SECTION II

ECOLOGICAL ENERGETICS

INTRODUCTION

All organisms need materials such as carbon, nitrogen, and phosphorus to build molecules, cells, and other structures, and energy to build and maintain those structures against the relentless forces of entropy. Not surprisingly, the two main branches of ecosystem science deal with the movement and fate of materials and energy (*biogeochemistry* and *ecosystem energetics*, respectively). This section of the book (Chapters 2–4) introduces ecosystem energetics (primary production, secondary production and consumer energetics, and decomposition), and Section III deals with biogeochemistry (Chapters 5–8).

Studies of energy flow through individuals, populations, communities, and ecosystems form a large part of past and present-day ecosystem science. Historically, ecosystem scientists studied energy flow for several reasons. Many of the earliest studies (i.e., before 1950) were motivated by the idea that the allowable harvest from a wild population (e.g., a fishery) would be related to the amount of energy flowing into that population, so that studies of energy flow would help to estimate sustainable yield. Although historically important, this is no longer a primary motivation for ecological energetics (but see Libralato et al. 2008 for a modern example). More generally, ecologists recognize that energy is essential for *all* life; thus, studies of energy flow track the movement of a key resource. Because all organisms require energy, it provides a common currency that allows ecologists to make comparisons across all organisms and habitats. That is, it allows ecologists to compare the activities of such disparate organisms as plants, mice, moose, and microbes using the same single currency that is required by all of them.

Some ecologists have gone further to regard energy as *the* key resource, making the case that energy can be substitutable with other resources (e.g., water, nutrients) so that deficiencies in any resource can be ameliorated if enough energy is available. In this world view, which was held by a minority of ecologists, energy is the ultimate limiting resource, so pathways of energy flow might reveal pathways of control in ecosystems. Finally, energy flow often is roughly proportional to other key activities (e.g., grazing, flows of elements), so it could be argued that energy flow is the most appropriate single measure of the importance of a population (if we *must* reduce a population to a single number), because it roughly summarizes the multiple activities that the population performs.

UNITS USED IN STUDIES OF ECOLOGICAL ENERGETICS

If you've taken a physics class recently, you know that the proper units of energy content and flow are joules (kg-m^2/s^2) and watts (joules/s), respectively. It may seem confusing, then, that ecologists studying energy flow almost never express their results in terms of joules or watts. Rather, most ecologists implicitly equate energy with biomass, because biomass is the carrier of energy in organisms, and is easier to measure than energy content. Biomass thus implies energy content, and the production or destruction of biomass implies energy flow. Consequently, ecologists usually express energy in units of biomass (i.e., grams of live mass, dry mass, ash-free dry mass, or organic carbon). Other units sometimes used in ecological energetics are the mass of oxygen produced or consumed by photosynthesis or respiration, or calories (an obsolete unit of energy content). Table 1 shows conversions between units commonly used in ecological energetics.

TABLE 1 Approximate conversion factors between energetic units used in ecological studies. Except for the conversion between joules and calories (which is exact), the conversion factors are approximate and can vary substantially among organisms and among tissues in an individual organism. Both the photosynthetic quotient and the respiratory quotient are assumed to equal 1.

Units Converted From	Units Converted To						
	Joules	**Calories**	**Carbon (g)**	**Oxygen (g)**	**Dry Mass**	**Wet Mass**	**Ash-Free Dry Mass**
Joules	1	0.239	2×10^{-5}	6×10^{-5}	5×10^{-5}	2.5×10^{-4}	4.3×10^{-5}
Calories	4.18	1	9×10^{-5}	2.5×10^{-4}	2×10^{-4}	1×10^{-3}	1.8×10^{-4}
Carbon (g)	4.5×10^{4}	1×10^{4}	1	2.7	2.2	11	1.9
Oxygen (g)	1.7×10^{4}	4×10^{3}	0.375	1	0.8	4	0.7
Dry mass	2×10^{4}	5×10^{3}	0.45	1.2	1	5	0.9
Wet mass	4×10^{3}	1×10^{3}	0.09	0.24	0.2	1	0.17
Ash-free dry mass	2.3×10^{4}	6×10^{3}	0.5	1.4	1.2	6	1

Modified from Cummins and Wuycheck (1971), Peters (1983), Benke (1993), Cattaneo and Mousseau (1995), and other sources.

