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ECOSYSTEMS

Plumbing the Global Carbon Cycle: Integrating Inland Waters into the Terrestrial Carbon Budget

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ABSTRACT

Because freshwater covers such a small fraction of the Earth's surface area, inland freshwater ecosystems (particularly lakes, rivers, and reservoirs) have rarely been considered as potentially important quantitative components of the carbon cycle at either global or regional scales. By taking published estimates of gas exchange, sediment accumulation, and carbon transport for a variety of aquatic systems, we have constructed a budget for the role of inland water ecosystems in the global carbon cycle. Our analysis conservatively estimates that inland waters annually receive, from a combination of background and anthropogenically altered sources, on the order of 1.9 Pg C y^{-1} from the terrestrial landscape, of which about 0.2 is buried in aquatic sediments, at least 0.8 (possibly much more) is returned to the atmosphere as gas exchange while the remaining 0.9 Pg y^{-1} is delivered to the oceans, roughly equally as inorganic and organic carbon. Thus, roughly twice as much C enters inland aquatic systems from land as is exported from land to the sea. Over prolonged time net carbon fluxes in aquatic systems tend to be greater per unit area than in much of the surrounding land. Although their area is small, these freshwater aquatic systems can affect regional C balances. Further, the inclusion of inland, freshwater ecosystems provides useful insight about the storage, oxidation and transport of terrestrial C, and may warrant a revision of how the modern net C sink on land is described.

Key words: global carbon; freshwater-ecosystems; inland-waters.

INTRODUCTION

Carbon in the biosphere is unevenly distributed among three major reservoirs: terrestrial, oceanic and atmospheric. Simplified depictions of the global carbon cycle have generally consisted of two biologically active boxes (oceans and land) connected through gas exchanges with a third box, the atmosphere (Bolin 1981; Siegenthaler and Sarmiento 1993; IPCC 2001). This approach has been

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*Corresponding author; e-mail: colej@ecostudies.org informative, and has led to the identification of major knowledge gaps, such as apparent imbalances in the global budget. It has also been valuable in understanding and evaluating the likely response of these reservoirs to large-scale phenomena such as global change. As models developed further, more sub-compartments and processes have been added in an attempt to unravel the more intricate interactions among them (for example, Parton and others 1994; Foley and others 1996; Canadell and others 2000; Cramer and others 2001). A feature of this generation of models is that the role of inland aquatic environments is rarely explicitly included. Work during the 1970s and 1980s demonstrated that rivers deliver significant amounts of terrestrially-derived organic and inorganic C from land to the sea (Degens and others 1991; Schlesinger and Melack 1981). This riverine ''pipe'' transports C from land to the ocean.

When inland aquatic systems are included in global models, it is usually only for the transport of C through the riverine pipe. This delivery of terrestrial C through the riverine drainage network is in fact the end result of a number of transformations and losses in aquatic systems en route. In this paper, we review the current knowledge on global rates for inland aquatic systems of C storage in sediments, C exchange with the atmosphere and transport along the flow path from upland systems to the ocean. We compare these net losses en route to both the amount of C transported by rivers and to the net amount of C sequestered on land. We show that the transfer of terrestrial C to inland aquatic ecosystems is considerably larger than delivery of that C to the sea and nearly co-equal with estimates of net ecosystem productivity (NEP) of the terrestrial biosphere.

FORMULATING INTEGRATED C BUDGETS

For the biosphere as a whole, and for the vast majority of terrestrial environments, carbon enters the biological part of the system via photosynthetic assimilation of atmospheric CO_2 [gross primary production (GPP)]. This assimilated carbon then supports the respiration (R) of all organisms (plant, microbe and animal), plus some abiotic oxidation to CO_2 in fire and photo-oxidation (Bertilsson and others 1999; Randerson and others 2002). The portion of GPP not remineralized, called net ecosystem production (NEP), has only two possible fates: storage within the system (S, as increased living plus dead biomass or additional abiotic storage), and export (E). Abiotic storage of CO_2 can also be significant. In the ocean, for example, recent increases in the partial pressure of CO_2 in the atmosphere above that in the surface ocean drive CO_2 into solution (Revelle and Suess 1957; Falkowski and others 2000). This abiotic process is the major way that atmospheric C is sequestered in the ocean at present and is much larger than biotic pathways. For terrestrial environments, the weathering of carbonate and aluminosilicate minerals into bicarbonate (largely by the CO_2 from soil respiration) is the major abiotic pathway, but is small in comparison to biotic pathways (Ittekkot and others 2004).

