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Organic matter breakdown and ecosystem metabolism: functional indicators for assessing river ecosystem health

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Abstract. River health monitoring traditionally has made use of structural measurements (water quality or taxonomic composition of aquatic organisms). We argue that a more complete assessment of river health should include functional metrics, such as rates of organic matter decomposition and ecosystem metabolism. Leaf breakdown links the characteristics of riparian vegetation with the activity of both aquatic invertebrates and microbial organisms and is affected by natural and human-induced variation in a wide range of environmental factors. Measurement of leaf breakdown is relatively simple and has modest equipment requirements. River metabolism (gross primary productivity and ecosystem respiration) measures the rates of production and use of organic C in river ecosystems as a whole, providing a direct estimate of the food base that determines life-supporting capacity. Metabolism measurements require more sophisticated equipment than do measurements of leaf breakdown, but improvements in technology have made metabolism measurements relatively easy. We review the factors that influence leaf breakdown and river metabolism and pay particular attention to the effects of human-induced environmental stressors. We also describe how measurements can be standardized and suggest criteria for interpreting functional measures in terms of river ecosystem health. Last, we consider the strengths and weaknesses of both methods as functional measures and provide recommendations for their use as biomonitoring tools.

Key words: river health, ecosystem function, organic matter decomposition, leaf litter, ecosystem metabolism, respiration, gross primary production, ecological integrity, environmental monitoring.

The state of a river can vary along a gradient of impairment from pristine to severely impacted. A critical part of improving the state of rivers is the ability to assess their ecological state accurately, so that the causes of degradation or the success of rehabilitation efforts can be measured. Resource managers can use 1 or more measures of condition to assess or monitor river health. River health traditionally has been assessed with structural measures related to physicochemistry or community composition (macroinvertebrates, algae, or microbes) (Barbour et al. 1999, Boulton 1999). However, river ecosystems also have functional components (Meyer 1997), which include rates, patterns, and relative importance of ecosystem processes. Adequate characterization of ecosystems requires information on both structure and function (Gessner and Chauvet 2002) because stressors might cause changes to structure but not function, to function but not structure, or to both (e.g., Matthews et al. 1982, Bunn and Davies 2000, Riipinen et al. 2008). Direct measurements of ecosystem function also might enable better discrimination among classes along a gradient of biological condition (Davies and Jackson 2006).

The only functional metric that is used routinely in water-quality assessment is biochemical O_2 demand (BOD), which is a measure of the total potential respiration within the water column and is most suited to sites influenced by wastewater discharges. Other ecosystem processes potentially could be used as functional indicators of river ecosystem health. These processes include rates of nutrient uptake (Sabater et al. 2000), microbial respiration (Hill et al. 2002), nitrification (Bernhardt et al. 2002), fine particulate organic matter export (Wallace et al. 1996), coarse

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particulate organic matter retention (Quinn et al. 2007), and invertebrate production (Buffagni and Comin 2000). However, some of these measures involve large effort or sophisticated and expensive equipment. Rates of leaf breakdown (Young et al. 1994, Benfield 1996, Gessner and Chauvet 2002) and ecosystem metabolism (the combination of algal productivity and ecosystem respiration; Hornberger et al. 1977, Bott 1996, Hill et al. 1997, Young and Huryn 1999, Bunn and Davies 2000, Fellows et al. 2006) are sensitive to environmental stressors and are relatively inexpensive and easy to measure. Leaf breakdown is an integrative process that links riparian vegetation and microbial and invertebrate activities. River metabolism measures the rates of production and use of organic C and, thus, provides a direct estimate of the food base and the way energy moves through the river food web. Both factors respond to many physical and chemical stressors (Mulholland et al. 2001, Pascoal et al. 2003).

An ideal indicator would respond predictably to anthropogenic stressors but be relatively insensitive to natural spatial or temporal variation (Norris and Hawkins 2000). This ideal is difficult to achieve because sensitive indicators, such as leaf breakdown and metabolism, respond to natural variation and to human-induced changes to ecosystems. Tradeoffs among generality, sensitivity, and robustness are inevitable when choices must be made among appropriate indicators (Gessner and Chauvet 2002). If possible, indicators of ecosystem health should be set against a local baseline of (more or less) pristine sites that have natural physicochemical characteristics equivalent to what would be expected in the (potentially) impaired sites under study. Good indicators should be economical to measure, provide easily interpreted outputs, relate to appropriate scales and management goals, and be scientifically defensible (Norris and Hawkins 2000).

We discuss natural variation in rates of leaf breakdown and river metabolism in relation to in-stream physicochemistry and geographic and landscape features and pay particular attention to the influence of a wide variety of human effects. We consider advantages and disadvantages of alternative measurement protocols for each indicator and provide a framework for distinguishing between healthy and unhealthy systems.

Leaf Decomposition

Review of factors controlling leaf decomposition

The many factors that control leaf decomposition range from those that vary naturally from site to site (e.g., climate, longitudinal position in the river) to those that are strongly influenced by anthropogenic disturbance to ecosystems (e.g., toxic chemicals, organic pollution). Most of these factors vary as a result of both natural and anthropogenic causes (e.g., nutrients, pH, sediment, riparian vegetation, temperature). The role of terrestrial leaf litter as an energy source to stream ecosystems has been widely studied since the 1970s (Table 1).

Leaf decomposition responds systematically to certain natural features of a river, and these responses must be taken into account when using leaf decomposition as a measure of ecosystem health. For example, leaf breakdown usually is faster in warm than in cold water (Table 1). Therefore, breakdown rates often differ between rivers with different altitudes or climates or that are in different ecoregions. Rivers at different altitudes or in different ecoregions also show systematic variation in naturally occurring nutrient concentrations, hydrological regimes, river geomorphology and bed substrate, and the nature of the riparian vegetation (which influences stream temperature via shading). Even in identical physicochemical settings, particular species that have strong effects in the food web might have far-reaching effects on leaf decomposition. Within a given river, leaves generally decompose faster at sites where leaf-eating invertebrates are more abundant. Distributions of leaf-eating insects, crayfish, or fish that prey upon the leaf eaters are patchy at a range of scales, and species might be present or absent at the catchment scale, in individual tributaries, or even in reaches within a tributary. Unexpected variation in breakdown rates might be caused by patchy distributions of particularly influential consumers (Table 1). The influence of those natural features that might affect the process of leaf decomposition must be removed from assessments of the influence of anthropogenic activities, such as input of fine sediment, organic matter, plant nutrients, and toxic chemicals, and changes to pH, temperature, and hydrology.

Human activities in a catchment often are reflected by changes in >1 stressor (Table 1). For example, when riparian vegetation is removed for agricultural or urban development, temperature, nutrient concentrations, and fine sediment input into the stream all are likely to increase. Multiple stressors might operate in concert to increase leaf breakdown rates, as would be the case when temperature and nutrient concentrations are increased simultaneously. On the other hand, positive effects of higher nutrient concentrations have counteracted negative effects of more fine sediment in streams in catchments developed for grazing (Niyogi et al. 2003). Similarly, the negative effects of increased heavy metal concentrations have counteracted the positive effects of high nutrient concentrations (Sridhar

et al. 2001). Pascoal et al. (2001) also reported that declines in leaf processing by invertebrates, caused by inputs of treated sewage effluent, were more than compensated by increased microbial activity.