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CHAPTER

2

Primary Production: The Foundation of Ecosystems

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INTRODUCTION

Primary production is the storage of energy through the formation of organic matter from inorganic carbon compounds. Primary production is carried out by autotrophic organisms. The term *autotrophic* is derived from the Greek words *autos*, meaning self, and *trophikos*, meaning pertaining to food. Autotrophs are "self-feeders." Higher plants as well as some microbes (e.g., algae) are autotrophs. Plants and algae conduct the most familiar form of primary production—photosynthesis—where carbon dioxide is incorporated into organic matter using energy from sunlight. In most ecosystems primary production is carried out by a variety of species and the diversity of autotrophs influences primary production (e.g., Tilman et al. 2006). The accrual of organic matter by primary producers represents the first step in the capture, storage, and transfer of energy in most ecosystems.

There are several reasons why ecologists consider primary production a fundamental ecosystem process. The ecosystem carbon cycle begins with the fixation of carbon (i.e., incorporation of CO_2 into organic matter). Herbivores consume this organic carbon produced by autotrophs to support their growth and metabolism. Other components of the food web such as detritivores and predators also depend directly or indirectly on primary production for their energy supply. Primary producers require nutrients such as nitrogen and phosphorus to build biomolecules such as proteins and nucleic acids. The uptake and cycling of nitrogen, phosphorus, and other elements accompanies primary production, and the ratio of elements that ultimately comprises primary producers influences many ecological processes (Sterner and Elser 2002). The formation of organic matter

by primary producers is also a key process of the global carbon cycle. Primary production and the short- and long-term fate of this fixed carbon influences atmospheric carbon dioxide concentration. The study of primary production in terms of rates, controls, trophic interactions, biogeochemical cycles, and storage of the end-products of primary production is, therefore, central to ecosystem science.

The results of primary production are often quite evident as, for example, the rapid growth of lawn grass during spring. In terrestrial ecosystems the accumulation of biomass by primary producers provides important structure. For example, in forests, tree growth leads to branch and root formation and the accumulation of wood. These structural elements are critical components affecting many physical, chemical, and biological processes in a forest (Box 11.1). Analogous growth of marine kelp forests in the sea creates structure and habitat that support many types of organisms.

Primary production may also be cryptic. Measurement of phytoplankton biomass day to day in the sea or in a lake would usually reveal little variation. It would seem that no biomass is being produced because there is no accumulation, but in this case, loss processes such as grazing by herbivores are as rapid as the increase in phytoplankton. Production might be high even though biomass of the phytoplankton does not change. In contrast, when growth rates are consistently in excess of loss rates, so-called "blooms" of phytoplankton result and can lead to massive, sometimes noxious, accumulations of algal scums. Rather than being cryptic, these scums caused by excess primary production are conspicuous and represent a serious environmental problem in many water bodies.

COMPONENTS OF PRIMARY PRODUCTION

Primary production is by definition a rate with units of mass per area (or volume, if measured in water) per time. For example, primary production data are often presented as grams carbon per square meter per day (g C m^{-2} d^{-1}). The absolute amount of plant material produced in an ecosystem is sometimes referred to as production or yield (mass per unit area or volume) as, for example, the total mass of corn plants generated in a field. Time, however, is generally implicit in this use of production and yield. For example, the production of a corn field typically refers to a mass per unit area for a growing season. In this chapter the terms *production* and *primary production* will always refer explicitly to rates with the time attribute of the rate specified.

Biomass is distinct from primary production. The biomass of primary producers is mass per area or volume independent of time. Biomass is often approximately correlated with primary production. However, it is possible as noted earlier to have low biomass but relatively high rates of primary production as often observed in the ocean. Alternatively, slow-growing plants may represent a substantial biomass but have relatively low rates of primary production.

Primary production encompasses a number of processes that require definition and that pose problems for measurement. The components of primary production are clarified by following the flow and fates of carbon through a generalized ecosystem (Figure 2.1). Primary production begins with the fixation of CO_2 into organic matter. Gross primary production (GPP) represents this first step accounting for all the carbon dioxide fixed into