Terrestrial ecosystems have a large capacity to sequester atmospheric CO_2 when growing. Values of NEP in excess of $100\ \mathrm{g\ C\ m^{-2}\ y^{-1}}$ are not uncommon for actively growing forested ecosystems (Hollinger and others 2004; Canadell and others 2000). At broad spatial scales, and when averaged over longer time scales, accumulation rates are considerably lower (for example, Schimel and others 2001) and storage occurs primarily as soil organic matter. Boreal peatlands, for example, one of the most consistent long term C stores on land, have accumulated about 2–7 $\mathrm{g\ C\ m^{-2} y^{-1}}$ over the Holocene (Post and others 1982; Smith and others 2004). Except for rapidly aggrading ecosystems, much of terrestrial NEP is exported by fluvial processes (Schlesinger and Melack 1981; Fahey and others 2005), consistent with the slow accumulation rate of soil carbon observed in many regions (Tremblay and others 2002; Liski and Westman 1997).

In addition to their own primary production, freshwater ecosystems are subsidized by imported carbon (I) from land. This imported carbon can be both organic and inorganic, with different implications for the ecology and C dynamics of the receiving water bodies. The subsidy of organic carbon can alter the metabolic balance of freshwaters (Caraco and Cole 2004; Hanson and others 2004). Because organic C inputs can be co-equal or larger than aquatic GPP, respiration, export, or storage can also be significantly larger than aquatic GPP, a condition very rarely met on land (Polis and Power 2004). Lakes, for example, are commonly net sources of CO_2 to the atmosphere while simultaneously burying organic C in their sediments (Dillon and Molot 1997; Kortelainen and others 2004; Duarte and Prairie 2005; Pace and Prairie 2005; Rantakari and Kortelainen 2005; Sobek et al. 2005). In lakes, R often exceeds GPP (that is, NEP is negative) because a portion of the organic C imported from land is respired (del Giorgio and Peters 1994; Prairie and others 2002). That there is also net storage necessarily implies that total inputs are greater than the sum of carbon gas exchange and fluvial export.

Streams and rivers are usually net sources of CO_2 to the atmosphere as well. This excess CO_2 is derived from groundwater inputs of organic carbon respired in either the soil system (Jones and Mulholland 1998; Telmer and Vezier 1999), the hyporheic zone (Schindler and Krabbenhoft 1998), or within the stream or river itself. Further, most of the HCO_3 transported in flowing waters represents CO_2 that has been altered during weathering of either aluminosilicate or carbonate rocks (Gaillardet and others 1999; Humborg and others 2000). Ultimately of metabolic origin, this soil CO_2 is derived from respiration of organic matter of terrestrial origin. Rather than returning to the atmosphere as CO_2 evading from the soil surface, which could in principle be measured as efflux by current techniques (for example, eddy-covariance towers, Valentíni and others 2000), this CO_2 returns to the atmosphere meters to kilometers downstream of its origin when it evades across the stream surface. Similarly, the HCO_3 transported by rivers represents mostly the CO_2 of soil *R* that due to weathering reactions does not evade back into the atmosphere on the continents (Stallard 1998; Jones and others 2003; Raymond and Cole 2003). The net gaseous loss of CO_2 from flowing waters, and much of the transported HCO_3, thus represents terrestrial *R* that is not measured as such.