Measurement of leaf breakdown

Leaf breakdown is measured by securing bunches of preweighed leaves to the streambed (as leaf packs or in mesh bags) and retrieving them after a certain period. Enclosing the leaves in mesh bags standardizes the approach and reduces abrasion-induced mass losses of large leaf fragments that have not been totally decomposed (Meyer 1980, Boulton and Boon 1991). On the other hand, leaf decay might be underestimated in mesh bags because of size-selective exclusion of some or all macroinvertebrates, the potential for anoxic conditions to develop in the center of the bag (Boulton and Boon 1991), and the tendency for fine sediment to accumulate within the bag (Dangles et al. 2001). However, these problems can be circumvented by using appropriate mesh sizes and relatively small leaf bags and by exposing leaf bags for relatively short periods of time (Boulton and Boon 1991). Coarse-mesh bags (0.5–1-cm aperture) allow colonization by leaf-eating macroinvertebrates, and, thus, conditions in coarse-mesh bags simulate natural leaf breakdown more closely than do conditions in fine-mesh bags (e.g., Chergui and Pattee 1988, Stewart and Davies 1989, Gonzalez et al. 1998, Gessner and Chauvet 2002, Menendez et al. 2003). Both coarse- and fine-mesh bags ($\leq$1 mm) should be used (e.g., Gonzalez et al. 1998, Menendez et al. 2003, Pascoal et al. 2003), if feasible, to permit assessment of the relative contributions of macroinvertebrates and microorganisms (fungi and bacteria) to leaf breakdown (Gessner and Chauvet 2002).

Many studies have provided information on relative decay rates of leaf species in different parts of the world (e.g., Bärlocher et al. 1995, Quinn et al. 2000, Haapala et al. 2001, Sampaio et al. 2001, Hieber and Gessner 2002, Pascoal et al. 2003). Most researchers have emphasized realism in leaf breakdown studies by selecting leaves from the riparian zone (Boulton and Boon 1991). However, when leaf breakdown is used as a functional measure of river health, relative measures (i.e., comparisons between polluted and unpolluted reference sites) are often more important than absolute breakdown rates, and leaf type and treatment should be standardized among sites. A species that decays relatively fast has the advantage of a possibly shorter exposure period. On the other hand, a more slowly decomposing species could be selected if retrieval might be delayed for logistic reasons. Use of freshly fallen leaves allows assessment of the natural decomposition process (Boulton and Boon 1991), but logistic constraints are likely to preclude this approach if comparable studies are to be carried out in many locations. To minimize variability, leaves should be picked from trees at a single location and air-dried prior to exposure in leaf bags (Boulton and Boon 1991).

A promising alternative technique is the *cellulose decomposition potential* method (Hildrew et al. 1984, Boulton and Quinn 2000, Tiegs et al. 2007), which was first used in streams by Egglishaw (1972). Strips of standard cotton cloth are deployed in the stream, and the extent of cellulose decomposition is measured as loss in tensile strength. Other standard substrates, such as wooden sticks, also have potential (Tank and Winterbourn 1996, McTammany et al. 2008). Use of standard substrates ensures that comparisons of decay rates among sites are not confounded by variability in the chemical composition of the initial substrate (Tiegs et al. 2007). Standard substrates are relatively inexpensive and are less prone to fragmentation and are easier to transport than leaves (Egglishaw 1972, Tiegs et al. 2007).

In most studies, replicate leaf packs or bags are retrieved after various periods of exposure (e.g., Hill et al. 1992, Gonzalez et al. 1998, Haapala et al. 2001, Hieber and Gessner 2002, Menendez et al. 2003), but a single retrieval period (e.g., 1 mo) might be adequate if effort must be minimized. Decomposition rates vary with time of year, and the most realistic values will be obtained at the time of peak leaffall (Garden and Davies 1988, Boulton and Boon 1991, Lopez et al. 2001, Menendez et al. 2003, Pascoal et al. 2003). Complete decay of leaves reduces power to detect differences among sites. Thus, the ideal period of deployment is one that results in $\sim$50% loss of mass or strength. This period provides sufficient time for detection of differences among sites but insufficient time for complete leaf decay at most sites.

Leaf bags should be securely fastened to metal pegs ($\geq$15–20 cm long) anchored to the stream bottom and driven beneath the bed surface so that hydraulic conditions are not dramatically altered. Bags should not be allowed to float in the water column because of potential effects on decay rates (Mutch et al. 1983). Leaf bags should be tethered in areas where leaves are likely to accumulate naturally to mimic the natural rate of leaf decomposition (Boulton and Boon 1991). Breakdown rates differ among habitat types within streams. Leaves buried in debris dams and pools typically decompose slowly, whereas leaves in riffles decompose faster (Meyer 1980, Casas 1996). Measures of ecosystem health rely on comparisons among sites, so the habitat types in which leaves are positioned

TABLE 1. Expected patterns in leaf breakdown in relation to natural variation and responses to environmental stressors.

Factor	Change	Leaf breakdown response
Climatic zone	Warmer water	Faster
Position from headwater to river mouth	Shredding invertebrate density higher in small streams	Faster in small streams
	Shredding invertebrate density or fungal biomass higher downstream	Faster downstream
	Higher nutrient concentrations downstream	Faster downstream
Streambed characteristics	Riffles vs pools or debris dams	Faster in riffles
	Fine vs coarse sediment	Lowest on silt
	Stable vs unstable bed	Faster on stable bed
Influential species	Action of efficient shredders (or of predators of shredders)	Faster where shredders occur without predators
Water temperature	Warmer water	Faster in warm streams or warm season
Sediment	More fine sediment	Slower
pH	Acid conditions	Slower
Conductivity	Hard vs soft water	Faster in hard-water streams
Nutrients	Nutrient enrichment	Faster as long as nutrient was limiting
Organic pollution	Increased pollution	Faster
Toxic chemicals	Heavy metal inputs	Slower
	Insecticide	Slower
Riparian vegetation	Loss of stream-side vegetation or reduced canopy cover	Faster
	Different leaf species	Systematic variation in breakdown rates
River regulation	Damming of a river	Faster
Channelization	Simplification of habitat	Slower
Water abstraction	Reduced flows	Minimal

should be as consistent as possible among sites. We recommend that riffles be used as a standard habitat type because leaves naturally accumulate (Speaker et al. 1984), invertebrate density and diversity are often high (Brown and Brussock 1991), and sediment deposition and leaf pack burial are less likely in riffles than in other habitats. In larger rivers, riffles also are the shallowest areas, so leaf bag deployment and recovery often are easier in riffles.

The simplest way to assess leaf breakdown is to measure mass loss (as ash-free dry mass to circumvent the problem of inorganic sediment accumulation) of leaves during the period of deployment. One of the problems associated with mass-loss measurements is that some of the measured loss might result from loss of large leaf fragments through physical abrasion rather than biological or chemical decomposition. An alternative measure that could be used on remaining

TABLE 1. Extended.