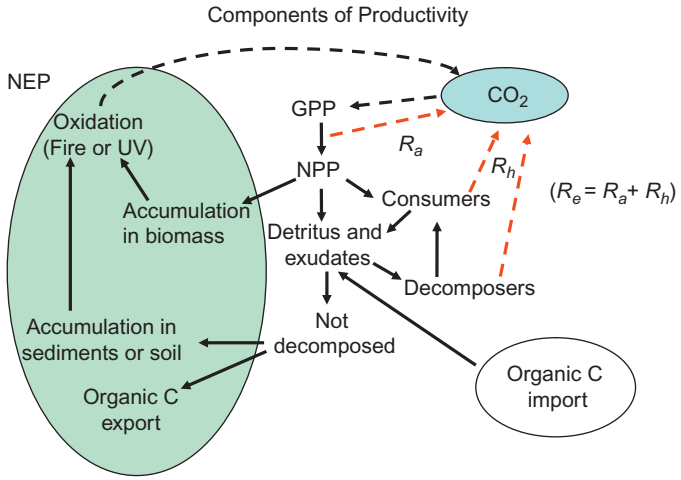

FIGURE 2.1 Components of productivity; see text for definitions. *(Figure modified from Lovett et al. 2006.)*

organic matter irrespective of any respiratory losses (Figure 2.1). Net primary production (NPP) is the difference between GPP and autotrophic respiration (R_a):

$$\text{NPP} = \text{GPP} - R_a \tag{2.1}$$

Conceptually, NPP is the rate at which organic matter is made available for other uses beyond simply supporting energy costs (i.e., respiration) of the primary producers. Net primary production is consumed, converted to detritus, or accumulated in biomass. The portion of the NPP that is consumed and respired by heterotrophic organisms (R_h) is cycled back to the atmosphere as CO_2. Ecosystem respiration (R_e) is the sum of R_a and R_h (Figure 2.1).

Ecosystem respiration typically does not consume all the organic carbon that is either produced within or imported to the ecosystem (Figure 2.1). Some organic carbon accumulates in biomass (e.g., wood in trees) and detritus (e.g., organic matter in soils and sediments). Some organic matter is exported (e.g., organic carbon exiting a river ecosystem and entering the ocean). Together these rates of accumulation and export represent net ecosystem production (NEP). The balance of carbon flows requires that NEP is equivalent to the difference between GPP and R_e:

$$\text{NEP} = \text{GPP} - R_e \tag{2.2}$$

Because R_e is the sum of R_a and R_h and NPP is the difference between GPP and R_a, NEP can also be expressed as:

$$\text{NEP} = \text{GPP} - R_a - R_h = \text{NPP} - R_h \tag{2.3}$$

In other words, *NEP is the portion of gross primary production that is not respired by autotrophs or heterotrophs*. This residual production either accumulates as carbon in biomass or detritus, is exported from an ecosystem, or is lost through fire or photo-oxidation.

Interestingly, NEP can be either positive or negative. How is this possible? One way this can occur is if the primary production of an ecosystem is stopped or severely reduced (the GPP in Eq. 2.2 ~ 0), but the respiration of stored organic matter continues. For instance, consider a forest that has just been clear-cut so that there is little or no primary production but decomposers are still consuming (and respiring) the organic matter in the forest floor. Another way that negative NEP can occur is if an ecosystem imports organic carbon, and these imports are respired by heterotrophs along with the carbon produced within an ecosystem. In both cases the total respiration of the ecosystem exceeds gross primary production ($R_e > \text{GPP}$), thus NEP is negative. Ecosystems with negative NEP are referred to as heterotrophic ecosystems—these systems respire more carbon than they produce and the excess respiration either depletes carbon stored in the system or is subsidized by imports of carbon from outside the ecosystem. In contrast, ecosystems with positive NEP are autotrophic ecosystems. Ecosystems with negative NEP are quite common and include many lakes, streams, rivers, and estuaries (Caraco and Cole 2004). These distinctions about relative NEP are important in considering carbon sequestration by ecosystems (Box 2.1; Chapter 6).

We can also consider NEP in the context of organic carbon accumulation (dC_{org}) in an ecosystem by considering a mass balance of inputs and losses:

$$dC_{org} = \text{GPP} + I - R_e - Ex - Ox_{nb} \tag{2.4}$$

where the new terms are:

I = imported organic carbon
Ex = exported organic carbon
Ox_{nb} = nonbiological oxidation of organic carbon (e.g., fire or photo-oxidation)

Since NEP is equal to GPP $- R_e$, Eq. (2.4) can be written as:

$$dC_{org} = \text{NEP} + I - Ex - Ox_{nb} \tag{2.5}$$

Organic carbon accumulation (dC_{org}) in ecosystems sequestered over long time periods (centuries to millennia) provides a sink for atmospheric CO_2 and is very important to those studying global carbon budgets (Box 2.1; Chapter 6).

