant Sci. 5:482–488.

King, J.S., K.S. Pregitzer, D.R. Zak, J. Sober, J.G. Isebrands, R.E. Dickson, G.R. Hendrey and D.F. Karnosky. 2001. Fine-root biomass and fluxes of soil carbon in young stands of paper birch and trembling aspen as affected by elevated atmospheric CO_2 and tropospheric O_3. Oecologia 128:237–250.

Kramer, K., I. Leinonen, H.H. Bartelink et al. 2002. Evaluation of six process-based forest growth models using eddy-covariance measurements of CO_2 and H_2O fluxes at six forest sites in Europe. Global Change Biol. 8:213–230.

Kull, O. and I. Tulva. 2002. Shoot structure and growth along a vertical profile within a *Populus–Tilia* canopy. Tree Physiol. 22: 1167–1175.

Landsberg, J.J. and S.T. Gower. 1997. Applications of physiological ecology to forest management. Academic Press, San Diego, 354 p.

Landsberg, J.J. and R.H. Waring. 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. For. Ecol. Manage. 95:209–228.

Landsberg, J.J., M.R. Kaufmann, D. Binkley, J. Isebrands and P.G. Jarvis. 1991. Evaluating progress toward closed forest models based on fluxes of carbon, water, and nutrients. Tree Physiol. 9:1–15.

Lassoie, J.P. and T.M. Hinckley. 1991. Techniques and approaches in forest tree ecophysiology. CRC Press, Boston, 616 p.

Lavigne, M.B., M.G. Ryan, D.E. Anderson et al. 1997. Comparing nocturnal eddy covariance measurements to estimates of ecosystem respiration made by scaling chamber measurements. J. Geophys. Res. 102(D24):28,977–28,986.

Law, B.E., A. Cescatti and D.D. Baldocchi. 2001*a*. Leaf area distribution and radiative transfer in open-canopy forests: implications for mass and energy exchange. Tree Physiol. 21:777–788.

Law, B.E., P.E. Thornton, J. Irvine, P.M. Anthoni and S. Van Tuyl. 2001*b*. Carbon storage and fluxes in ponderosa pine forests at different developmental stages. Global Change Biol. 7:755–777.

Lefsky, M.A., D.J. Harding, W.B. Cohen, G.G. Parker and H.H. Shugart. 1999. Surface lidar remote sensing of basal area and biomass in deciduous forests of eastern Maryland, USA. Remote Sens. Environ. 67:83–98.

Lefsky, M.A., W.B. Cohen, G.G. Parker and D.J. Harding. 2002. Lidar remote sensing for ecosystem studies. BioScience 52:19–30.

Maier, C.A., K.H. Johnsen, J. Butnor, L.W. Kress and P.H. Anderson. 2002. Branch growth and gas exchange in 13-year-old loblolly pine (*Pinus taeda*) trees in response to elevated carbon dioxide concentration and fertilization. Tree Physiol. 22:1093–1106.

Malhi, Y., D.D. Baldocchi and P.G. Jarvis. 1999. The carbon balance of tropical, temperate and boreal forests. Plant Cell Environ. 22: 715–740.

Mann, C.C. and M.L. Plummer. 2002. Biotechnology: forest biotech edges out of the lab. Science 295:1626–1629.

Margolis, H.A. and M.G. Ryan. 1997. A physiological basis for biosphere–atmosphere interactions in the boreal forest: an overview. Tree Physiol. 17:491–499.

Martin, T.A., K.H. Johnsen and T.L. White. 2001. Ideotype development in southern pines: rationale and strategies for overcoming scale-related obstacles. For. Sci. 47:21–28.

McDowell, N.G., H.R. Barnard, B.J. Bond et al. 2002*a*. The relationship between tree height and leaf area:sapwood area ratio. Oecologia 132:12–20.

McDowell, N.G., N. Phillips, C. Lunch, B.J. Bond and M.G. Ryan. 2002*b*. An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. Tree Physiol. 22:763–774.

McMurtrie, R.E. and Y.P. Wang. 1993. Mathematical-models of the photosynthetic response of tree stands to rising CO_2 concentrations and temperatures. Plant Cell Environ. 16:1–13.