We can formulate a simplified mass balance equation to track the fate of carbon (organic plus inorganic) in an integrated freshwater and terrestrial C budget as:

$$I=G+S+E1 \qquad (1)$$

where the carbon imported to aquatic systems (*I*) can be estimated as the net carbon gas balance of the aquatic system with the atmosphere (*G*), plus storage (*S*) and export in drainage waters (*E*). A number of different processes generate CO_2 in addition to metabolism. Both photo-oxidation and import, for example, are non-metabolic inputs of CO_2. The simple mass-balance equation [equation (1)] can be used to describe the integrated C balance for a single lake, a region or the terrestrial biosphere. When applied to the entire terrestrial system, *E* is the export via rivers (plus direct groundwater discharge) to the sea plus the export of any volatile organics to the air, and *I* is the total C of terrestrial origin entering aquatic ecosystems. Thus, the difference between *I* and *E* represents the net C loss from terrestrial ecosystems that meets a fate other than export in freshwaters. If $I = E$, then freshwaters, from a mass balance point of view, function as neutral passive pipes (Figure 1a). To the extent that *I* may exceed *E*, the loss of C from land exceeds its export into the ocean, meaning that significant gas flux and or storage must occur during its transit through freshwater ecosystems. That is, the freshwater ''pipe'' would not be a passive conduit but a place of active transformation (Figure 1b).

QUANTIFYING THE GLOBAL ROLE OF INLAND AQUATIC SYSTEMS

We review the recent literature on the components of the mass balance model [equation (1)] for inland waters to test the ''neutral pipe'' hypothesis. We examine the extent to which there is a quantitatively significant fraction of the carbon entering these systems that is either stored permanently or lost to the atmosphere as net gas exchange. We then further consider the consequences of an explicit consideration of the role of inland aquatic systems for the terrestrial C balance.

GAS EFFLUX

Net gaseous carbon flux [*G* in equation (1)] is one pathway for which inland waters are not passive transport pipes. The sources of the carbon evading from freshwaters cannot at present be fully partitioned into advective input from soil respiratory products or the oxidation of terrestrially derived organic carbon within the aquatic system. Also for some systems such as wetlands and the floodplains of large rivers, the distinction between CO_2 from terrestrial inputs and CO_2 from aquatic inputs is problematic. Nevertheless, we are able to estimate a conservative value for the overall magnitude of CO_2 efflux as the sum of published worldwide efflux estimates from large rivers (Cole and Caraco 2001), lakes (Cole and others 1994; Sobek and others 2005), reservoirs (St. Louis and others 2000), and groundwater withdrawal (Table 1). The carbon dioxide released when groundwater withdrawn for various purposes that completely reequilibrates with the atmosphere was estimated, crudely, as the product of the total groundwater volume withdrawn (658 $km^3\ y^{-1}$; FAO Aquastat 2003, available at http://www.fao.org/ag/agl/aglw/aquastat/main/index.stm) and the average excess CO_2 concentration above atmospheric equilibrium calculated from a newly compiled dataset of 283 published measurements (data available upon