Comments	References
See "Water temperature" below	Gessner et al. 1998, Robinson et al. 1998, Mathuriau and Chauvet 2002, but see Chergui and Pattee 1991
Depends on rate of invertebrate shredding	Baldy et al. 1995, Jonsson et al. 2001, but see Graça et al. 2001 Fabre and Chauvet 1998, Fleituch 2001
See "Nutrients" below	Pozo 1993
Invertebrate density or leaf abrasion higher in riffles	Meyer 1980, Smith 1986, Casas 1996
Invertebrate densities lower or anaerobic	Reice 1974
Higher invertebrate density	Rounick and Winterbourn 1983
Crayfish very important, but fish might reduce shredder activity	Rosemond et al. 1998, Usio 2000, Konishi et al. 2001, Schofield et al. 2001
Microorganisms most responsive to temperature; if invertebrate density is high in cold season, leaf decay is faster	Webster and Benfield 1986, Bunn 1988, Garden and Davies 1988, 1989, McArthur et al. 1988, Short and Smith 1989, Lopez et al. 2001, Menendez et al. 2003
Lower invertebrate density or anaerobic conditions	Reice 1974, Triska and Buckley 1978, Herbst 1980, Meyer 1980, Chauvet 1988, Chergui and Pattee 1990, Rader et al. 1994, Niyogi et al. 2003
Reduced invertebrate or microorganism activity	Allard and Moreau 1986, Collier and Winterbourn 1987, Garden and Davies 1989, Griffith and Perry 1994, Rowe et al. 1996, Dangles and Guerold 1998, 2001, Siefert and Mutz 2001, Dangles and Chauvet 2003, Riipinen et al. 2008
Shredding invertebrate density or microorganism activity increases with conductivity	Rosset et al. 1982
Response might be counteracted by increased sediment	Elwood et al. 1981, Meyer and Johnson 1983, Young et al. 1994, Suberkropp and Chauvet 1995, Pozo et al. 1998, Robinson and Gessner 2000, Graça et al. 2001, Huryn et al. 2002, Rosemond et al. 2002, Gulis and Suberkropp 2003, Niyogi et al. 2003, Menendez et al. 2003, Gulis et al. 2006, Hagen et al. 2006, Paul et al. 2006, Mesquita et al. 2007
Response to nutrient stimulation but might be counteracted by changes to invertebrate community	Pascoal et al. 2001, 2003, but see Raviraja et al. 1998
Via reduced invertebrate and microbial activity	Schultheis and Hendricks 1999, Sridhar et al. 2001, Niyogi et al. 2001, but see Nelson 2000
Via reduced invertebrate density (experiment with herbicide had no effect)	Wallace et al. 1982, Kreutzweiser et al. 1998
Via warmer water temperatures, but counteracted by increased sedimentation soon after logging	Webster and Waide 1982, Griffith and Perry 1991, Whiles and Wallace 1997, Benfield et al. 2001, but see Bird and Kaushik 1992
Depends on leaf chemistry (nutrients and toxins) and fiber content	Webster and Benfield 1986, Enriquez et al. 1993, Ostrofsky 1993, 1997, Campbell and Fuchshuber 1995, Hutchens and Benfield 2000, Royer and Minshall 2001, Chadwick and Huryn 2003, Riipinen et al. 2008
Warmer temperatures in winter, but depends on nature of invertebrate community	Short and Ward 1980, Casas et al. 2000, Nelson and Roline 2000
Via loss of natural leaf accumulations and leaf-eating invertebrates	Gelroth and Marzolf 1978
Probably depends on magnitude of flow reduction and effect on other factors	Dewson et al. 2007

leaf material is a measure of leaf toughness as the force required to drive a blunt metal pin through a leaf (Suberkropp and Klug 1980, Young et al. 1994, Quinn et al. 2000, Huryn et al. 2002, Chadwick and Huryn 2003, Niyogi et al. 2003). This force can be measured in Newtons with a commercially available penetrometer or as the mass (lead shot or water added to a container directly above the pin) required to force the pin through the leaf. Other measurements, such as concentrations of polysaccharides, total N, protein, tannin, lignin, and ergosterol (an indicator of fungal biomass) in the leaves (Suberkropp et al. 1976) also could be made (Boulton and Boon 1991). Microbial growth and activity can be measured as radioactive thymidine uptake and respiration rates, respectively. These measurements can help determine the relative

importance of bacteria, fungi, and invertebrates, but many are time-consuming and require specialized equipment and, therefore, probably are beyond the scope of monitoring programs that use leaf breakdown as a routine measurement of river ecosystem health.

The simplest method of reporting breakdown rates is to use the percentage of the initial mass of leaf material remaining after a certain time period. This method assumes that decomposition is linear and that a constant amount of material is lost throughout the decomposition process. Studies on leaf breakdown often report exponential decay of the leaf material, where a constant proportion of the material remaining at any time is lost throughout the decomposition process. In these situations, breakdown rates are more accurately described in terms of an exponential decay coefficient (k) than by percentage of mass remaining (Petersen and Cummins 1974). However, exponential decay coefficients represent a simplification of the actual process in streams (Boulton and Boon 1991). Leaf decay begins with the fast leaching of soluble compounds, followed by relatively fast decay of the fleshy parts of the leaf. The tougher veins decompose at the slowest rates. Therefore, at least 3 distinct decay rates might occur as a leaf decomposes. This fact can cause problems when trying to interpret decomposition rates, especially if the deployment period is fixed with only a single retrieval time. When only initial and final masses (or toughness) are measured, it is impossible to determine whether decomposition was linear or exponential. Nevertheless, we recommend use of exponential decay rates because they are the standard measure reported in the literature.

If natural differences in water temperature are expected between sites, and temperature has been measured continuously throughout the study, then the effect of temperature on decomposition rates can be removed by using degree days, rather than days, as the measurement of time (Minshall et al. 1983).

Ecosystem Metabolism

Review of factors controlling river metabolism

River ecosystem metabolism—the combination of gross primary production (GPP; photosynthesis [P]) and ecosystem respiration (ER)—is a measure of how much organic C is produced and consumed in rivers. Algae and other aquatic plants are responsible for primary production, whereas ER measures the rates of respiration of all life, including fish, invertebrates, algae, aquatic plants, and microbes. The ratio of these 2 variables (GPP/ER or P/R) also is informative and provides information on the relative importance of the 2 key sources of energy that fuel river ecosystems—algae and terrestrial organic matter. If organic C production is greater than C consumption, then organic matter produced within the system probably is supporting the food web, whereas if C consumption is greater than C production, then organic matter from upstream or the surrounding catchment probably is maintaining the system (Meyer 1989). Therefore, ecosystem metabolism provides a direct measurement of the food base of river ecosystems and helps to determine their life-supporting capacity.

