Throughout the history of science, innovative measuring techniques in combination with new theories have advanced our understanding of the natural world. The invention of the telescope allowed remotely based exploration of the solar system and modern telescopes, equipped with detectors that scan across the electromagnetic spectrum, have provided data to test the concepts and theories of cosmology and relativity; an application of x-ray crystallography led to the discovery of the structure of DNA and the subsequent revolution in molecular biology and genetics; and deep-sea drilling technologies – originally associated with petroleum and natural gas extraction – provided key support for the hypothesis of continental drift, to list just a few examples.

Our understanding of biogeochemical cycles has benefited considerably from both technical and conceptual advances. Here, we examine the important technological advances that have helped transform our knowledge of biogeochemistry in recent years and that will continue to do so as they are incorporated more extensively into ecological studies. We focus on carbon (C) because it is the major currency by which primary productivity and respiratory processes are assessed, illustrating how spaceborne remote-sensing innovations have made global-scale calculations of oceanic productivity at fine spatial and temporal scales possible, as well as the integration of inundation and vegetation dynamics into the calculation of methane (CH₄) and carbon dioxide (CO₂) exchanges in wetlands. We also discuss how adaptation of micrometeorological approaches in measuring terrestrial C balance has refined our understanding of ecosystem function. Characterization of the microbial organisms that perform many processes is integral to understanding biogeochemical cycles. It is also essential to determine the fluxes of materials among reservoirs, which requires measurements of transport processes and associated chemical constituents. We therefore discuss new analytical techniques in molecular biology and chemistry, as well as advances in the measurement of turbulent mixing required to compute fluxes.
Central to the biogeochemistry of C is the fixation of CO$_2$ through photosynthesis – that is, primary productivity. Although this process has been studied in individual plants or small samples of phytoplankton for decades, temporal and spatial variability of primary productivity has made regional and global estimates difficult to make with sufficient accuracy. Yet these estimates are critical for understanding interactions between the C cycle and changes in climate. Recent advances in remote sensing and micrometeorological techniques have revolutionized the ability to determine oceanic and terrestrial productivity. When combined with large-scale experimental manipulations, these techniques have led to an improved understanding of the ecological and biophysical mechanisms that control productivity. Wetlands process considerable amounts of C, some of which is either reduced to CH$_4$ or emitted as CO$_2$. However, the extensive and remote areas covered by tropical and northern wetlands, and their spatial and temporal heterogeneity, complicate the assessment of these ecosystems’ roles in C dynamics on a regional scale. Innovations in remote sensing have greatly helped in addressing these challenges.

**Ocean-color remote sensing**

The chlorophyll content, or “green-ness”, of a water body provides an index of its primary productivity. With the launch, in the 1990s, of satellite-borne sensors capable of measuring the faint signals of blue and green light emitted from the oceans, it became possible to estimate oceanic chlorophyll concentrations globally (McClain 2009). Recent algorithms have enabled calculation of backscattering of underwater light by particulate matter suspended in the ocean, a measure of phytoplankton C (Behrenfeld et al. 2005). The ability to determine chlorophyll content and C concentrations independently allows estimation of the chlorophyll-to-phytoplankton C (Chl:C) ratio; laboratory observations indicate that this ratio varies as a function of light and nutrient levels. It is therefore now possible to assess phytoplankton physiological status on global scales, a key step toward developing mechanistic models for the estimation of net primary production (Behrenfeld et al. 2005).

As an example, we describe an application of these new tools in studying the linkages between phytoplankton and biogeochemical processes in the waters of the sub-Arctic Pacific Ocean. Because of the region’s high nitrogen (N) and phosphorus (P) levels, phytoplankton should be abundant; however, the area is characterized by relatively low chlorophyll levels – iron limitation is thought to be the causal factor (Miller et al. 1991). Satellite imagery collected at a site after a large-scale iron-addition experiment indicated increased concentrations of chlorophyll and phytoplankton C (Figure 1). In particular, the observed Chl:C ratio increase was consistent with the idea that the addition of iron reduces nutrient stresses on phytoplankton, enabling more energy to be used to increase light-harvesting capabilities. Other researchers have used the signal from chlorophyll fluorescence to assess the physiological state of phytoplankton and its relationship to iron stress (Behrenfeld et al. 2009).

**Eddy covariance measurements in terrestrial systems**

Through the photosynthetic process, plants take up CO$_2$ and release water vapor (H$_2$O) and oxygen (O$_2$) to the atmosphere. Conversely, respiration by plants and decomposition of organic C in soils by microorganisms release CO$_2$ to the atmosphere. The difference between photosynthesis and respiration determines whether vegetation in a particular area is a sink or source of CO$_2$.

