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ECOSYSTEMS

SPECIAL FEATURE INTRODUCTION

Carbon Dynamics of an Old-growth Forest

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INTRODUCTION

Efforts are under way to evaluate the carbon storage capacity for a variety of terrestrial ecosystems in the United States [for example, see Canadell and others (2000) and Schimel and others (2000)]. The distribution and strengths of terrestrial carbon sources and sinks have gained increasing attention in recent years because of their relevance to changes in atmospheric carbon dioxide (CO_2) concentrations (Pacala and others 2001; Wofsy 2001) and because this information has significant implications for national and international carbon cycle policy. The AmeriFlux and FLUXNET Networks of carbon-flux measurement stations distributed throughout the globe were established as part of this effort (Kaiser 1998; Buchmann and Schulze 1999; Canadell and others 2000). Improving the accuracy of forest carbon-sequestration estimates will lessen the international controversy over carbon-accounting systems and carbon trading. Finally, better process-level understanding may enable the use of these systems in an "early warning" capacity. Although flux networks provide a basis for quantifying the magnitude of fluxes, they do not explain the environmental controls over these processes. We still lack fundamental information on the carbon dynamics of various ecosystem types, especially for mature forests, due to the difficulty in making direct measurements. Here we focus on measurements from an old-growth conifer forest to develop a baseline for understanding the consequences of human-induced landscape changes on carbon dynamics.

The dynamics of carbon exchange and storage within old-growth forests remain poorly understood. Thus, it is important to document the functioning of mature forests, especially for carbon cycling, and interactions with the surrounding biosphere to understand the consequences of shifting age-class distributions to younger aged stands. Because of their enormous biomass, both aboveground and belowground, old-growth systems play a significant role in regional/global carbon budgets and are simultaneously an important resource to the forest products industry. Although currently comprising only about 3.5 million acres (approximately 10%) of the forested landscape of the Pacific Northwest (USA) (compared with 32%–70% of historic coverage), they provide insights on the importance of structure and age on carbon balance, especially when compared to allocation processes in younger aged stands. Understanding the full range of carbon budgets is an important step to implementing carbon-management recommendations of the United Nations Committee of the Parties (COP) (http://unfccc.int/resource/docs/convkp/kpeng.pdf) at Kyoto (IGBP Terrestrial Carbon Working Group 1998), Buenos Aires, the

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Hague, Bonn (Royden 2001), Marrakech, New Delhi and Milan.

For decades, it has been assumed that old-growth forests are at or near equilibrium with respect to carbon exchange between the forest and the atmosphere (Odum 1953, 1963; DeBell and Franklin 1987; Franklin and DeBell 1988; Ryan and others 1997; Waring and Running 1998). Results from recent studies, however, vary widely and imply a more dynamic relationship with age. In a review by Buchmann and Schulze (1999) of 41 forest studies, only 28 (including data on broad-leaved and coniferous stands up to approximately 300 years of age) included information on stand age. For those 28 studies, results suggest that net ecosystem flux rates of CO_2 were lowest in young stands (less than 20 years old, but with some notable exceptions), highest in stands of intermediate age (30–80 years), and intermediate rather than negligible in forests older than 160 years.

The Wind River Old-growth Forest

We report on a series of interdisciplinary ecosystem studies begun in 1996 that elucidate the carbon dynamics of the 500-year-old Wind River old-growth forest located in the T. T. Munger Research Natural Area of the Gifford Pinchot National Forest in southern Washington, and the site of the Wind River Canopy Crane Research Facility (WRCCRF) (see Shaw and others 2004). The availability of a 75-m-tall construction crane within this old-growth forest presents a valuable opportunity to obtain measurements within and throughout the three-dimensional space of the entire canopy over a 2.3-ha area embedded within a much larger old-growth stand (approximately 500 ha). This site is the oldest forest ecosystem participating in the AmeriFlux Network of carbon flux measurement sites (Kaiser 1998; Buchmann and Schulze 1999).

