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Estimating autotrophic respiration in streams using daily metabolism data

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Abstract. The fraction of gross primary production (GPP) that is immediately respired by autotrophs and their closely associated heterotrophs (AR_f) is unknown. This value is necessary to calculate the autotrophic base of food webs, which requires knowing production available for grazers. AR_f is also necessary for estimating heterotrophic respiration (HR) which is needed to calculate C spiraling in streams and rivers. We suggest a way to estimate AR_f from daily metabolism data using quantile regression between GPP and 90% quantile of ecosystem respiration (ER). We reasoned that autotrophic respiration represents the lower limit for ER on any one day and used quantile regression to estimate the relationship of the lower quantile of ER with respect to GPP. We examined this approach with simulation modeling and application of quantile regression to estimates of continuous GPP and ER from >20 streams. Simulation modeling showed that low-uncertainty estimates of AR_f required large variation in daily GPP. Covariance between HR and GPP, which might be observed if the processes were temperature controlled, biased estimates of AR_f. Seasonal estimates of AR_f were robust to daily variation in AR_f as a function of GPP. AR_f calculated from previously published estimates of daily metabolism from streams averaged 0.44 (SD = 0.19) with high variation among streams. This value is higher than most physiological measurements, probably because of light limitation of algae and from HR closely associated with daily GPP. How much of AR_f was from algal respiration vs closely associated heterotrophic respiration is not known, but we suggest that the value $(1 - AR_f)$GPP represents the amount of C available to animals.

Key words: autotrophic respiration, gross primary production, ecosystem respiration, quantile regression, daily metabolism.

Metabolism, i.e., gross primary production (GPP) and ecosystem respiration (ER), is a fundamental process that describes C accumulation and breakdown in ecosystems. Measurements of GPP and ER allow budgeting of C in ecosystems (Lovett et al. 2006) and provide insight into the coupling of C cycling with other elements such as N and P (Hoellein et al. 2007, Hall et al. 2009, Norby et al. 2010). For both terrestrial and aquatic ecosystems, metabolism can be measured accurately at the ecosystem level using CO_2 or O_2 fluxes (Odum 1956, Law et al. 2002), allowing for consideration of various ecosystems in landscape-level C budgets (Battin et al. 2009). However, ecosystem-level, gas-flux methods cannot differentiate autotrophic respiration (AR), the respiration of C by plants, from heterotrophic respiration (HR), the respiration of organic C by heterotrophs (Newbold et al. 1982, DeLucia et al. 2007). Resolving the relative contribution of AR and HR to ER is needed for many ecological analyses, including estimates of the response of the terrestrial C budget to future climate change (Wei et al. 2010) and estimates of organic C spiraling lengths in streams (Newbold et al. 1982, Webster 2007). Organic C spiraling length is the ratio of downstream C flux to HR. HR is necessarily assumed and not measured (Taylor et al. 2006, Griffiths et al. 2012).

How much of the ER in aquatic ecosystems is from AR is unknown. In terrestrial ecosystems, this calculation can be done by comparing gross CO_2 uptake with estimates of net primary production (NPP) based on biomass accumulation rates (DeLucia et al. 2007). In algae-based freshwater ecosystems, biomass accumulation rates are very difficult to measure because the biomass turns over rapidly and

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a fraction of GPP is leaked as dissolved organic C (DOC) and not added to biomass (Baines and Pace 1991). Consequently, when authors have needed to estimate AR in aquatic ecosystems they have done so based on the results of laboratory or model studies (Webster and Meyer 1997, Young and Huryn 1999), which are rarely verified at the ecosystem level (Solomon et al., in press).

We present a statistical approach to estimating the fraction of GPP respired by autotrophs and their closely associated heterotrophic bacteria that is based on whole-stream metabolism measurements. For simplicity, we define this respiration as AR, though we recognize that the approach cannot separate photosynthesized C that is immediately respired by heterotrophs from that respired by photoautotrophs themselves. Following del Giorgio and Williams (2005) and Solomon et al. (in press) we define HR_c as heterotrophic respiration coupled to GPP at a time scale of ≤ 1 d that composes an unknown fraction of AR. Base heterotrophic respiration (HR_b) is respiration not associated with daily algal production, but rather is respiration of allochthonous inputs or autotrophic biomass at a time scale >1 d after C fixation. Daily variation in GPP does not control HR_b and is the quantity that we measured in our study. Our objectives were to: 1) design a statistical approach to estimate AR based on daily metabolism estimates for streams, 2) use simulation modeling to estimate conditions under which it is feasible to estimate AR from daily metabolism time series, and 3) estimate values of AR from published daily metabolism data sets.