Eddy covariance measurements take advantage of the fact that when wind passes across vegetated surfaces, turbulent eddies cause vertical fluxes, such that gases are exchanged between the atmosphere above the plant canopy, within the canopy, and along the ground’s surface (Figure 2). By rigging towers with sensors capable of taking high-frequency measurements of wind speed/direc-
tion and airborne CO$_2$ concentrations within and immediately above the plant canopy, the net flux of CO$_2$ (ie the difference between photosynthesis and respiration) into or out of an ecosystem may be estimated.

The use of eddy covariance to measure C exchange between vegetation and the atmosphere demonstrates how technology from one specialty can aid in the development of another specialty. Originally developed and applied in micrometeorology, eddy covariance tower sites are now found at numerous locations worldwide. Important benefits of this technique (summarized in Baldocchi et al. 1988) include: (1) the ability to conduct in situ measurements with minimal damage to the surrounding vegetation; (2) automated measurement and data-handling capability, enabling continuous, high-frequency observations of vegetation–atmosphere C exchanges; and (3) information on C exchange over areas measuring tens to hundreds of square kilometers, rather than tens to hundreds of square meters typical of plot-scale studies. Of course, no technique is without limitations. Eddy covariance estimates of C exchange involve a host of assumptions estimating photosynthesis and respiration from atmospheric CO$_2$ concentrations, and low wind speeds can cause measurement problems (Baldocchi et al. 1988).

In combination with ground- and satellite-based observations and experiments, the eddy covariance technique has provided a wealth of data on the patterns and processes regulating C uptake and storage in the terrestrial biosphere (Law et al. 2002). Eddy covariance data have also been invaluable in developing state-of-the-art, global-scale models of the C cycle (Dolman et al. 2003) and in testing theories about the C balance of terrestrial ecosystems. For example, Luyssaert et al. (2008) found that old-growth forests sequester atmospheric CO$_2$ at rates similar to those of young forests. This result conflicts with a long-held theory that old-growth forests become “carbon neutral” as inputs of C through photosynthesis are balanced by C outputs via plant and microbial respiration.

**Free-air CO$_2$ enrichment (FACE)**

A critical innovation in the field of elevated CO$_2$ research was the development of free-air CO$_2$ enrichment (FACE) technology (Figure 3), the key feature of which enables the enrichment of atmospheric CO$_2$ without modification of other environmental variables. At FACE sites, pure CO$_2$ gas is mixed with ambient air to artificially elevate atmospheric CO$_2$ levels (Pepin and Korner 2002). FACE sites contain many instruments measuring wind speed/direction and CO$_2$ concentrations, enabling rapid adjustments in the rate at which CO$_2$ is introduced into experimental plots.

With a substantial commitment from governments to fund FACE experiments, studies have extended over a decade in intact ecosystems, providing insights about whole-ecosystem responses to rising CO$_2$ levels. The unexpected outcome of these long-term experiments is the variety of ecosystem responses to elevated CO$_2$. Indeed, the response of primary productivity to elevated CO$_2$ spans a gradient, from experiments in which (1) there is no response to elevated CO$_2$, alone (Korner et al. 2005) to experiments in which (2) the response is initially high but then declines to levels observed under ambient CO$_2$ (Reich et al. 2006; Seiler et al. 2009), or (3) the response is sustained through time (Finzi et al. 2006). Increases in primary production associated with high CO$_2$ concentrations require sufficient availability of other resources, and much of the variation in net primary productivity in response to CO$_2$ enrichment can be tied to nutrient limitation (Finzi et al. 2001; Reich et al. 2006).

In an era of rising atmospheric CO$_2$ concentrations, increased transport and deposition of reactive nitrogen, warming temperatures, and shifting quantities and patterns of precipitation, it is important to study the effects of multiple changes simultaneously. As so-called multifactor global-change experiments increase in number and scope, it will be interesting to see whether and how theories developed from single-factor experiments (eg CO$_2$ fertilization) will apply in a multivariable context. Emerging technologies, such as eddy covariance, along with novel methods for rapidly assessing nutrient pools and fluxes, will be needed to maximize the benefits of these experiments.

**Remote sensing of wetlands**

Wetlands cover extensive areas, are widely dispersed across Earth, and include a diversity of plant communi-
ties. However, wetland habitats – particularly those in tropical and northern regions – are not well characterized in terms of their ecological importance, in part because of difficulties in determining the varying extent and timing of inundation among the diversity of vegetative cover types. Fortunately, the past two decades have seen the development of a new suite of optical and microwave remote-sensing systems and analysis algorithms that largely overcome these obstacles (Melack 2004). An especially promising approach is synthetic aperture radar (SAR), a technique that transmits and receives microwave signals from and to a sensor and, therefore, allows for accurate classification of digital radar images into various vegetative classes and by inundation status. With the advent of SAR-equipped satellites, studies of inundation and wetland vegetation worldwide have become feasible. Complementary use of aircraft and satellite-borne sensors of a few to hundreds of bands of visible light allow detection of chlorophyll in plants and algae (Melack and Gastil 2001; Novo et al. 2006).