The Wind River old-growth forest lies at the extremes of several gradients of organization for temperate forests: age, biomass, height, leaf-area index (LAI), structural complexity, gross primary production (GPP), and low albedo, but is quite representative of this type of forest in the Pacific Northwest region, especially with respect to general species composition and physical/biological organization. Empirical data have shown that the Pacific Northwest region has the highest levels of potential carbon accumulation of any forest region in the world, including tropical forests (Franklin and Waring 1980). And recent ecosystem model intercomparisons (Schimel and others 2000) suggest that the Pacific Northwest is the bioclimatic region within the continental United States that has the greatest potential to sequester additional net carbon storage. For these reasons, the Wind River old-growth forest provides an extremely valuable opportunity to examine how a forest of this stature interfaces with its physical and biological environment, especially with respect to the cycling of carbon. Because many authors have hypothesized that old-growth forests are at equilibrium with respect to carbon balance, we need to investigate more thoroughly the validity of these hypotheses and the age at which forests become nonproductive. The integrated research at the Wind River old-growth forest site provides an unusual opportunity to compare fluxes, process, and inventory data with other temperate forests in North America and Eurasia.

The articles that follow have used environmental data, forest structural and physiological measurements, models, eddy-covariance measurements, and remote sensing techniques to provide the most complete view to date of carbon balance for an old-growth forest. The species composition of this forest is typical of many other Pacific Northwest forests, yet because of its age, stature, and structure provides the opportunity to document carbon dynamics for an old-growth forest. In addition, a diversity of approaches to measuring the carbon budget in this forest enables a comparison between traditional ecological methods and eddy covariance.

Integrated Studies at Wind River

The physical, geological, climatological, and basic biological setting of the Wind River old-growth forest, described by Shaw and colleagues (2004), forms the foundation for the studies described in this special feature. Specifically, their database ensures that consistent information on site conditions exists for all other studies. Foundation data for a 4-ha plot immediately surrounding the canopy crane includes carbon (C) and nitrogen concentrations in forest litter and soil, dominant plant associations, and densities, heights, basal area, and DBH (diameter at breast height) for all (live and dead standing) tree species.

Equally fundamental are the three-dimensional structural components reported by Parker and colleagues (2004) that include data on the vertical distribution of the canopy. These data contribute to a greater understanding of how the architecture of the forest affects the fluxes and storage of carbon. In addition, Parker and colleagues (2004) quantify the topography of the outer canopy surface area. The range of values obtained using different approaches for measuring/quantifying LAI and vertical structure has significant implications for cross-site comparisons and highlights the need to develop standard methodologies.

Photosynthetic CO_2 uptake is largely light limited in Pacific Northwest forests, and the complex vertical structure of the canopy makes scaling leaf measurements to the canopy difficult or impossible. Recently it has become possible to model the transmission of photosynthetically active radiation (PAR) light in a three-dimensional canopy to evaluate CO_2 fluxes. Mariscal and colleagues (2004) used two spatially explicit radiative transfer models with empirical data from three-dimensional profiles for every crown in the 4-ha plot around the crane to simulate the vertical PAR transmission in this system. The results agree with observations of vertical profiles at specific locations and with canopy measurements of albedo. These model simulations can be used to test our understanding of the light environment within the canopy and its significance for controlling physiological productivity at new sites.

Availability of soil water in summer months is a significant factor controlling the overall annual carbon budget. Integrated experimental data elucidate diurnal variations in evapotranspiration and processes controlling ecosystem water use for dominant tree species and the relative contributions of water flux from understory, lichens, mosses, and coarse woody debris (Unsworth and others 2004).