Not all primary production results from aerobic photosynthesis where water is split and oxygen is produced in the fixation of carbon. Under anoxic conditions, some microorganisms can fix carbon, for example, using hydrogen sulfide (H_2S) instead of water and producing sulfur instead of oxygen. Further, some microorganisms, primarily archaea and bacteria, have chemosynthetic abilities and are also primary producers. There are many types of chemosynthetic reactions but all oxidize inorganic molecules to produce energy, which is used to fix CO_2 as organic matter (Box 2.2). For example, nitrifying bacteria convert ammonia to nitrite or nitrite to nitrate, and in the process derive energy sufficient to convert CO_2 to organic matter.

BOX 2.1

NET ECOSYSTEM PRODUCTION AND CARBON SEQUESTRATION

The fate and especially long-term storage of primary production in the biosphere can influence carbon dioxide in the atmosphere. For example, the current burning of fossil fuels by humans that is causing atmospheric CO_2 to increase represents the mining of ancient primary production long stored in the earth. Is it possible to partially reverse the current course of CO_2 increase by storing increased amounts of contemporary primary production in long-term reservoirs? This type of question drives research on the carbon cycle and carbon sequestration in ecosystems. Consideration of carbon sequestration, however, requires clarity in terminology and specification about timescales over which sequestration occurs. In some systems NEP is equated to carbon sequestration; however, this is not necessarily correct. For instance, a portion of NEP may be exported as organic carbon rather than sequestered in the ecosystem. In addition, today's sequestered carbon might become tomorrow's atmospheric CO_2. Consider a regenerating forest that grows for 50 years accumulating carbon in wood (90%) and soil organic matter (10%) at a rate of 100 g C m^{-2} y^{-1} so that 5000 g C m^{-2} is stored after 50 years. If the forest burns in year 51 and all the wood is consumed in the fire, the sequestered carbon is only the 10% stored in the soil (assuming it did not burn). Consideration of the timescale of carbon storage is important given discussions to develop carbon markets and global sinks for CO_2.

These general issues can be clarified by revisiting the definition of NEP in the context of an ecosystem budget for organic carbon (Lovett et al. 2006). Remember Eq. (2.5) that $dC_{org} = \text{NEP} + I - Ex - Ox_{nb}$.

Clearly, NEP is not simply equivalent to carbon sequestration (dC_{org}). It is possible that in some ecosystems I, Ex, and Ox_{nb} are low, but most ecosystems lose some carbon (Ex) as dissolved organic carbon and receive organic inputs (I) from the atmosphere and/or adjacent ecosystems. Further, if an area burns, Ox_{nb} is high and dC_{org} is strongly affected but NEP is not. Schemes for carbon sequestration must consider NEP and the fluxes I, Ex, and Ox_{nb} in the context of the particular ecosystems where carbon will be stored. Because some measurement systems provide an instantaneous estimate of NEP, the imports, exports, and nonbiological oxidation must be accounted for before organic carbon accumulation can be calculated. Moreover, the timescale of probable carbon sequestration should be explicit so that periodic events like fires and floods can be incorporated into calculations.

In most ecosystems that receive significant light energy, chemosynthesis is only a small proportion of primary production. For example, in three Swedish lakes chemosynthetic primary production by methane-oxidizing bacteria (which transform methane to acquire energy, Box 2.2) was only 0.3% to 7% of total primary production (Bastviken et al. 2003). However, in unlighted ecosystems such as the deep realms of soils, sediments, and caves where suitable reduced compounds are present (e.g., ammonium, sulfides, methane, and hydrogen),

BOX 2.2

CHEMOSYNTHESIS

Chemosynthesis exploits chemical energy to convert inorganic carbon compounds into organic matter, in contrast with photosynthesis, which exploits the energy of light to produce organic matter. Chemosynthetic reactions are carried out by prokaryotic microorganisms, principally bacteria and archaea (referred to as "bacteria" in the following). Energy is produced in chemosynthetic reactions from oxidizing reduced compounds. There are a variety of chemosynthetic bacteria that carry out these reactions including nitrifying bacteria (oxidizing NH_4 or NO_2), sulfur bacteria (oxidizing H_2S, S, and other sulfur compounds), hydrogen bacteria (oxidizing H_2), methane bacteria (oxidizing CH_4), iron and manganese bacteria (oxidizing reduced iron and manganese compounds), and carbon monoxide bacteria (oxidizing CO). This is not an exhaustive list and new modes of chemosynthesis as well as new chemosynthetic bacteria are still being discovered.