Methods

Approach

We estimated AR by relating ER to GPP. Consider a hypothetical ecosystem that receives no allochthonous sources of C and has no heterotrophic respiration of accumulated NPP. All respiration would be from the plants themselves. The value of the slope of a line relating ER to GPP would be the fraction of daily GPP that is respired by these plants. However, in real ecosystems, ER represents the sum of AR and HR_b. We reasoned that AR represents the minimum amount of ER that can occur on any one day above some level of HR_b (Fig. 1). Therefore, AR should correspond to the upper limit of the relationship between ER (where ER is negative) and GPP. We used quantile regression to quantify the relationship between the upper quantile of ER vs GPP (Koenker and Hallock 2001, Cade and Noon 2003) (Fig. 1). Ordinary least squares regression estimates the mean of y as conditioned on x, but quantile regression estimates quantiles of y as conditioned on x (Cade and Noon 2003). We chose the 0.9 quantile as a tradeoff between describing the upper edge of the data and having enough data points to describe that quantile.

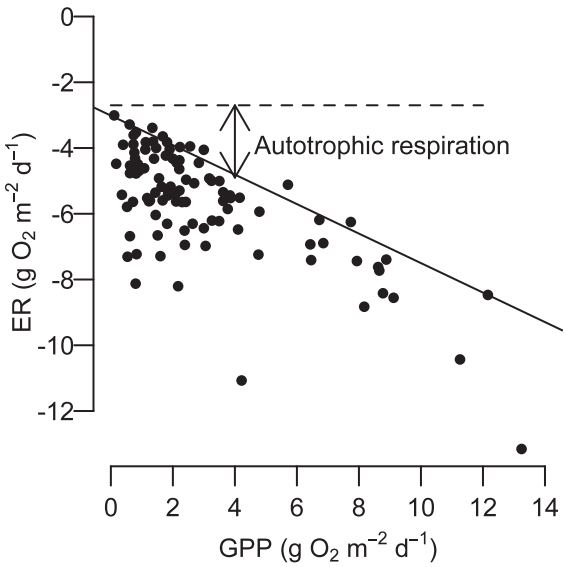

FIG. 1. Simulated data showing calculation of autotrophic respiration. Data are 100 d of metabolism with gross primary productivity (GPP) drawn from a log-normal distribution with mean = ln2 and SD = 1 and base heterotrophic respiration (HR_b) drawn from a log-normal distribution with mean = ln2 and SD = 0.5. Base level HR_b was -2 g O_2 m^{-2} d^{-1} plus the random variation (hence predicted y-intercept is -2.7 g O_2 m^{-2} d^{-1}). Autotrophic respiration was set at 0.45GPP. The solid line is the quantile regression of the 0.9 quantile of these randomly generated data, where ecosystem respiration (ER) = -0.46GPP $- 3.04$. The double-headed arrow indicates the amount of ER that is from autotrophic respiration.

Simulation

We used simulation to identify the conditions under which we could use quantile regression successfully to estimate the fraction of GPP immediately respired by algae and closely associated heterotrophs (AR_f) from daily metabolism data. We predicted that a large range in GPP would provide a more constrained estimate of AR_f simply because we extended the x-axis in the regression. However, we also predicted that highly variable HR_b would add error to the regression slope, and thus, to AR_f. We used a Monte Carlo simulation to test these predictions as follows. First, we assumed that GPP and HR_b are log-normally distributed. This distribution is skewed right, with all values >0 and is phenomenologically similar to the distribution of time-series data of metabolism (see *Data* section). We created a range

of variability for GPP and HR by generating a vector of 20 standard deviations (SDs) ranging from 0.05–1.5, given a mean for both HR and GPP of ln2. These means and SDs of lnGPP and $-\ln HR_b$ were similar to those from Walker Branch and Shepherd Creek (see Results). For each of the 400 combinations of $\ln HR_b$ SD and lnGPP SD, we simulated 1000 data sets, each of which comprised 100 d of GPP and HR_b values that were randomly selected from a log-normal distribution defined by these 400 combinations of SDs. On each day we calculated AR and ER as:

$$AR = (AR_f)(GPP) \quad [1]$$

$$ER = AR + HR_b \quad [2]$$

For the simulations we used $AR_f = 0.45$, close to the mean AR_f estimate from literature data (see Results). From each of the 1000 data sets, we estimated the slope of the regression of the 0.9 quantile of the ER vs GPP data ($\tau = 0.9$) for a total of 40,000 estimates of quantile slope. We used package *quantreg* in R to calculate quantile regressions (R Development Core Team 2011, Vienna, Austria; Koenker 2011). We subtracted the 0.05 and 0.95 quantiles from this distribution of the 1000 slope estimates as an estimate of the measurement error for any 1 of 400 combinations of GPP and HR range. All simulations were run in R.