Ecosystem metabolism is influenced by a wide range of factors. Some factors vary naturally (e.g., longitudinal position in the river, climate), whereas others are influenced primarily by anthropogenic disturbance to ecosystems (e.g., organic pollution, river regulation, toxic chemicals, aquatic plant management). However, many of the factors that control ecosystem metabolism vary as a result of both natural and anthropogenic causes (e.g., light, substrate composition, turbidity, nutrients, pH, riparian vegetation, flow fluctuations). Considerable research has been done on river ecosystem metabolism (Table 2), especially in the last 10 y, as improvements in technology have made measurements easier.

The probable effects of natural variation on rates of metabolism must be understood and taken into account when designing monitoring programs or when interpreting data. For example, a key prediction of the river continuum concept is that GPP/ER should change in a predictable manner from the headwaters to the lower reaches of natural river systems (Vannote et al. 1980). This prediction has been tested in many locations and generally has been supported by data (Table 2; Naiman 1983, Bott et al. 1985, Chessman 1985, Naiman et al. 1987, Minshall et al. 1992, McTammany et al. 2003), although some fundamental differences have been seen in grassland/prairie systems (Wiley et al. 1990, Young and Huryn 1996) and in rivers with strong floodplain connections (Junk et al. 1989, Meyer and Edwards 1990). Thus, metabolic rates at potentially impacted sites should be compared with rates measured at (more) pristine sites that are characterized by similar stream order and size.

The amount of light reaching primary producers on the streambed appears to be the main factor influencing GPP in rivers (Bott et al. 1985, Young and Huryn 1999, Mulholland et al. 2001, Fellows et al. 2006). Many factors control the amount of light reaching a particular reach. These factors include the amount and type of riparian vegetation, orientation of the valley, and slope of the banks. Light input also varies with cloud cover and seasonally with changes in day length and sun angle. The amount of light passing through the water column depends on water clarity (Davies-Colley et al. 1992). Shading from riparian

vegetation is particularly important, and changes associated with leaffall or removal of riparian vegetation can have dramatic effects on stream metabolism. For example, GPP declined 75% after leaves emerged and shaded the streambed in 2 deciduous forest streams in Tennessee (Hill et al. 2001). Light intensity is unlikely to affect respiration rates directly, but light intensity and ER could be correlated when respiration is mainly associated with algal biomass, which can be abundant in well-lit streams (Bunn et al. 1999). Differences in turbidity and riparian shading could be related to human-induced disturbance to river ecosystems, but natural changes in light input, such as cloud cover and season, should be factored out as much as possible in monitoring programs.

Effects of climate on ecosystem metabolism probably are mediated through light inputs, rather than through water temperature, which is the primary factor affecting leaf breakdown. Increases in temperature (to a certain tolerance limit) should enhance GPP and ER (Phinney and McIntire 1965). However, temperature effects appear weak at the ecosystem scale (DeNicola 1996, Mulholland et al. 2001). We are unaware of any studies that have conclusively shown a link between GPP and temperature in natural streams. However, several studies have suggested modest effects of temperature on ER (Bott et al. 1985, Hill and Gardner 1987, Hedin 1990, Howarth et al. 1992, Sinsabaugh 1997, Hill et al. 1998, 2000, 2002), and many studies have shown that ER is significantly greater in summer than in winter (Webster et al. 1995).

Another point to consider when using metabolism as an index of health is that some factors affect both GPP and ER, whereas others primarily influence only one of these processes (Table 2). For example, GPP appears to be more sensitive to flow fluctuations than does ER, so bed-moving high flows tend to cause dramatic reductions in P/R (Young and Huryn 1996, Uehlinger and Naegeli 1998, Uehlinger 2000, 2006, Uehlinger et al. 2003). Increased light input caused by loss of stream-side vegetation is likely to affect GPP more strongly than ER (Table 2). In contrast, a reduction in connectivity between surface and hyporheic flows should affect ER strongly, because a relatively large proportion of the ER appears to occur in the hyporheic zone (Mulholland et al. 1997, Fellows et al. 2001), without influencing GPP, which occurs primarily on the surface of the streambed.

The presence of particular species that strongly influence the food web does not appear to affect metabolism to the same extent as it does leaf-litter processing. Nevertheless, trophic cascades, in which changes at one trophic level influence other trophic levels, are well known in streams. Biggs et al. (2000) compared periphyton biomass and production among 6 streams with different top-level fish predators (*Salmo trutta* [brown trout], and *Galaxias* spp.) to determine the strength and implications of trophic cascading that had been observed in earlier experiments in artificial stream channels (Flecker and Townsend 1994). Periphyton biomass was significantly higher in the trout streams than in the *Galaxias* streams, but differences in periphyton biomass were not associated with differences in GPP. In a more intensive study at 2 of the same sites, Huryn (1998) observed a 6× difference in annual net primary production between a trout stream and a *Galaxias* stream. This result suggests that particular species can sometimes affect metabolism.

Human-induced stressors often tend to co-occur, and co-occurring effects might be either complementary or antagonistic. For example, agricultural development often is associated with removal of riparian vegetation and with increased nutrient and sediment delivery to streams. Removal of riparian vegetation increases light available for GPP, and this effect is enhanced by an increased supply of nutrients. High rates of GPP and ER in response to abundant light and nutrient levels have been observed in agricultural streams and rivers (Wiley et al. 1990, Wilcock et al. 1998, Young and Huryn 1999). However, increased concentrations of suspended fine sediment and turbidity tend to counteract these positive effects and lead to declines in GPP at sites where the combination of water depth and turbidity restricts light availability at the riverbed (Wiley et al. 1990, Young and Huryn 1996). Similar antagonistic effects might occur in streams receiving waste discharges in which increased organic C would tend to increase ER, but industrial toxins might reduce GPP and ER (Rama Rao et al. 1979).

Measurement of river ecosystem metabolism

GPP involves uptake of CO_2 and release of O_2 into the water, whereas ER is essentially the reverse process. Therefore, ecosystem metabolism can be measured using changes in either O_2 or CO_2 (Bott et al. 1978). CO_2 is relatively difficult to measure directly in water, so some researchers have measured pH, which closely corresponds with CO_2 (Simonsen and Harremoes 1978, Cushing and Wolf 1984). Radioactive $^{14}CO_2$ uptake also can be used to measure rates of photosynthesis (Bott and Ritter 1981), but we recommend using changes in dissolved O_2 because this variable is relatively easy to measure, and the magnitude of O_2 change is typically large.

Metabolism can be estimated by measuring natural changes in O_2 concentration in the river, or by enclosing part of the river in an air-tight chamber and measuring

TABLE 2. Expected patterns in gross primary productivity (GPP) and ecosystem respiration (ER), and in the ratio of photosynthesis to respiration (P/R) in relation to natural variation and responses to environmental stressors.