Chemosynthetic reactions often occur at the interface of aerobic and anaerobic environments where the end-products of anaerobic decomposition as well as oxygen are available. Thus, these reactions are most often apparent in soils and sediments where oxygen is depleted. For example, methane is produced by anaerobic bacteria that convert fermentative end-products like acetate to methane. Methane builds up in anaerobic zones of soils, sediments, and stratified water columns. Methane-oxidizing bacteria grow at the interface of the aerobic–anaerobic zone exploiting methane that moves out of the anaerobic area. The chemosynthetic reaction of methane oxidation is:

$$CH_4 + O_2 \rightarrow CO_2 + 4\,H^+ \text{and } 2\,e^-$$

The energy generated by this reaction is represented by the reducing power of the hydrogen ions and electrons produced. These are coupled to biochemical reactions used to fix inorganic carbon. For methane-oxidizing bacteria the initial organic compound produced in the coupled oxidation-reduction reaction is formaldehyde (HCHO), which is a precursor for further organic synthesis.

Understanding of chemosynthetic processes is still advancing with new findings that reveal reactions in environments where they were not previously believed to occur. For example, methane oxidation can occur in anaerobic environments where microbes use sulfate or nitrate to oxidize methane. Raghoebarsing et al. (2006) studied a freshwater canal polluted with high concentrations of agricultural runoff and documented anaerobic methane oxidation conforming to the following reaction:

$$5\,CH_4 + 8\,NO_3^- + 8\,H^+ \rightarrow \begin{matrix} 5\,CO_2 + 4\,N_2 \\ + 14\,H_2O \end{matrix}$$

The microbial community found in the canal was able to use methane and nitrate as a sole energy source and did not require oxygen to convert methane to carbon dioxide. The energy gained from this reaction is used to fuel growth (via the fixed CO_2). Further research is likely to bring to light novel mechanisms by which microbes use chemicals in their environment as energy sources to fix carbon.

chemosynthetic organisms can be the main primary producers (e.g., Sarbu et al. 1996). Indeed, in the thermal vent regions of the deep sea entire ecosystems run on energy derived from chemosynthetic microorganisms. Sulfides and other reduced compounds that emerge with geothermal fluids from these vents are converted by microorganisms to energy through chemosynthetic reactions. In these settings chemosynthetic primary production supports a variety of consumers with high local biomass (Lutz and Kennish 1993; Van Dover et al. 2002). Regardless of whether gross primary production is powered by chemosynthesis or photosynthesis, the carbon flow pathways in Figure 2.1 still apply and the definitions of GPP, NPP, R, and NEP are equivalent.

MEASURING PRIMARY PRODUCTION

Methods to measure primary production vary as a function of the types of autotrophs in an ecosystem—an algal assemblage in a lake or stream requires a different approach compared to trees in a forest. Primary production methods also vary in terms of the processes that are included or excluded. For example, some methods measure GPP while other methods include autotrophic respiration and therefore measure NPP. The timescale of the measurement may determine which of the processes in Figure 2.1 are included. For example, measurement of grassland primary production is often accomplished by clipping and weighing plant material produced over a given time interval (e.g., a growing season). This measurement represents NPP not GPP because R_a has occurred during the course of the measurement. Furthermore, any losses to herbivores that were not excluded and that occur in this period are not measured in the biomass accumulation and must either be considered negligible or estimated to provide a correction.

In aquatic ecosystems, "bottle methods" are often used wherein a sample is collected and incubated for a few hours to measure the uptake of radioactive inorganic carbon (^{14}C) or a change of dissolved oxygen. Other techniques include continuously monitoring chemical constituents such as oxygen or pH to assess overall ecosystem respiration and primary production. For aquatic and wetland vascular plants various harvest and morphometric methods are used.

In terrestrial ecosystems, including fields and forests, both harvest and incremental growth observations are used to measure production. More recently, continuous monitoring of CO_2 exchange over terrestrial ecosystems has been employed to estimate production over large areas. The actual area measured by these latter approaches varies substantially from system to system as a function of plant cover, terrain complexity, wind, and weather conditions.