We also used simulation modeling to test 2 other assumptions in our approach. One assumption is that HR_b does not covary with GPP. Reasons exist to think that HR_b might covary with GPP, e.g., warmer summer temperatures may increase HR_b and GPP. To examine the effect of covarying HR_b on GPP, we generated 1000 data sets of 100 random daily observations of GPP and HR_b, where HR_b varied log-normally with mean of ln2 and SD of 0.5 and GPP varied log-normally with mean of ln2 and SD of 1. We chose these SDs as a combination that allowed estimation of AR_f with a confidence interval (CI) of ~0.1. We forced HR to covary with GPP (HR_{corr}) as:

$$HR_{corr} = a\text{GPP} + \text{HR} \quad [3]$$

where a ranged from -0.15 to $+0.15$ corresponding to Pearson correlation coefficients (r) between HR and GPP ranging from -0.29 to 0.29. For each simulation, we recorded the median and 5 and 95% quantiles of the resulting distribution of the slope of the 0.9 quantile between ER and GPP.

In another simulation, we examined how variation in AR_f as a function of GPP would affect overall estimates of AR_f. GPP may vary as a function of algal species composition, and different algal assemblages may have different AR_f. Alternatively, the fraction of AR that is HR_c may vary with GPP, which would result in a positive correlation between GPP and AR_f. We varied AR_f as:

$$AR_f = \frac{b\text{GPP}}{GPP_{max}} + 0.45 - \frac{b}{2} \quad [4]$$

for b ranging from -0.3 to 0.3. For example $b = 0.3$ meant that AR_f ranged from 0.3 to 0.6 with a center of 0.45, as GPP increased from 0 to its maximal value, GPP_{max}. For $b = -0.1$, AR_f declined from 0.5 to 0.4 as GPP increased to its maximum.

Data

We used quantile regression to estimate AR_f from continuous GPP and ER measurements reported for 25 streams and rivers in the USA, Spain, and Australia. We used winter, spring, and summer data from Walker Branch, a forested stream in southeastern USA (Roberts et al. 2007), because this time period encompassed a large range in GPP, but excluded autumn litterfall when ER values increase as a consequence of litter inputs (B. Roberts, Louisiana University Marine Consortium, personal communication). We also used data from an open canopy, western USA river, the Portneuf (Marcarelli et al. 2010). Some GPP values were <0, and we deleted these values from the data set. Another data set came from 19 streams in the Basque region of Spain (Izagirre et al. 2008). These streams had continuous metabolism measurements for an average of 217 d/stream. We also used data from 3 sites distributed along 366 km of the Mitchell River in the Australian tropics. These sites had continuous metabolism measurements on 76 to 124 d (Hunt et al. 2012). Last, we used 23 mo of daily data from Shepherd Creek, a 2nd-order, urban stream in the midwestern USA (Beaulieu et al., in press). For each stream, we used quantile regression to estimate the slope and 90% CIs for the 0.9 quantile of the data (Koenker and Hallock 2001, Cade and Noon 2003, Koenker 2011). We also used quantile regression to estimate AR_f from a pooled data set of 305 individual measurements of GPP and ER in streams in the USA, Europe, Japan, New Zealand, and South America (Bernot et al. 2010, Marcarelli et al. 2011).

Results

Simulation modeling

Estimating AR_f with high precision required metabolism data spanning a wide range of GPP. For example, the simulation showed that if SD of $\ln HR_b$ was ≥ 0.5, SD of lnGPP had to be >1 to estimate AR_f

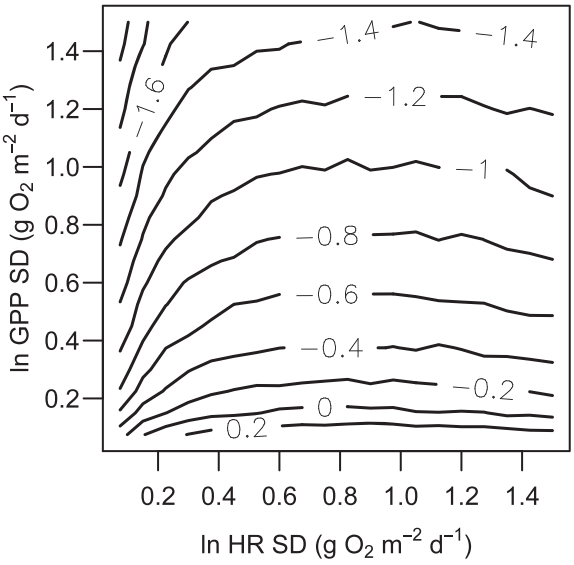

FIG. 2. Error analysis (contours) as a function of ecosystem respiration (ER) and gross primary production (GPP) variation in simulated 100-d data sets. Error on quantile slopes between GPP and ER decreases as the range in GPP increases and range in base heterotrophic respiration (HR_b) decreases. The *x*-axis is variability in HR_b, and the *y*-axis is variability in GPP for any 1 simulated data set of 100 metabolism days. Variability is reported as the standard deviation (SD) of lnHR_b or GPP, with a mean of ln2 for both. Contours correspond to the $\log_{10}$ confidence interval (CI) of the slope estimate, e.g., −1.0 corresponds to a CI of ±0.05, and −0.8 corresponds to a CI of ±0.08.