Ecosystem constraints of light and water availability are further explored at the leaf level for physiological processes that regulate carbon gain and water loss for dominant tree species (Douglas-fir, western hemlock and western red cedar) at different vertical positions within the canopy by Winner and colleagues (2004). They quantify net losses of carbon from this forest by emissions of volatile biogenic hydrocarbons (specifically terpenes). These leaf-level data are then used to scale fluxes to the canopy level and to estimate annual latent heat flux and GPP by using a physiologically based process model, MBL-SPA. Within-crown PAR estimates by Mariscal and colleagues (2004) predict that most crowns are near photosynthetic saturation as observed by Winner and colleagues (2004) during all but winter months. Despite declining soil moisture levels during summer (Unsworth and others 2004), Winner and colleagues (2004) show that Douglas-fir maintains constant midday minimum water potentials, indicating regulation of transpiration and water-use efficiency, consistent with patterns observed elsewhere in conifers.

Other contrasting approaches with vastly different assumptions also have been used to estimate productivity for this forest. A classical ground-based allometric approach was used by Harmon and colleagues (2004) to estimate changes in aboveground carbon stores [see Field and Kaduk (2004, Figure 3) for a description of carbon pools]. Carbon-store contributions from epiphytes, live and dead fine-root biomass, coarse and fine woody detritus, soil carbon, and decomposition rates were estimated. Harmon and colleagues (2004) calculated GPP, autotrophic respiration (R_a), heterotrophic respiration (R_h), net primary production (NPP), and net ecosystem production (NEP). These calculations were used in a Monte Carlo simulation to yield a long-term probability estimate of NEP from −116 to +156 (mean = 20) g C m^{-2} y^{-1}, which indicates, for the mean value of this range, that the Wind River old-growth forest may be a small carbon sink.

A micrometerological approach was employed by Paw U and colleagues (2004), who applied eddy-covariance techniques to measure the exchange of CO_2 between the forest and the atmosphere to produce an estimate of net ecosystem exchange (NEE). They estimated NEE (by using a 0.21 advection correction) at +20 to +360 (mean = 190) g C m^{-2} y^{-1}, which overlaps considerably with the estimates of Harmon and colleagues (2004). In contrast to the inherently longer period of integration in the allometric approach (Harmon and others 2004), Paw U and colleagues (2004) demonstrate sensitivity of carbon sequestration to climate conditions at seasonal and interannual scales. They also note that, despite extreme winter cold and summer drought, there was no extended period in which carbon sequestration did not occur.

These approaches were further compared by Field and Kaduk (2004) in an evaluation of three independent approaches for estimating the carbon balance of the Wind River forest: (a) the leaf model approach (Winner and others 2004), (b) the ground-based allometric approach (Harmon and others 2004), and (c) the micrometeorologic eddy-covariance approach (Paw U and others 2004). The initial results of these three approaches, which span significantly different spatial and temporal scales and diverse methodologies, appear to be moderately consistent (within an order of magnitude), but with some unique differences that permit differing conclusions. By all approaches considered, Field and Kaduk (2004) place this old-growth forest near the high end of GPP for temperate forests. As noted, NPP is also at the high end for temperate forests (Franklin and Waring 1980).

The magnitude of differences in carbon fluxes between young and old forests was explored by Chen and colleagues (2004). Using a micrometeorologic eddy-covariance approach comparable to that of Paw U and colleagues (2004), they compared the Wind River old-growth stand with two nearby similarly structured younger forests (20 and 40 years old) during July to September for NEE, CO_2, and water exchanges. During this period, all three can be net carbon sinks, even during dry warm summers, with the 40-year-old stand exhibiting the greatest net carbon assimilation and losing the least water through evapotranspiration.