Medlyn, B.E., C.V.M. Barton, M.S.J. Broadmeadow et al. 2001. Stomatal conductance of forest species after long-term exposure to elevated CO_2 concentration: a synthesis. New Phytol. 149: 247–264.

Nemani, R., M. White, P. Thornton, K. Nishida, S. Reddy, J. Jenkins and S. Running. 2002. Recent trends in hydrologic balance have enhanced the terrestrial carbon sink in the United States. Geophys. Res. Let. 29:10.1029/2002GL014867.

Norby, R.J., S.D. Wullschleger, C.A. Gunderson, D.W. Johnson and R. Ceulemans. 1999. Tree responses to rising CO_2 in field experiments: implications for the future forest. Plant Cell Environ. 22: 683–714.

Oren, R., D.S. Ellsworth, K.H. Johnsen, N. Phillips, B.E. Ewers, C. Maier, K.V.R. Schafer, H. McCarthy, G. Hendrey, S.G. McNulty and G.G. Katul. 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO_2-enriched atmosphere. Nature 411:469–472.

Palmroth, S., P. Stenberg, S. Smolander, P. Voipio and H. Smolander. 2002. Fertilization has little effect on light-interception efficiency of *Picea abies* shoots. Tree Physiol. 22:1185–1192.

Parker, G.G. 1995. Structure and microclimate of forest canopies. *In* Forest Canopies. Eds. M.D. Lowman and N.N. Nadkarni. Academic Press, San Diego, pp 73–106.

Parker, G.G., M.M. Davis and S.M. Chapotin. 2002. Canopy light transmittance in Douglas-fir–western hemlock stands. Tree Physiol. 22:147–157.

Phillips, N., B.J. Bond, N.G. McDowell and M.G. Ryan. 2002. Canopy and hydraulic conductance in young, mature and old Douglas-fir trees. Tree Physiol. 22:205–211.

Prescott, C.E. 2002. The influence of the forest canopy on nutrient cycling. Tree Physiol. 22:1193–1200.

Pruyn, M.L., B.L. Gartner and M.E. Harmon. 2002. Respiratory potential in sapwood of old versus young ponderosa pine trees in the Pacific Northwest. Tree Physiol. 22:105–116.

Pye, J.M. 1988. Impact of ozone on the growth and yield of trees—a review. J. Environ. Qual. 17:347–360.

Raich, J.W., E.B. Rastetter, J.M. Melillo, D.W. Kicklighter, P.A. Steudler, B.J. Peterson, A.L. Grace, B. Moore, III and C.J. Vorosmarty. 1991. Potential net primary productivity in South America: application of a global model. Ecol. Appl. 1:399–429.

Raulier, F., P.Y. Bernier, C.-H. Ung and R. Boutin. 2002. Structural differences and functional similarities between two sugar maple (*Acer saccharum*) stands. Tree Physiol. 22:1147–1156.

Rayment, M.B., D. Loustau and P.G. Jarvis. 2002. Photosynthesis and respiration of black spruce at three organizational scales: shoot, branch and canopy. Tree Physiol. 22:219–229.

Running, S.W. and E.R. Hunt, Jr. 1993. Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an application for global-scale models. *In* Scaling Physiological Processes: Leaf to Globe. Eds. J.R. Ehleringer and C.B. Field. Academic Press, San Diego, pp 141–158.

Ryan, M.G. and R.H. Waring. 1992. Maintenance respiration and stand development in a subalpine lodgepole pine forest. Ecology 73:2100–2108.

Ryan, M.G., S. Linder, J.M. Vose and R.M. Hubbard. 1994. Dark respiration in pines. *In* Environmental Constraints on the Structure and Productivity of Pine Forest Ecosystems: A Comparative Analysis. Eds. H.L. Gholz, S. Linder and R.E. McMurtrie. Ecol. Bull. 43:50–63.

Ryan, M.G., R.M. Hubbard, S. Pongracic, R.J. Raison and R.E. McMurtrie. 1996. Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nutrient status. Tree Physiol. 16:333–343.