with a CI of ±0.05 (Fig. 2). The effect of increasing HR_b saturated at ~0.6 for this combination of parameters, such that very high variation in HR_b did not decrease precision of the estimate. In contrast, increasing variation in GPP always provided more precise estimates of AR_f (Fig. 2). These simulation results showed that high variation in GPP was required and, therefore, we would be unable to estimate AR_f in all data sets. Thus, we did not consider quantile regression estimates from metabolism time-series data where the CI of AR_f was >0.4. We considered estimates of AR_f with error >0.4 too uncertain to be ecologically insightful. A more restrictive CI would have depleted the number of studies for analysis.

Simulation modeling showed that estimates of AR_f were sensitive to correlation between HR and GPP. If HR was correlated to GPP with $r = 0.29$, then the estimate of AR_f was 0.31, ~⅔ of the true estimate of 0.45 (Fig. 3A). Conversely, if HR_b was negatively correlated with GPP to the same extent, then the estimate of AR_f was 0.61, ~⅝ of the true estimate (Fig. 3A).

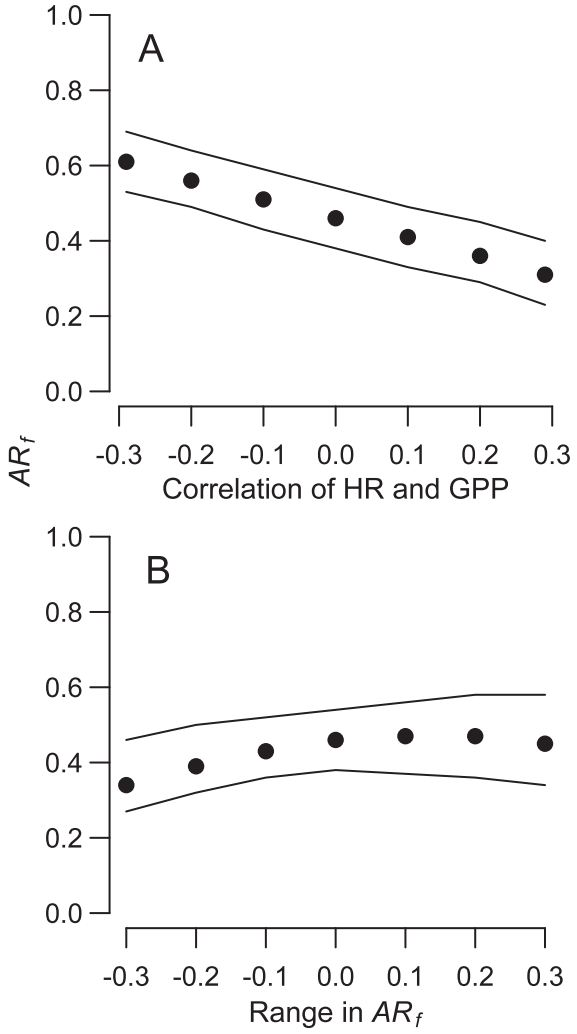

FIG. 3. A.—Positive correlation between HR_b and GPP decreases the estimate of the fraction of GPP respired by autotrophs (AR_f), and negative correlation between HR_b and GPP increases the estimate of AR_f. Simulation is based on log-normally distributed HR_b and GPP with mean of ln2 and standard deviations (SD) of 0.5 for HR_b and 1.0 for GPP. *x*-axis values are Pearson correlation coefficients. Points are medians of 1000 simulations of data sets corresponding to 100 d. Lines are the upper and lower 2.5% quantiles. B.—Varying AR_f with GPP moderately affected the estimate of AR_f. Simulations were as for panel A, but AR_f was allowed to covary on a day-to-day basis as a function of GPP. At the lowest GPP level, the modeled AR_f was offset from the mean value by −0.3. At maximum GPP, modeled AR_f was offset from the mean value by +0.3.

Varying AR_f as a function of GPP did not strongly affect estimates of AR_f. If daily AR_f increased by 0.3 across the range of GPP, the increase in the seasonal estimate of AR_f was ~0.02, much smaller than the estimation error (Fig. 3B). If AR_f decreased 0.3 across

TABLE 1. Estimates of the fraction of gross primary productivity respired by autotrophs and closely associated heterotrophs (AR_f) for 13 streams. AR_f was calculated as the slope of the quantile regression of gross primary productivity and ecosystem respiration for the 0.9 quantile. Only slopes from streams with 95% confidence interval <0.4 are shown.