Factor	Change	Response
Position from headwaters to river mouth	Forested headwaters: dense shade	Decrease GPP ($P/R << 1$)
	Middle section: more light	Increase GPP ($P/R \approx 1$)
	Lower river: deep, turbid	Decrease GPP ($P/R < 1$)
Influential species	Trout reduce insect grazing, increase algae	Increase GPP and P/R
Light	More sunlight	Increase GPP and P/R
Temperature	Warmer water	Increase ER, possibly GPP
Nature of substrate	More fine sediment	Increase ER, decrease P/R
	Less stable or more heterogeneous substrate	Decrease GPP, decrease P/R
	Impaired connection with hyporheic zone	Decrease ER, increase P/R
Turbidity	More suspended sediment	Decrease GPP, decrease P/R
pH	Acid conditions	Decrease GPP and ER
Nutrients	Nutrient enrichment	Increase GPP and ER
Organic pollution	Input of organic waste	Increase ER, decrease P/R
Toxic chemicals	Toxic inputs	Decrease GPP and ER
Riparian vegetation	Lose stream-side vegetation, increase light	Increase GPP and P/R
	Increase organic matter inputs	Increase ER, decrease P/R
Channelization	Loss of habitat heterogeneity	Increase GPP, increase P/R
Flow fluctuations	Floods	Decrease GPP, ER (a little), decrease P/R
	River drying	Increase GPP, P/R
	River regulation	Increase GPP and ER
Aquatic plant management	Plant removal	Decrease GPP and ER

O_2 changes in the chamber. Open-system methods have the advantage that they include the whole ecosystem, and, in many situations, measurements are relatively simple and require just 1 data-logging O_2 meter (Owens 1974, Young and Huryn 1996). O_2 concentrations are measured at regular intervals over at least one 24-h period, and changes in concentration are related to O_2 input via photosynthesis and O_2 removal via respiration. The main difficulty with open-system measurements is that they require an estimate of the amount of O_2 diffusing between the air and water (reaeration). Reaeration rates can be estimated relatively easily in most rivers and streams from the O_2 record (Owens 1974, Kosinski 1984, McBride 2002) or by applying empirical equations that use mean reach depth and mean velocity to estimate reaeration coefficients (Wilcock 1982, Young and Huryn 1999). However, more-complicated techniques involving injection of tracer gases are required in small, turbulent streams with low primary productivity (Marzolf et al. 1994, Young and Huryn 1998, 1999). We think that open-system O_2 change methods are the most appropriate methods for routine monitoring of ecosystem metabolism.

Measurements of metabolism made within chambers usually also use changes in O_2 concentration over at least one 24-h period (Bott et al. 1978). However, ER and maximum GPP can be estimated over shorter periods by comparing O_2 changes in chambers exposed to high light intensities with those in artificially darkened chambers (Hickey 1988). Chamber measurements have been used to assess the contribution of different components of river ecosystems to overall metabolism (Naiman 1983, Mulholland et al. 1997, Naegeli and Uehlinger 1997, Oliver and Merrick 2006). The O_2 changes are measured within an air-tight chamber, so estimates of metabolism can be made without measurements of diffusion rates. However, the use of such chambers has many disadvantages: 1) material placed

TABLE 2. Extended.

Comments	References
GPP light limited, but not in grassland (P/R high)	Junk et al. 1989, Meyer and Edwards 1990, Wiley et al. 1990, Young and Huryn 1996
P/R decreases downstream in grassland	Young and Huryn 1996
Where strong floodplain connection, high organic input and ER (P/R<<1)	Naiman 1983, Bott et al. 1985, Chessman 1985, Naiman et al. 1987, Junk et al. 1989, Meyer and Edwards 1990, Minshall et al. 1992, McTammany et al. 2003
Algal biomass higher, GPP sometimes higher	Flecker and Townsend 1994, Huryn 1998, Biggs et al. 2000
Mainly based on the amount of light reaching the riverbed; affected by season, cloud cover, canopy cover, and turbidity	Naiman 1983, Bott et al. 1985, 2006, Webster et al. 1995, Hill et al. 2001, Mulholland et al. 2001, Acuña et al. 2004, Ortiz-Zayas et al. 2005, McTammany et al. 2007
Only weak evidence	Phinney and McIntire 1965, Bott et al. 1985, Hill and Gardner 1987, Hedin 1990, Howarth et al. 1992, Webster et al. 1995, DeNicola 1996, Sinsabaugh 1997, Hill et al. 1998, 2000, 2002, Mulholland et al. 2001
More organic matter	Hedin 1990, Hill et al. 1998
Algal production higher on large stable particles	Rosenfeld and Roff 1991, Rier and King 1996, Biggs et al. 2001, Houser et al. 2005
Large proportion of ER occurs in hyporheic zone	Mulholland et al. 1997, 2001, Fellows et al. 2001
If river depth is sufficient to limit light	Davies-Colley et al. 1992, Peterson 1996, Young and Huryn 1996 Niyogi et al. 2002 Odum 1956, Bott et al. 1985, Bowden et al. 1992, Guasch et al. 1995, Wilcock et al. 1995, 1998, Young 1998, Hill et al. 2000, Mulholland et al. 2001
Possible increase in GPP too, if nutrients released	Odum 1956, Rama Rao et al. 1979, Quinn and McFarlane 1989, Paul and Meyer 2001, Bott et al. 2006, Gücker et al. 2006
May be offset by nutrients in toxic discharge	Maki and Johnson 1976, Crossey and La Point 1988, Hill et al. 1997, Niyogi et al. 2002
ER may also increase if system is dominated by algal respiration	Bunn et al. 1999, Young and Huryn 1999, McTammany et al. 2007
Some trees (especially deciduous) drop more leaves	Hedin 1990, McTammany et al. 2007
Loss of riparian cover partly responsible	Gelroth and Marzolf 1978
High flows and abrasion reduce algal biomass	Peterson 1996, Young and Huryn 1996, Uehlinger and Naegeli 1998, Uehlinger 2000, 2006, Uehlinger et al. 2003
Pattern reverses after flow resumes	Hill and Gardner 1987, Mollá et al. 1996, Acuña et al. 2004
Loss of flushing flows	Uehlinger et al. 2003, Munn and Brusven 2004
Only if macrophytes contribute strongly to metabolism	Simonsen and Harremoes 1978, Wilcock et al. 1999, Kaenel et al. 2000

within the chamber invariably is disturbed during the process; 2) water velocity, light, nutrient concentrations, and temperature within the chamber differ from natural conditions in the river; and 3) errors can occur when trying to relate small-scale measurements of different components of the ecosystem to processes occurring at the whole-reach scale. Considerable effort has been made to overcome some of these disadvantages (Bott et al. 1997, Dodds and Brock 1998, Bunn et al. 1999, Uzarski et al. 2001), but many of the problems cannot be solved simply by adjustments to chamber design. Therefore, we do not recommend chambers for use in routine measurements of river ecosystem health.

Discussion

Relationships of functional measures to ecosystem health

As with any biological indicator, river managers require guidance regarding the meaning of functional measurements for ecosystem health. Ideally, managers should know the specific values that might indicate a possible transition from "good" to "poor" ecosystem health. Gessner and Chauvet (2002) proposed a tentative framework for assessing functional stream integrity from leaf-litter processing rates (Table 3). This framework includes 2 approaches. The 1st compares values at test sites with values at appropriate reference sites and sets impairment criteria based on values at the reference sites. For example, a leaf-litter decay rate at a test site that is within 30% of the decay rate at reference sites would indicate good ecosystem health, whereas decay rates <50% or >200% of those at reference sites would indicate severely impaired ecosystem health. Values between the extremes would indicate milder effects. Scores could be assigned to each criterion as a simple way of indicating the health of different sites (Table 3).