This text does not emphasize methods but we turn now to a brief discussion of some aquatic and terrestrial methods for measuring primary production. Our purpose is to compare and contrast the methods in terms of the components of primary production (Figure 2.1) that are included in or excluded by the technique. By considering the methods we hope to deepen understanding of the process of primary production and to increase the reader's appreciation of some of the complexities inherent in this measurement.

Aquatic Methods

One of the most common primary production methods used in aquatic ecosystems dominated by fast-growing phytoplankton and benthic algae is measurement of the incorporation of ^{14}C. The technique is extremely sensitive so even very low rates of primary production can be measured. To measure phytoplankton production, water samples are collected, a trace amount of ^{14}C-labeled bicarbonate ($H^{14}CO_3$) is added, and the sample is incubated in situ or in the laboratory under specified light conditions. At the end of the incubation, the water is filtered. The ^{14}C captured on the filter after any residual bicarbonate is removed by acidification represents primary production. The length of incubation determines whether significant respiration of ^{14}C by phytoplankton occurs (R_a) and the method typically measures a quantity that falls somewhere between GPP and NPP. Other complexities need to be considered including the loss of radioactive dissolved organic compounds, death of phytoplankton during the incubation, temporal variations of light (e.g., daily light cycle), and possible artifacts from enclosing phytoplankton in bottles. The incubation time, and hence measurement period, is usually a few hours, and rates are typically extrapolated to represent daily production.

Terrestrial Methods

The phytoplankton ^{14}C method contrasts with approaches to forest production. One standard approach to measuring forest primary production is through a combination of leaf fall (foliar production) and wood production estimates. The estimate of wood production takes advantage of the strong correlation of woody biomass with tree diameter. Allometric equations that quantify the relationship between diameter and mass are available in the literature for many tree species. These equations are generated by harvesting trees and measuring both morphometric characteristics and the biomass of selective components. With these relationships, repeated measurements (usually over several years) of tree diameters in a stand of trees can be used to calculate the accumulation of woody biomass. This approach estimates NPP rather than GPP because R_a is occurring during the measurement period. Foliar and wood production constitute most of the NPP in forests, but it is important to note that this method ignores many other parts of the total NPP, each of which can be important in some places and times. For instance, understory plants can contribute significantly to NPP in some ecosystems. Losses to herbivory are usually small but can sometimes be very important, as for example, during insect outbreaks or in grasslands. Seed production can be important but is sometimes episodic (e.g., masting) and therefore difficult to measure accurately. Root production is also part of the primary production but is also very difficult to measure, thus most terrestrial primary production data are presented as ANPP, above-ground net primary production. Root production can be equal to or greater than ANPP in some ecosystems, but measurement of this process has vexed ecologists for decades. One current method is to use a video camera to repeatedly measure the growth of individual roots along the face of a clear sampling tube inserted into the ground. Although this method is promising, all root production estimates involve great uncertainties.

The aquatic and terrestrial methods outlined earlier have been used extensively but are being supplemented or replaced by methods that rely on in situ measurement of gas exchange to estimate primary production. These new techniques provide much greater temporal resolution and increase the spatial scale of the estimates of primary production (because the gas measurements are typically representative of larger spatial areas). To illustrate these approaches, consider measurements of oxygen concentration made continuously in a water body with an in situ oxygen electrode (Figure 2.2). Oxygen increases during the day as a consequence of oxygen production by photosynthesis (GPP) and decreases at night as a consequence of oxygen consumption by respiration (R_e). In addition, oxygen exchanges (D) with the atmosphere as a consequence of the relative concentrations of oxygen in the water and atmosphere. D can be positive or negative depending on whether oxygen in the water is undersaturated or oversaturated relative to the atmosphere. Thus, the daily change in oxygen is described as:

$$\Delta O_2 = \text{GPP} - R_e + D \tag{2.6}$$

where $R_e = R_a + R_h$ (Figure 2.1). The loss of oxygen at night plus or minus atmospheric exchange is equal to respiration (R_{night}):

$$\Delta O_{2\text{night}} = R_{\text{night}} + D \tag{2.7}$$

Assuming respiration at night equals respiration during the day (R_{day}), the gain of oxygen during the day is equal to GPP plus respiration ($R_{\text{day}} = R_{\text{night}}$) plus atmospheric exchange (D). Hence, GPP can be readily calculated as:

$$\text{GPP} = \Delta O_{2\text{day}} + (R_{\text{night}}) + D \tag{2.8}$$

The advantages of this method are numerous. Instruments to measure oxygen allow continuous observations so that production can be estimated repeatedly rather than just a