Ryan, M.G., B.J. Bond, B.E. Law, R.M. Hubbard, D. Woodruff, E. Cienciala and J. Kucera. 2000. Transpiration and whole-tree conductance in ponderosa pine trees of different heights. Oecologia 124:553–560.

Saxe, H., M.G.R. Cannell, O. Johnsen, M.G. Ryan and G. Vourlitis. 2001. Tree and forest functioning in response to global warming. New Phytol. 149:369–399.

Schoettle, A.W. 1994. Influence of tree size on shoot structure and physiology of *Pinus contorta* and *Pinus aristata*. Tree Physiol. 14:1055–1068.

Sellers, P.J., F.G. Hall, R.D. Kelly et al. 1997. BOREAS in 1997: experiment overview, scientific results, and future directions. J. Geophys. Res. Atmos. 102:28,731–28,769.

Sperry, J.S., U.G. Hacke, R. Oren and J.P. Comstock. 2002. Water deficits and hydraulic limits to leaf water supply. Plant Cell Environ. 25:251–263.

Sprugel, D.G. 2002. When branch autonomy fails: Milton's Law of resource availability and allocation. Tree Physiol. 22:1119–1124.

Thomas, S.C. and W.E. Winner. 2002. Photosynthetic differences between saplings and adult trees: an integration of field results by meta-analysis. Tree Physiol. 22:117–127.

Thornley, J.H.M. 1998. Modelling shoot:root relations: the only way forward? Ann. Bot. 81:165–171.

Thornley, J.H.M. and M.G.R. Cannell. 2000. Modelling the components of plant respiration: representation and realism. Ann. Bot. 85:55–67.

Tissue, D.T., J.D. Lewis, S.D. Wullschleger, J.S. Amthor, K.L. Griffin and O.R. Anderson. 2002. Leaf respiration at different canopy positions in sweetgum (*Liquidambar styraciflua*) grown in ambient and elevated concentrations of carbon dioxide in the field. Tree Physiol. 22:1157–1166.

Valentini, R., G. Matteucci, A.J. Dolman et al. 2000. Respiration as the main determinant of carbon balance in European forests. Nature 404:861–865.

VEMAP Members. 1995. Vegetation/ecosystem modeling and analysis project: comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO_2 doubling. Global Biogeochem. Cycle 9: 407–437.

Wang, Y.P. and P.G. Jarvis. 1990. Description and validation of an array model–MAESTRO. Agric. For. Meteorol. 51:257–280.

Waring, R.H. and S.W. Running. 1978. Sapwood water storage: its contribution to transpiration and effect upon water conductance through the stems of old-growth Douglas-fir. Plant Cell Environ. 1: 131–140.

Waring, R.H. and S.W. Running. 1998. Forest ecosystems: analysis at multiple scales. Academic Press, San Diego, 370 p.

Waring, R.H. and G.B. Pitman. 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. Ecology 66:889–897.

Waring, R.H., J.J. Landsberg and M. Williams. 1998. Net primary production of forests: a constant fraction of gross primary production? Tree Physiol. 18:129–134.

Warren, J.M., J.H. Bassman and S. Eigenbrode. 2002. Leaf chemical changes induced in *Populus trichocarpa* by enhanced UV-B radiation and concomitant effects on herbivory by *Chrysomela scripta* (Coleoptera: Chrysomelidae). Tree Physiol. 22:1137–1146.

Williams, M., E.B. Rastetter, D.N. Fernandes et al. 1996. Modelling the soil–plant–atmosphere continuum in a *Quercus–Acer* stand at Harvard Forest: the regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties. Plant Cell Environ. 19: 911–927.

Yoder, B.J., M.G. Ryan, R.H. Waring, A.W. Schoettle and M.R. Kaufmann. 1994. Evidence of reduced photosynthetic rates in old trees. For. Sci. 40:513–527.

Zweifel, R., J.P. Böhm and R. Häsler. 2002. Midday stomatal closure in Norway spruce—reactions in the upper and lower crown. Tree Physiol. 22:1125–1136.

Zwieniecki, M.A., P.J. Melcher and N.M. Holbrook. 2001. Hydrogel control of xylem hydraulic resistance in plants. Science 291: 1059–1062.