The 2nd approach compares values at test sites with

TABLE 3. Framework for assessing functional stream health using leaf-litter processing rates (from Gessner and Chauvet 2002). Scores indicate the health of the test site: 2 = no evidence of an impact on ecosystem function, 1 = mild effect on ecosystem function, 0 = severely impaired ecosystem function. k_t = decomposition rate at test sites, k_r = decomposition rate at reference sites.

Method	Assessment parameter	Criterion	Score
Comparison with reference	k_t/k_r	$k_t/k_r = 0.75$–1.33	2
		$k_t/k_r = 0.5$–0.75 or $k_t/k_r = 1.33$–2.0	1
		$k_t/k_r < 0.5$ or $k_t/k_r > 2.0$	0
Absolute value	k_t (/d)	$k_t = 0.01$–0.03	2
		$k_t = 0.005$–0.01 or $k_t = 0.03$–0.05	1
		$k_t < 0.005$ or $k_t/k_r > 0.05$	0

set absolute values (Table 3). For example, Gessner and Chauvet (2002) suggested that leaf-litter processing rates between 0.01 and 0.03/d generally indicate good ecosystem health, whereas values outside this range indicate either mild or severe impairment of ecosystem health (Table 3). However, sensible absolute values cannot be set without knowing the type of leaves used or the characteristics of the test sites. If rivers within a given biomonitoring region were classified into types and sufficient information on breakdown rates in reference streams of each type were obtained, a series of absolute values could be devised for comparison with test sites of the same type.

We extended the framework proposed by Gessner and Chauvet (2002) to assessing ecosystem health based on ecosystem metabolism. We did a meta-analysis of river metabolism data in the scientific literature (Wiley et al. 1990, Young and Huryn 1996, 1999, Webster and Meyer 1997, Wilcock et al. 1998, Young 1998, Mulholland et al. 2001, 2006, Hall and Tank 2003, McTammany et al. 2003, 2007, Houser et al. 2005, Meyer et al. 2005, Ortiz-Zayas et al. 2005, Bott et al. 2006, Gücker et al. 2006), and split study sites into 2 groups. *Reference* sites drained relatively natural catchments, and *impact* sites drained intensively modified land. We used data from the reference sites to develop interim criteria for interpreting metabolism data (Fig. 1A–C, Table 4).

We assumed that GPP and ER values between the lower and upper quartiles of the reference-site distributions (25^{th}–75^{th} percentiles) indicated good ecosystem health, as has been done previously for other biological indices (Gerritsen 1995, Barbour et al. 1996, Maxted et al. 2000). We categorized GPP values outside this range such that values $<25^{th}$ percentile also indicated good ecosystem health, values between the 75^{th} and 95^{th} percentiles indicated satisfactory ecosystem health, and values $>95^{th}$ percentile indicated poor ecosystem health (Fig. 1A). We categorized ER values outside the 25^{th} to 75^{th} percentile range such that values between the 5^{th} and 25^{th} percentiles or between the 75^{th} and 95^{th} percentiles indicated satisfactory ecosystem health and values $<5^{th}$ percentile or $>95^{th}$ percentile indicated poor ecosystem health (Fig. 1B). The differences between the GPP and ER criteria reflect the fact that low GPP values do not necessarily indicate poor ecosystem health, e.g., small, pristine forested streams can have very low rates of GPP. However, extremely low rates of ER are more likely than low rates of GPP to indicate poor ecosystem health. Our analysis yielded absolute target values that seemed to be applicable for GPP and ER measurements (Table 4). We derived tentative thresholds for comparing test sites with reference sites by comparing the average rates of GPP and ER for the reference sites with the appropriate lower and upper limits of each range. We assigned scores to each criterion as a simple way to indicate ecosystem health of sites (Table 4; Gessner and Chauvet 2002).

We tested whether these criteria could distinguish healthy from unhealthy systems by comparing metabolism data from reference sites with data from impact sites (log-transformed analysis of variance [ANOVA]; Fig. 2A–C). Almost all data from the impact sites indicated either poor or satisfactory health according to the criteria. Data from only 16 of 82 impact sites indicated good ecosystem health. Therefore, our proposed framework has the potential to identify sites where ecosystem metabolism has been impaired.

The framework presented here is very broad and could be tightened by developing criteria based on appropriate local reference sites rather than the broad range of sites used in our meta-analysis. For example, light input and shading affect GPP, and patterns of GPP vs ER differed markedly between reference sites with closed canopies (smaller or forested sites) and open canopies (larger or grassland sites) (log-transformed ANOVA, Fig. 3A, B). Reference sites with closed canopies would provide a more appropriate basis of comparison than reference sites with both open and closed canopies when a study is designed to investigate the effect of loss of riparian vegetation on small forested streams. Similarly, ephemeral streams