Stream	Reference	AR_f	Confidence interval
Walker Branch	Roberts et al. 2007	0.43	0.40–0.46
Portneuf River	Marcarelli et al. 2010	0.34	0.13–0.58
Shepherd Creek	Beaulieu et al. in press	0.69	0.62–0.71
Aitzu	Izagirre et al. 2008	0.64	0.45–0.79
Aizarnazabal	Izagirre et al. 2008	0.47	0.41–0.53
Alegia	Izagirre et al. 2008	0.64	0.45–0.75
Anorebieta	Izagirre et al. 2008	0.65	0.41–0.79
Berriatua	Izagirre et al. 2008	0.11	0.05–0.31
Erenozu	Izagirre et al. 2008	0.17	0.14–0.23
Gardea	Izagirre et al. 2008	0.35	0.30–0.49
Lasarte	Izagirre et al. 2008	0.47	0.38–0.60
Nuxika	Izagirre et al. 2008	0.41	0.36–0.47
Oiartzun	Izagirre et al. 2008	0.30	0.12–0.41

the range in GPP then the estimate of AR_f was 0.34, ~75% of the seasonal estimate (Fig. 3B).

Empirical estimates

We estimated AR_f with variable success among 25 streams and rivers. Walker Branch, Portneuf River, and Shepherd Creek provided constrained estimates of AR_f (Table 1, Fig. 4A–C). Three rivers in Australia had narrow GPP ranges (0.8 to 3.4 g O_2 m^{-2} d^{-1}) and, therefore, highly unconstrained estimates of AR_f (CI > 0.5, data not shown). Among the 19 Basque streams, 10 estimates of AR_f had CIs <0.4 (Fig. 5, Table 1). The mean of all 13 streams with constrained estimates of AR_f was 0.44 with an SD of 0.19 (Table 1). Differences in AR_f between several streams were statistically significant (i.e., 95% CI did not overlap) suggesting that the value of AR_f is not universal among stream ecosystems.

We applied this statistical approach to a pooled data set of daily estimates of GPP and ER from many streams and found that the slope of the 0.9 quantile of AR_f was 0.63 (CI = 0.53–0.66), which was within the range of AR_f values estimated for individual streams (Fig. 6, Table 1).

Discussion

We presented an approach that, under circumstances of high range in GPP, can estimate the fraction of GPP consumed by respiration each day. We based this approach on the assumption that AR represents the lower limit for ER on any one day above some level of HR_b (Fig. 1). AR averaged 44% of GPP for 13 streams that had constrained quantile regression slope. For our approach to be valid, we necessarily made several assumptions, which we outline below.

Assumptions

What we call *autotrophic respiration* is not a physiological measure of immediate algal respiration, but rather a measure of the total respiration supported by GPP on the same day. That is, our estimate of AR includes an unknown fraction of HR_c that is tightly coupled to GPP. One mechanism for this tight coupling is the release of photosynthetically produced dissolved organic C (DOC), which can fuel immediate bacterial respiration (Cole et al. 1982). Therefore, the quantity $(1 - AR_f)$GPP is not a true estimate of NPP because HR_c somewhat inflates the estimate of AR_f. Obtaining true estimates of NPP in algae-dominated stream ecosystems is difficult because algae turn over their biomass quickly (1–21 d; Odum 1957, Dodds et al. 2000) and release 2 to 40% of their C as DOC (Baines and Pace 1991). From a foodweb or an ecosystem standpoint, GPP that is immediately respired by bacteria or algae is not available for higher trophic levels or storage as biomass. Thus, $(1 - AR_f)$GPP represents the amount of autochthonously produced C available for storage, transport, or consumption by higher trophic levels. We suggest that it is an appropriate quantity with which to assess net autotrophic production in freshwater ecosystems.

If HR_b covaries with GPP, then estimates of AR_f can be highly biased. Correlation of HR_b and GPP with $r = 0.3$ can decrease the estimate of AR_f by 0.15. Negative correlation between HR_b and GPP can increase the estimate of AR_f by the same amount. We may expect correlation between HR_b and GPP as temperatures warm, which can increase both photosynthesis and respiration, albeit at different rates because the activation energy for respiration is higher than that for photosynthesis (Yvon-Durocher