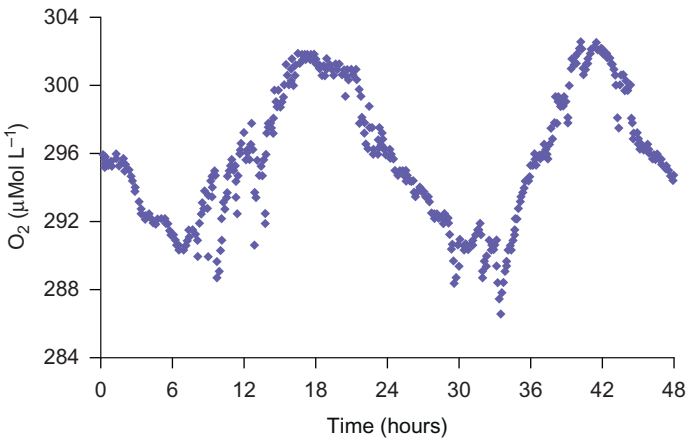

FIGURE 2.2 Oxygen dynamics in Peter Lake, a small lake in Michigan, over 48 hours beginning at midnight. Oxygen declines at night are due to respiration and increases during the day are due to photosynthesis. These daily changes in oxygen provide a basis for estimating primary production. *(From data from the authors.)*

few times. Potential artifacts related to sample enclosure as required in the ^{14}C method are eliminated. The technique is less subject to problems of extrapolation of primary production for an ecosystem, because the method inherently provides estimates across broad scales (e.g., an entire lake each day). This method, as for any technique, also has important uncertainties such as the assumptions about the equivalence of day and night respiration as well as questions of scale (e.g., what portion of an aquatic ecosystem is represented by the oxygen measurements). Nevertheless, this type of method is greatly improving the resolution and the accuracy of primary production measurements of ecosystems (e.g., Roberts et al. 2007).

An analogous gas-exchange approach in terrestrial ecosystems is called *eddy covariance* (sometimes called eddy flux or eddy correlation). In this method a fast-response CO_2 sensor is paired with a multidirectional wind speed sensor on a tower extending above a vegetation canopy. The sensors measure the CO_2 concentrations associated with updrafts and downdrafts as the turbulent air mixes into the canopy. The flux of CO_2 into and out of the canopy on these air currents is calculated using algorithms programmed into a computer, and the difference (efflux − influx), integrated over time, is termed the *net ecosystem exchange*, or NEE. (By convention, NEE is negative if the net flux of CO_2 is into the canopy and positive if the net flux is out of the canopy.) Because the release of CO_2 from the ecosystem includes both autotrophic and heterotrophic respiration, NEE is essentially an instantaneous measurement of NEP. In some cases, nighttime measurement of NEE (CO_2 efflux at night) is used to estimate ecosystem respiration (R_e, including both R_a and R_h), and GPP is calculated as the sum of NEE and R_e. NPP cannot be readily calculated because it is very difficult to separate the autotrophic and heterotrophic components of R_e.

This method has some major advantages—its fast response allows for observation of short-term physiological and meteorological controls on production, and it naturally integrates over a substantial area (typically on the order of hectares) upwind of the tower. It also allows direct measurement of NEP, which, if organic carbon losses from the system are negligible, is a good estimate of the organic carbon accumulation rate in the ecosystem. On the other hand, it is difficult to apply in areas where the terrain or the vegetation canopy is uneven, and it does not measure NPP, which is very important in terrestrial ecological studies.

REGULATION OF PRIMARY PRODUCTION

Primary production by photosynthesis obviously requires light, which attenuates rapidly with depth in water and from the top of the canopy to the ground on land. This limits maximum light to upper waters of aquatic ecosystems and to terrestrial plant canopies. Primary producers found in deeper waters and on the ground beneath canopies are shaded and exhibit adaptations that enhance carbon fixation at low light intensities. Primary production tends to increase with increasing light concentration up to a maximum (Figure 2.3) and can often be described by a saturating function (Jassby and Platt 1976). This relationship is useful for modeling primary production. The relationship can be quantified by measuring primary production per unit biomass at different light intensities and fitting a two-parameter model that includes the initial slope of the