Recent applications of remote sensing to wetland studies in Amazonia provide excellent examples of how these new techniques are advancing biogeochemical understanding (Melack et al. 2009). In particular, Hess et al. (2003) developed a method of classifying vegetative–hydrological states using SAR mosaic images captured by the Japanese Environmental Resource Satellite and validated their results using high-resolution digital videography (Figure 4). Such vegetative–hydrological classification schemes are essential for studying wetland biogeochemistry. Because CH4 is produced predominantly in anoxic environments associated with flooded habitats, Melack et al. (2004) were able to calculate regional rates of CH4 emission by combining habitat-specific field measurements with passive and active microwave data that revealed temporal variations in the extent of both flooding and vegetation. On the basis of extensive field data and measurements of inundation areas derived from remotely sensed data, Richey et al. (2002) reported that CO2 evasion (e.g. outgassing from water to atmosphere) from lakes, rivers, and wetlands in the Amazon is an important term in the C balance for the Amazon Basin. Methane and CO2 are important greenhouse gases, and improved understanding of their evasion from large tropical wetlands, such as those in the Amazon, is a key component in predicting the role of the C cycle in global warming. A clever combination of satellite-derived observations of gravitational anomalies associated with flooding and atmospheric CH4 concentrations illustrates the promise for further advances in understanding global-scale CH4 fluxes made possible by new measurement tools (Bloom et al. 2010).

**Linking physical and biogeochemical processes in aquatic systems**

Crucial to studies of biogeochemical cycles is the determination of fluxes of materials between sediments, water, and the atmosphere and within these reservoirs, and calculation of these fluxes requires measurements of transport processes and associated chemical constituents. Over the past two decades, major advances in measuring and modeling aquatic systems’ physical processes – active in the dispersion and advection of gases, solutes, and particles – have been made, but these innovations have yet to be routinely incorporated within biogeochemical studies.

Improved understanding of turbulence has been critical to recent advances in measuring transport processes. Turbulent flows comprise three-dimensional eddies, with smaller eddies embedded in larger ones and with variations in eddy velocity, in part dependent upon eddy size. Turbulence is important because it induces fluxes across boundaries. Profiles of turbulence may be acquired with shear probes (Moum et al. 2008) or by millimeter-scale measurements of temperature (MacIntyre et al. 1999). Time series of turbulence can be obtained with acoustic Doppler velocimeters or acoustic Doppler current profilers (Figure 5). Long-term deployments of arrays of high-resolution, fast-response temperature sensors permit identification of regions of enhanced turbulence, sizes of turbulent eddies, and time series of eddy diffusivity.

Coupling measures of turbulence with estimates of biogeochemical fluxes can be accomplished by indirect or direct methods. In the indirect approach, either a mass transfer
coefficient or an eddy diffusivity coefficient is measured, and fluxes are computed as the product of the coefficient and a concentration gradient. The coefficient of eddy diffusivity is computed either based on fluxes of heat and tracers, or from measurements of the small-scale temperature or velocity fluctuations caused by turbulence (MacIntyre et al. 1999; MacIntyre et al. 2009). Fluxes at the benthic boundary layer and at the air–water interface are computed by way of mass transfer coefficients (Lorke et al. 2003; Laurion et al. 2010). Alternatively, a direct approach, known as eddy covariance and discussed above in a terrestrial-system application, involves simultaneous measurements of fluctuating solute concentrations and vertical velocities. This approach is being applied in lakes, estuaries, and coastal waters, and has been used successfully in studies of oxygen flux across the benthic boundary layer (Berg et al. 2003) and of gas flux across the air–water interface (Edson et al. 2008).

A major challenge in linking calculations of transport with biogeochemical processes is obtaining the biological or chemical measurements at a frequency appropriate to merge with the physical data. However, recent advances in sensor technology, such as the availability of in situ nitrate (NO$_3^-$) analyzers or optical oxygen sensors (Figure 5), are beginning to alleviate this problem. Profiling or moored fluorometers, which measure chlorophyll concentrations and states of fluorescence, when used with in situ temperature and light sensors or temperature microstructure profilers, have the potential to integrate stratification dynamics and variability of light climate for continuous estimates of primary productivity.