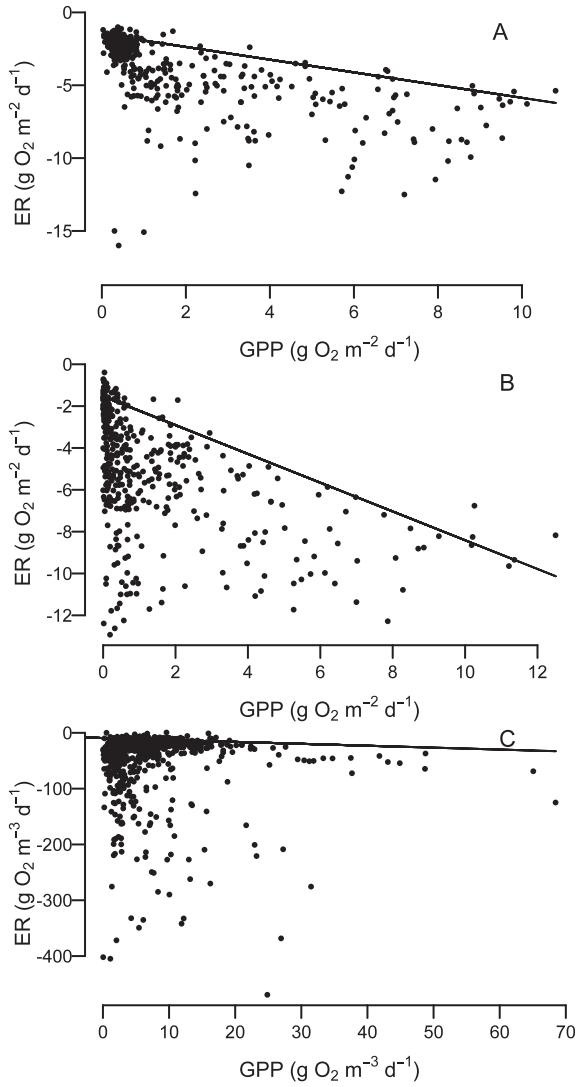

FIG. 4. Quantile regressions ($\tau = 0.9$) of ecosystem respiration (ER) and gross primary production (GPP) for Walker Branch (Roberts et al. 2007) (A), Shepherd Creek (Beaulieu et al., in press) (B), and Portneuf River (Marcarelli et al. 2010) (C). Lines are the 0.9 quantile regressions. Parameters are in Table 1. Note volumetric units of metabolism for the Portneuf River.

et al. 2010). In addition, warm temperatures correspond to sunny parts of the year when photosynthesis is high in open-canopy streams. GPP could also stimulate HR_b by releasing photosynthetically produced DOC into the water column. This DOC may support HR_b directly and may prime the bacterial degradation of more recalcitrant allochthonous organic matter (Bianchi 2011). Evidence for this possibility comes from tropical rivers where ER vs GPP had a slope >1 suggesting that HR_b increased with GPP (Townsend et al. 2011). Forested streams in temperate climates frequently exhibit predictable patterns in HR_b and GPP. Maximum HR_b typically is observed during autumn leaf fall, whereas maximum GPP is observed during high-light periods in winter and spring (Roberts et al. 2007). Therefore, our method may perform best in forested regions when applied to winter and spring metabolism data. We may expect negative correlation between HR and GPP in a forested stream during autumn, when HR_b increases during litter fall. A consideration when choosing the time of year to calculate AR_f is that the data set contain enough days to estimate the slope of the 0.9 quantile of ER precisely, but few enough days that big changes in HR_b caused by, e.g., litterfall or large floods, are not included. We suggest that this ideal number of days will vary from stream to stream, and investigators should consider the length of record needed to balance statistical power with low seasonal variation in HR_b. One can check the estimates of daily HR_b to estimate the degree to which they relate with GPP.

We assumed that AR_f does not change as a function of GPP. However, this assumption might not be met for several reasons. First, algal assemblages change seasonally, and some taxa may have higher rates of respiration per unit of growth than other taxa because of variation in maintenance metabolism (Geider and Osborne 1989). Algal cell size probably does not explain variation in respiration. Respiration scales isometrically with cell size in algae (Tang and Peters 1995). Second, the fraction of AR that consists of tightly coupled heterotrophic respiration (HR_c) may change with GPP, in that higher rates of GPP may increase HR_c and, therefore, AR_f. Regardless of the mechanism that might generate variability in AR_f, our simulation model results indicate that our method of estimating AR_f is fairly robust to changes in AR_f values linked to GPP. Even if daily AR_f were increased by 0.3 across the range of GPP, the overall seasonal mean estimate of AR_f would change little.

Estimating AR_f using the quantile-regression approach will not be possible in all streams. Based on output of our simulation model, the method requires high variation in GPP to produce constrained estimates of AR_f. In this case, simulation modeling provides a way to estimate the degree to which we can estimate the parameter AR_f because we programmed the true value. When we applied quantile regression to streams with low variation in GPP, our approach produced 95% CIs for AR_f that were >0.4. Other streams did have high variation in GPP, but estimates of AR were poorly constrained, possibly from too much variation in HR_b or HR_b that covaried with GPP very strongly.