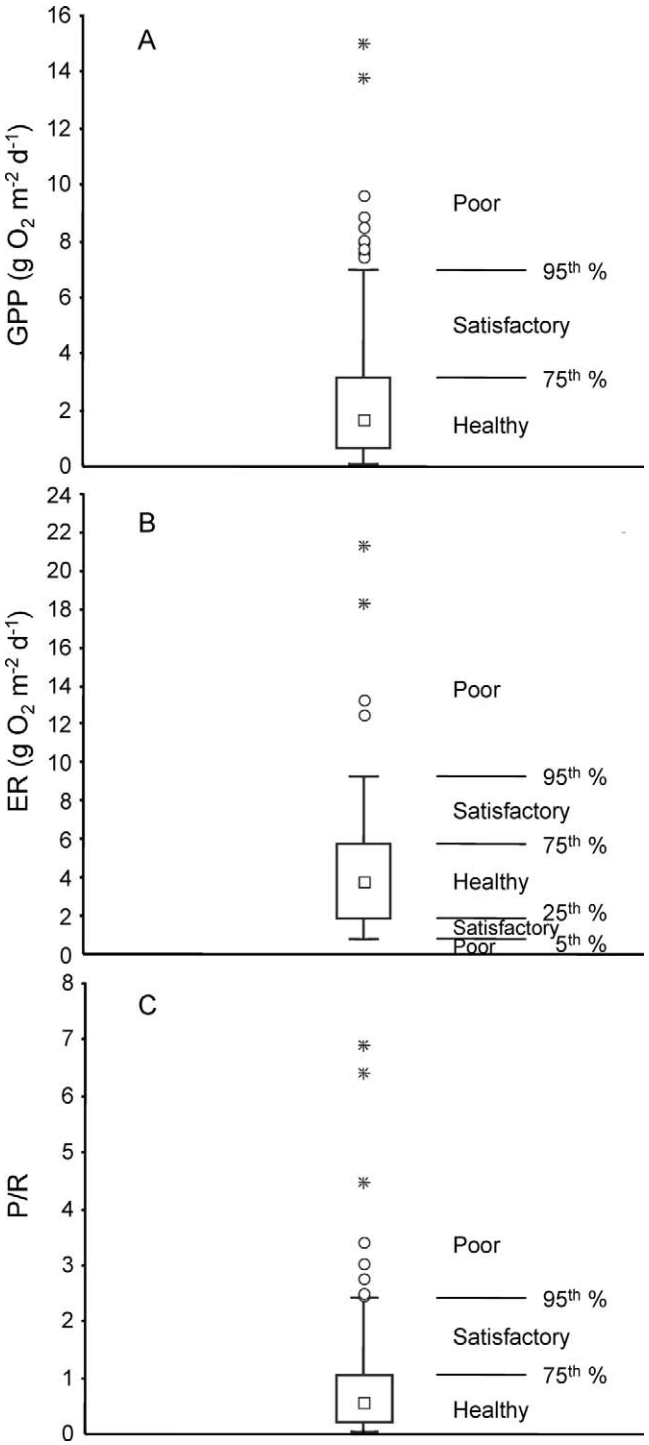

FIG. 1. Distribution of rates of gross primary production (GPP) (A), ecosystem respiration (ER) (B), and the ratio of GPP and ER (P/R) (C) from reference sites ($n = 213$) and proposed criteria that could be used to determine the health of streams. Values were taken from the scientific literature (Wiley et al. 1990, Young and Huryn 1996, 1999, Webster and Meyer 1997, Wilcock et al. 1998, Young 1998, Mulholland et al. 2001, 2006, Hall and Tank 2003, McTammany et al. 2003, 2007, Houser et al. 2005, Meyer et al. 2005, Ortiz-Zayas et al. 2005, Bott et al. 2006, Gücker et al. 2006).

have very high rates of ER associated with accumulation of organic matter during periods of low or no flow (Acuña et al. 2004), and conditions at reference sites for these streams should reflect this characteristic.

Other metrics, such as P/R, also might be useful for detecting particular types of environmental stress where the effects do not apply equally to both GPP and ER (Fig. 1C). For example, P/R was similar at reference and impact sites included in our meta-analysis (log-transformed ANOVA, $p > 0.05$; Fig. 2C), but P/R clearly differed between reference sites with closed and open canopies (log-transformed ANOVA, $p < 0.001$; Fig. 3B).

Advantages and disadvantages as biomonitoring tools

Leaf decomposition.—Leaf breakdown has specific advantages as a potential bioindicator: 1) Measurement is relatively simple and requires inexpensive equipment that is readily available. 2) Many scientific studies have examined the factors that control leaf breakdown, so responses to natural variation and most stressors can be predicted with confidence. 3) Leaf breakdown can be measured in any aquatic habitat, from tiny streams to large rivers, and the method can be used in lakes, wetlands, and estuaries. 4) Criteria for linking leaf breakdown rates and ecosystem health exist already (Gessner and Chauvet 2002).

Leaf breakdown also has disadvantages as a potential bioindicator: 1) Leaf breakdown is influenced by a wide variety of factors, and this broad response can sometimes make interpretation of results difficult. 2) Leaf breakdown is measured at a specific location in a stream and is indicative of conditions only at that location rather than throughout an entire reach; thus, the method is suited best for detecting small-scale effects of stressors. 3) The meaning of this measurement is not intuitive to the general public; therefore, simple and clear explanations are required to demonstrate how leaf breakdown rates can be used to measure river health.

Ecosystem metabolism.—Metabolism has several specific advantages as a potential bioindicator: 1) Metabolism measurements are representative of the entire reach and cover the range of habitat types present, even though the O_2 concentrations used to calculate metabolism are only measured at 1 or 2 specific locations, because of the natural movement and mixing of water in a river. 2) Metabolism directly assesses the balance between energy supply and demand in river ecosystems and, thus, gives an indication of what fuels the ecosystem. 3) Studies of metabolism at one particular site can be planned, conducted, and completed within as little as 2 d,

TABLE 4. Framework for assessing functional stream health using gross primary productivity (GPP) and ecosystem respiration (ER) data. The scores indicate the health of the test site: 2 = no evidence of an impact on ecosystem functioning, 1 = mild effect on ecosystem functioning, 0 = severely impaired ecosystem functioning; t = test site, r = reference site.

Method	Assessment parameter	Criterion	Score
Comparison with reference	GPP_t/GPP_r	$GPP_t/GPP_r < 2.5$	2
		$GPP_t/GPP_r = 2.5–5.0$	1
		$GPP_t/GPP_r > 5.0$	0
	ER_t/ER_r	$ER_t/ER_r = 0.4–1.6$	2
		$ER_t/ER_r = 0.2–0.4$ or 1.6–2.7	1
		$ER_t/ER_r < 0.2$ or $ER_t/ER_r > 2.7$	0
Absolute value	GPP_t (g O_2 m^{-2} d^{-1})	$GPP_t < 3.5$	2
		$GPP_t = 3.5–7.0$	1
		$GPP_t > 7.0$	0
	ER_t (g O_2 m^{-2} d^{-1})	$ER_t = 1.6–5.8$	2
		$ER_t = 0.8–1.6$ or $ER_t = 5.8–9.5$	1
		$ER_t < 0.8$ or $ER_t > 9.5$	0

assuming the necessary equipment is available. 4) Metabolism measurements are closely associated with O_2 dynamics within a river, and even raw O_2 measurements are of interest for assessments of river ecosystem health. 5) The reason for measuring O_2 concentrations in rivers is easily explained to members of the general public.

Metabolism also has potential disadvantages as a potential bioindicator: 1) At least 1 data-logging O_2 meter is required to make metabolism measurements feasible for biomonitoring, and this equipment is expensive. 2) Measurements of O_2 concentration are required over at least a 24-h period; therefore, equipment usually must be left unattended at the sampling site for several hours, with potential losses from theft, vandalism, or sudden changes in flow. 3) Metabolism is difficult to measure in small, turbulent streams with low productivity (e.g., Young and Huryn 1999), and this difficulty limits use of this method for routine biomonitoring in such streams.

Summary and Recommendations

A variety of ecosystem processes potentially could be used as functional indicators of river ecosystem health. However, in our opinion, rates of organic matter decomposition and ecosystem metabolism best meet the requirements of good indicators and, thus, offer the most potential as indicators of the functional aspects of river ecosystem health. These indicators should be seen as complementary to traditional monitoring tools that rely on structural measures. Measurement of both structural and functional aspects provides a more complete picture of ecosystem health than either aspect alone. Our review of the factors controlling these ecosystem processes should help to inform predictions of how the processes will respond to stressors.

We also outlined a framework for interpreting functional measures in terms of ecosystem health. We extended the approach used by Gessner and Chauvet (2002) for interpreting leaf breakdown rates to interpreting ecosystem metabolism on the basis of absolute target values or the degree of departure of measurements at test sites from measurements at equivalent reference sites. Use of absolute values seems to be well suited to metabolism measurements, but the criteria could be tightened by restricting the reference sites used to establish the statistical distributions to sites that are similar to the test sites.