New approaches that combine rapid bench-top or in situ measurements of the ultraviolet (UV)–visible or fluorescence spectrum with multivariate statistical techniques hold considerable potential for quantifying the C sources for aquatic ecosystems (McKnight et al. 2001; Hassouna et al. 2007). One such approach, fluorescence spectroscopy, subjects an intact water sample to a range of UV wavelengths while recording emission over a range of wavelengths. The approach has been used to distinguish algal from terrestrial vegetation sources of dissolved organic matter in streams and lakes (McKnight et al. 2001), and to link dissolved organic matter sources to changes in microbial community structure (Nelson 2009). Another analytical development poised to transform the ability to measure metabolic processes at high spatial and temporal resolution is in situ measurements of stable isotopes in CO$_2$ and H$_2$O (Bowling et al. 2003).

Continuous measurements are enabling the observation of biogeochemical and ecological properties at rates sufficient to test theories of ecosystem change. Regime shifts are one form of ecosystem change where switches between alternate states result in different ecosystem properties, and theory suggests that regime shifts are preceded by changes in system variability (Scheffer et al. 2009). High-frequency observations of ecosystem components offer a new potential for evaluating hypotheses about variance properties in relation to regime shifts, through sensors that measure attributes of productivity, biomass, and respiration (Cole et al. 2000).

### Roles of genomics

By allowing direct assessment of the identity and spatio-temporal dynamics of gene and protein sequences in the environment, genomics and proteomics have revolutionized our understanding of the types of microbial cells present in the environment and their potential role in biogeochemical cycles. The age of environmental genomics began with work demonstrating that the diversity of microbial ribosomal gene sequences in the environment far surpassed diversity estimates from microscopic and culture-based methods (Stahl et al. 1985). Sequence-based methods of community fingerprinting (Liu et al. 1997) and phylogenetic staining (Giovannoni et al. 1988) have since allowed tracking of natural, uncultivated microbial populations through time and space, and have been used widely to develop correlational linkages between microbial community structure and biogeochemical processes in diverse environments (Nelson 2009).

Perhaps the strongest demonstration of the power of genomics to revise assumptions about ecosystem biogeochemistry came with the discovery of abundant and diverse genes that code for proteorhodopsin and nitrogenase in free-living oceanic microbial communities (Beja et al. 2000; Zehr et al. 2001). The occurrence of diverse and abundant marine bacterioplankton lineages – contain-
The development of metagenomic (the collective genetic sequence of all organisms in a sampled habitat) approaches has made functional genomic snapshots of ecosystems possible. In extreme microbial ecosystems, such as acid mine drainages and hydrothermal vents, this approach has permitted mechanistic detailing of biogeochemical cycles and the involvement of specific microbial taxa in the various cycles (Reyesenbach and Shock 2002; Tyson et al. 2004). In more diverse systems, such as the open ocean or human gut, these datasets clarify the relative abundance of different taxa and functional genes and allow for reconstruction of community metabolic pathways and modeling of biogeochemical interactions among consortia (DeLong et al. 2006; Gill et al. 2006). Metagenomes have now been successfully complemented with other “post-genomic” approaches, including the use of transcriptomic (ie collective messenger RNA sequence data) and proteomic (ie collective protein sequence data) methods to clarify the differences between genetic potential and actively expressed metabolic products (Frias-Lopez et al. 2008; Sowell et al. 2009).

Methods are rapidly emerging to link genomic data directly to biogeochemical processes. Stable isotope probing permits separation of community nucleic acids based on incorporation of labeled substrates, allowing metagenomic or transcriptomic characterization of a select subset of genomes associated with specific biogeochemical processes (Kalyuzhnaya et al. 2008). New sequencing technologies have reduced the cost and increased the efficiency of gene sequencing, permitting researchers to develop and analyze multiple metagenomes and transcriptomes along environmental or temporal gradients (Willner et al. 2009). In the coming decades, genomics and related fields in systems biology (eg proteomics and metagenomics) will take center stage in defining ecosystem biogeochemical dynamics, developing management strategies, and predicting ecological responses to global change.

**Future challenges and opportunities**

Challenges that result from technological advances, such as those discussed here, include the costs of supporting the continued operation of remote-sensing and data systems, maintaining long-term, whole-ecosystem experiments, and sustaining state-of-the-art analytical facilities. The reward of doing so is an increased capacity to measure and model coupled biogeochemical cycles. One essential element in this increased capacity is, and will be, the invention and application of new technologies. As members of the ecological scientific community continue to learn how to distribute and creatively use the ever-increasing volume and kinds of data on biogeochemical processes and fluxes, the resulting integrated analyses will enhance our understanding of ecosystems and their short-term variability and long-term changes. With the resulting increased understanding, ecologists will be better able to inform policies that influence human societies and their environment.

**References**


**Figure 5. Diver installing acoustic Doppler profiler, optical oxygen sensor, and irradiance sensor for benthic metabolism studies in Moorea, French Polynesia.**