The Wind River Valley landscape is a complex mosaic of forests of widely varying age classes and other nonforest land-cover types that inhibits ready extrapolation of carbon budgets to the regional level. Roberts and colleagues (2004) explored the factors controlling spectral variability at leaf, branch, and stand levels to the regional scale to improve the use of these data in regional carbon estimates. Data from an airborne visible infrared imaging spectrometer (AVIRIS) provided three remotely sensed structural measures: (a) the normalized difference vegetation index (NDVI), (b) cover fractions derived from spectral mixture analysis (SMA), and (c) equivalent water thickness (EWT). At the leaf scale, there were significant differences between conifers and broadleaf species, but differences were not distinguishable at the species level. In contrast, at the branch scale, most species were distinct, although conifers were less so than broadleaf species. At the landscape scale, measures of green vegetation, the nonphotosynthetic component of vegetation (litter and stems), and shade provide useful measures of canopy structure.

Caveats to Interpretation of Data

Climate and Variability

Interannual climate variability dramatically alters the magnitude and timing of carbon fluxes, and affects interpretations especially when used to generalize annual estimates of net productivity or carbon sequestration (Goulden and others 1998; Black and others 2000). Long-term weather datasets (1931–76) are available for this site (Shaw and others 2004), allowing extrapolation of results to longer-term conditions. Generally, the warmest and driest period occurs during June, July, and August. Climate measurements at the crane were begun in 1996, whereas ecosystem productivity comparisons started during the spring of 1998. There were significant climate differences between the 1998 (El Niño) and the 1999 (La Niña) years, which translated into dramatically different productivity estimates for the month of overlap (July) in the eddy-covariance NEP estimates. There does not appear to be any extended period throughout the year when carbon assimilation ceases for this coniferous forest (Paw U and others 2004). Continued long-term observations (5–10 years) are needed to characterize adequately this forest in terms of interannual variability in NEP to understand whether the forest is a small source or sink at the decadal scale.

Conventions/Terminology

The multidisciplinary and interdisciplinary nature of these integrated studies is a strength that adds breadth and rigor to these convergent results. Different disciplines have evolved independent conventions and terminology based on their own unique perspectives. For example, classical ground-based ecologists typically refer to the flux of carbon from the atmosphere to the biological system as an addition in carbon to the system (a positive change). However, atmospheric scientists usually view this same flux as a loss from the atmosphere (a negative change). Therefore, each of the studies reported in this special feature use the standard convention of their respective disciplines, which is clearly designated within each article and, where applicable in figures, carbon ‘‘source’’ or ‘‘sink’’ terms are labeled on the positive or negative side of the ordinate axis to avoid confusion. For example, Harmon and colleagues (2004) adopt the ecological convention, whereas Paw U and colleagues (2004) and Chen and coworkers (2004) use the atmospheric convention.

The carbon balance of the Wind River forest appears to be far more dynamic and variable in response to climatic and other drivers than previously thought for old-growth forest systems. Not only do these results have implications for forest management in western North America and for national and international policy decisions focused on managing greenhouse gases (especially carbon dioxide), they serve as an indication that potential climate change will present us with a far more dynamic response than previously envisioned. An important question is whether the estimated annual carbon sequestration (regardless of whether it is large or small) at the Wind River old-growth forest is sustained over long periods. How might the stand change over the next 100–200 years? The small carbon sequestration estimate of Harmon and colleagues (2004) was derived from measurements of properties that reflect changes over annual to century time scales, whereas meteorologic conditions alter GPP, NPP, and NEP at daily to annual time scales. Paw U and colleagues (2004) using the eddy-covariance approach estimated a sink for NEE from a single year (August 1998 to July 1999), at 150 g C m^{-2} y^{-1}, which has now been extended into a second year (August 1999 to July 2000), producing results consistent with the data reported in this issue [that is, 130 g C m^{-2} y^{-1} with the u* correction (Paw U personal communication)], suggesting that the Wind River old-growth forest is a significant carbon sink during both El Niño and La Niña years (Paw U and colleagues 2004). Whether this outcome is the result of two anomalous years of meteorologic forcing that produced unusually high levels of carbon sequestration or whether this will be sustained over longer periods remains to be determined. Currently, plans include continuing the eddy-covariance data collection for 10 years.

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