Leaf breakdown and ecosystem metabolism are affected by a wide range of factors, both anthropogenic and natural. The problem of separating responses to natural and anthropogenic factors is not insurmountable. Stream invertebrate communities also are affected by a wide range of natural and anthropogenic factors but have been used successfully for biomonitoring purposes throughout the world. Where possible, naturally varying factors known to influence rates of decomposition or metabolism, such as water temperature, light, or nutrient concentrations, should be measured in the field, and statistical techniques, such as analysis of covariance, should be used to account for their effects during data analysis. Measures of antecedent conditions, such as time since the last bed-moving flood, also should be incorporated into data analysis because ecosystem metabolism, in particular, shows strong successional patterns following these natural disturbances (Uehlinger 2000, 2006). Alternatively, sampling could be avoided during the first 2 to 3 wk following a bed-moving flood to allow ecosystem function to recover to normal levels.

Accumulation of local data collected with standard

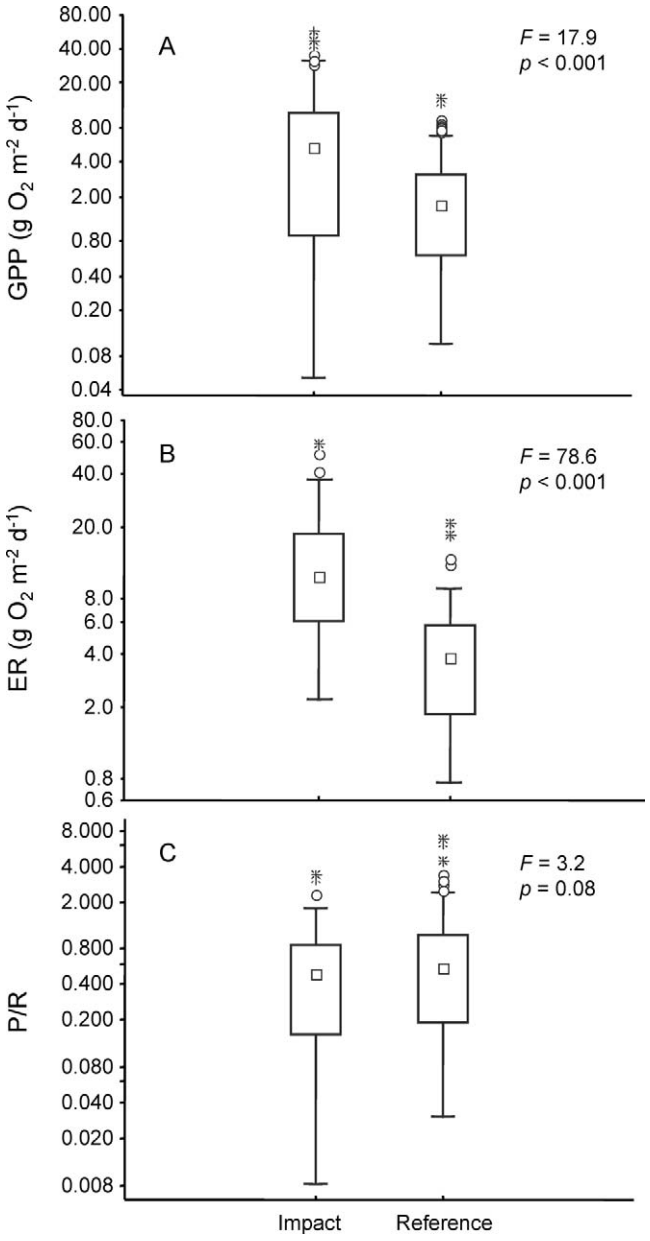

FIG. 2. Comparison of rates of gross primary production (GPP) (A), ecosystem respiration (ER) (B), and the ratio GPP/ER (P/R) (C) between reference sites ($n = 213$) and impact sites ($n = 82$) draining intensively modified land. Values were taken from references listed in Fig. 1.

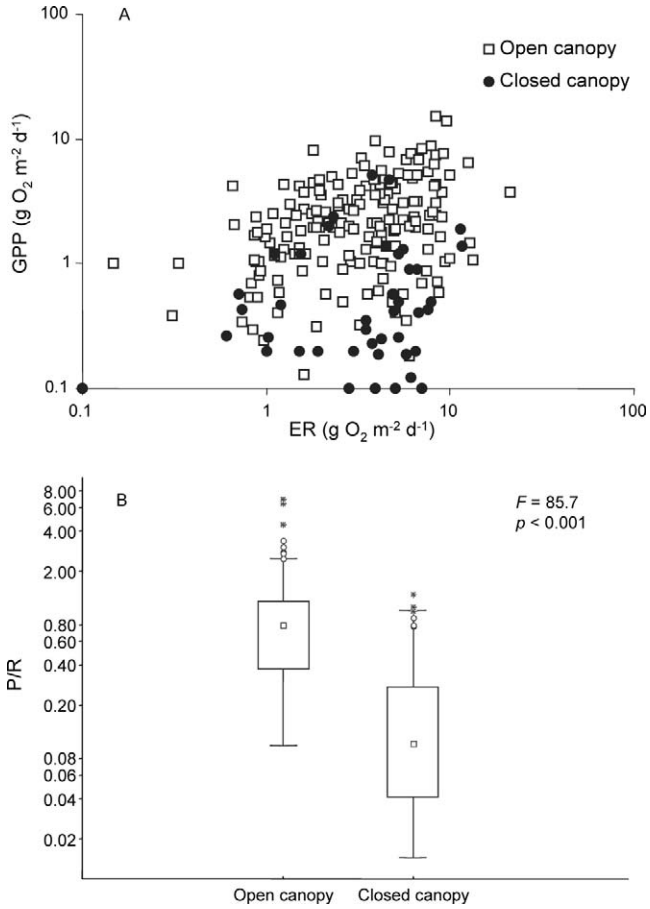

FIG. 3. Plots of ecosystem respiration (ER) vs gross primary production (GPP) (A) and the ratio GPP/ER (P/R) (B) for reference sites with closed ($n = 48$) and open canopies ($n = 165$). Values were taken from references listed in Fig. 1.

field procedures throughout a selected monitoring region should allow increasingly meaningful interpretations of results of individual studies. Local databases could be used to fine-tune tentative criteria for detecting impairment. This process has already begun in Europe (see Gulis et al. 2006, Lecerf et al. 2006, Izagirre et al. 2008). Database development should include trials that address a wide range of stress intensities to identify potentially nonlinear responses and to refine estimates of variability among reference sites. Further research on the influence of interacting stressors on indicator responses (e.g., Niyogi et al. 2003, Hagen et al. 2006, McTammany et al. 2008) also would be valuable.

We recommend methods for measuring organic matter decomposition and ecosystem metabolism that are economical and that limit method-related variability. Use of artificial substrates, such as cotton strips or wooden sticks, instead of highly variable natural leaves reduces within-site variation in decay rates and increases power to detect differences among sites (Tiegs et al. 2007). Methodological improvements also might aid interpretation of results. For example, fluorescence-quenching O_2 probes can be deployed for long periods without calibration and stirring problems, so continuous open-system measurements of O_2 concentrations should become more feasible and, therefore, more common. These data will allow better understanding of natural variability in rates of

ecosystem metabolism and, therefore, will increase our ability to characterize correctly rates that indicate healthy or unhealthy conditions.

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