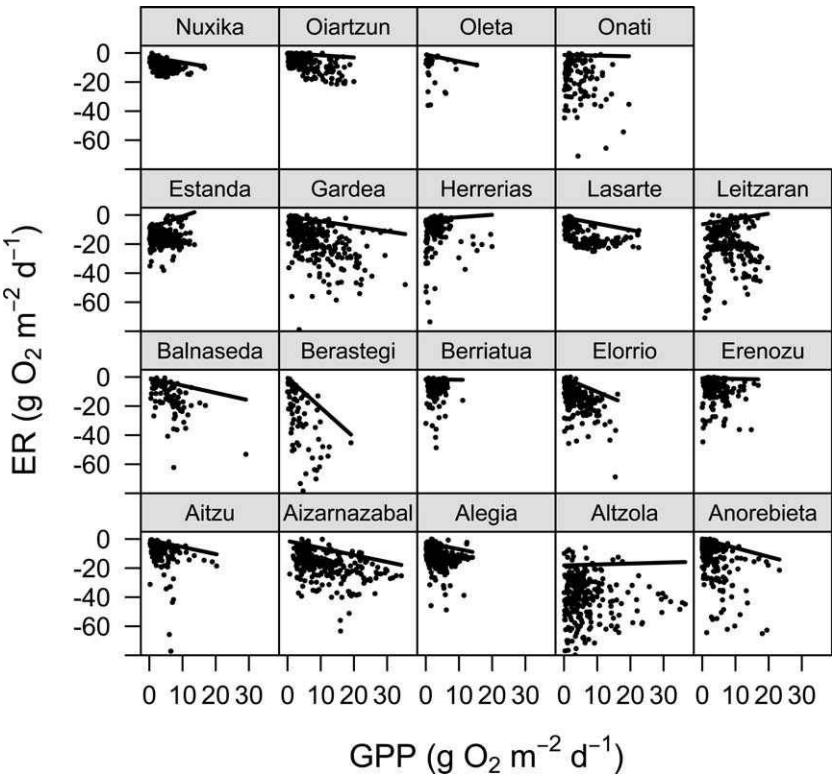

FIG. 5. Quantile regressions ($\tau = 0.9$) of ecosystem respiration (ER) and gross primary production (GPP) for 19 streams in the Basque region of Spain (Izagirre et al. 2008). Each panel is one of 19 named streams. Lines are the 0.9 quantile regressions. Parameters are in Table 1.

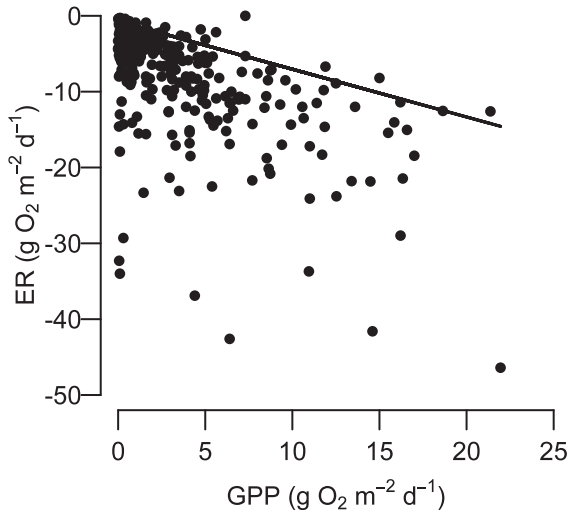

FIG. 6. Ecosystem respiration (ER) vs gross primary production (GPP) for 305 streams around the world. The line is the quantile regression ($\tau = 0.9$) with slope = 0.63 (95% CI = 0.53–0.66) indicating that across all streams autotrophic respiration (AR) constituted 0.63GPP.

Comparison of AR_f *among ecosystems*

The mean AR_f value calculated using long-term metabolism data sets from the 13 streams included in our study was 0.44 ± 0.19 (SD) (Table 1), indicating that roughly ½ of the recently fixed C was immediately respired in the streams. This finding was supported by the analysis of 1-time metabolism measurements made in 305 streams where we found a AR_f value of 0.63 (CI = 0.53–0.66). This value from the 305 streams is higher than those from continuous estimates, probably because the 0.90 quantile from this data set was dominated by those streams with the largest AR_f values. Streams with a lower AR_f would fall below the 0.90 quantile regression line. The AR_f values reported here were similar to but somewhat higher than values from other aquatic ecosystems and were much higher than AR_f derived from physiological measurements. For example, Graham et al. (1985) reported an AR_f of 0.2 for *Ulothrix*, a filamentous alga, under laboratory conditions. Similarly, Geider and Osborne (1989) reported that the ratio of dark respiration to light-saturated photosynthesis ranged from 0.07 to 0.35 (Geider and Osborne 1989) across several algal taxa under laboratory conditions. We

propose 2 reasons for our high estimates of AR_f: 1) our regression approach by necessity estimates immediate HR in addition to algal respiration, and 2) algae in ecosystems with substantial light limitation might struggle to maintain a positive C balance resulting in high algal respiration relative to GPP.

Light limitation may control AR_f in stream ecosystems such that highly light-limited algae might have high respiration demand relative to the rate of C fixation. Attached algae in stream ecosystems could be shaded by turbid water or dense riparian canopy cover. Variation in shading might explain the difference in AR_f values among the streams included in our study. However, canopy cover in Basque streams (Izagirre et al. 2008) was not related to AR_f values (Pearson correlation, $p > 0.05$). Another shading mechanism in small streams is self-shading, whereby the upper layers of the periphyton mat shade the bottom layers. The bottom layers support similar AR, but lower GPP. McIntire et al. (1996) used a modeling approach to suggest that AR_f increased from 0.2 to 0.4 when grazing was eliminated, probably because grazing reduced self-shading of the deeper periphyton layers and allowed the mat to support greater photosynthetic rates per unit mass of periphyton. Self-shading among periphyton mats in stream ecosystems is analogous to the effects of allometry of photosynthetic vs nonphotosynthetic tissue on AR_f in vascular plants. DeLucia et al. (2007) reported that forest ecosystems supported an average AR_f of 0.47, but this value increased with forest age and decreased with relative leaf mass, suggesting that bigger trees have higher AR_f due to allometry of photosynthetic tissue.

Planktonic algae can have variable AR_f, depending upon the degree of light limitation, and provide a useful comparison to AR_f for benthic algae. A survey of marine literature showed that AR_f for phytoplankton is 0.35 ± 0.02 (Duarte and Cebrian 1996), a value lower than we found for attached algae in stream ecosystems. However, at the ecosystem level, AR_f for phytoplankton-based ecosystems like large rivers, lakes, and estuaries probably is >0.35 because of the preponderance of algal dark respiration. Light availability in deep and turbid habitats may vary from full sunlight at the water surface to values too low to support photosynthesis below the photic zone. In these deep, light-limited waters, phytoplankton would continue to respire (i.e., dark algal respiration) whereas photosynthesis would cease, leading to high AR_f values. Cole et al. (1992) estimated that AR was sufficiently high in the turbid Hudson River to make algal growth impossible over much of the river during much of the year. Similarly, Lewis (1988) found that autotrophic respiration exceeded photosynthesis in the Orinoco River. Solomon et al. (in press) showed that daily coupling of ER and GPP, which is similar to our estimate of AR_f, varied between 0.4 and 1 in a suite of lakes, a result showing that much of daily GPP was respired immediately. Thus, it appears that on a per algal cell basis, phytoplankton may support lower AR_f values than reported here, but at the ecosystem level, phytoplankton-based ecosystems may support equivalent or even higher AR_f values than stream ecosystems. However, the mechanisms controlling variation in AR_f among streams remain unclear.

Prospectus

We emphasize that our approach to estimating AR_f is merely a step in the direction of solving the difficult problem of partitioning ER into HR and AR at the ecosystem level. Our approach is similar to that of Solomon et al. (in press). Several assumptions in our approach may represent research questions. One is the degree of covariance between GPP and HR_b, to the extent that GPP may control rates of HR via priming (Bianchi 2011). Another is to estimate the amount of HR_c associated with daily GPP. What fraction of GPP fuels HR_c? Does this fraction change as a function of GPP? We also do not know what controls variation in AR_f within or among streams. This knowledge will require additional data.

Estimating AR_f will allow investigators to partition AR and HR in aquatic ecosystems. Knowing AR will allow estimation of the C available for higher trophic levels, export, or storage. In addition, knowing HR_b will allow more accurate calculation of spiraling lengths of C in streams, which is the ratio of transported C to heterotrophically respired C. The caveat is that >50 continuous daily estimates of metabolism are required to estimate AR_f precisely for a stream. Fortunately, these data are becoming increasingly available. The downside is that like in forests, AR_f probably is not constant among freshwater ecosystems. If one does not have data to estimate AR_f , we suggest bounding the estimate based on the studies to date and estimating C spiraling or C available for higher trophic levels probabilistically rather than assuming a discrete AR_f value. Such an analysis will measure the sensitivity of the process of interest (e.g., C spiraling) to variation in the assumed AR_f value. However, with daily metabolism data coupled with frequent measures of C transport, it may be possible to generate real-time estimates of C spiraling, which will provide a clearer picture on the controls of upstream and downstream linkages in streams and rivers (Webster 2007).

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