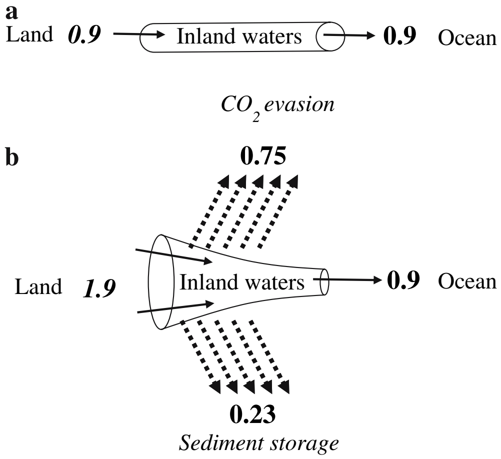

Figure 1. Simplified, schematic view of the role of inland aquatic systems in the global C balance. **a** The present view considers inland waters as a passive pipe that transports organic and inorganic carbon from land to sea. To the reported delivery of 0.7 Pg C y^{-1} from rivers to the sea, we have added a direct ground water load of 0.2 Pg C y^{-1} that discharges to the sea without entering rivers (see text). Assuming that carbon is transported passively, this implies that 0.9 Pg C y^{-1} leaves the terrestrial environment. **b** A proposed alternative view recognizes that inland waters are active components of the global C cycle that store terrestrially-derived carbon in sediments and lose CO_2 as emissions to the atmosphere (see Table 1), in addition to transporting it to the ocean. Because of the terrestrial subsidy inland waters are simultaneously net sources of CO_2 to the atmosphere and net sinks for C in sediments (see text). To balance these fluxes requires that 1.9 Pg C y^{-1} of terrestrial NEP is exported into inland waters. This terrestrial loss is a conservative estimate (see text) and represents a large fraction of total terrestrial NEP (from 50 to >70%; see text).

request). For surface water the individual published estimates of net gas exchange used in this synthesis were derived from the products of global averages of pCO_2 values, gas exchange velocities (k) appropriate for the different environments and their global coverage (Table 1).

Lakes

The published estimates of the global net CO_2 flux for lakes ranges from about 0.07–0.15 Pg C y^{-1}, with a mid-range value of 0.11 Pg C y^{-1} (Table 1). The data sets behind these estimates are large, covering about 5,000 individual lakes spanning the globe (Sobek and others 2005). The data are not evenly distributed geographically and although tropical lakes are included (see Cole and others 1994), lakes in the north temperate and boreal zones are better represented. Further, the data set includes some, but certainly not all of the world's largest lakes.

Reservoirs

Based on the data in St. Louis and others (2000) reservoirs are also a net source of CO_2 to the atmosphere that is about twice the magnitude of that from natural lakes (0.28 Pg C y^{-1}). The data set includes some of the largest reservoirs in the world but is limited in that the very small (and extremely numerous) reservoirs are not explicitly included.

Large Rivers, Floodplains, and Estuaries

The published estimate includes more than 80 of the world's largest rivers (Cole and Caraco 2001 and references therein). The estimates range from 0.15 to 0.3 Pg C y^{-1} (mid-range value 0.23 Pg C y^{-1}; Table 1). This estimate includes only the main channels of the rivers. Many rivers have large seasonal floodplains that also tend to be net sources of CO_2 to the atmosphere. The only large-scale estimate we have for this comes from the Amazon. Extrapolating from the Amazon, Richey and others (2002) estimate that the inundated floodplains of the humid tropics would have net emissions of about 0.9 Pg C y^{-1}, which would more than triple the global riverine main channel flux. Because we cannot provide a separate estimate for floodplains globally, we use the much more conservative mid range gas flux for rivers of 0.23 Pg C y^{-1} in Table 1. Further, to fully evaluate floodplains and wetlands would require some estimate of net storage during their dry phase. Estimates of net gas efflux from estuaries (Frankignoulle and others 1998; Borges 2005) scaled to the global extent of estuaries suggest an additional 0.12 Pg C y^{-1}. The estimate is based on 26 inner and outer estuarine systems with a global distribution. In Table 1, we use 0.35 Pg C y^{-1} as the combined net CO_2 flux for rivers and estuaries and point out that this is a quite conservative estimate.

Ground Water

Ground water is highly supersaturated in CO_2 and when it reaches the surface by either natural or anthropogenic processes it equilibrates with the atmosphere. We generated an estimated range by assuming that between 10 and 100% of the mean groundwater dissolved inorganic C (DIC; 4.7 mM) evades to the atmosphere. We estimate that ground water contributes a relatively small amount of CO_2 to the atmosphere (about 0.01 Pg C y^{-1} with large uncertainty, (0.003–0.03 Pg C y^{-1}; Table 1).

Table 1. Global Inland Water C Fluxes. Mid-range value estimates (min–max) of annual global transport of carbon (Pg) through major inland water components.

Inland water component		CO_2 efflux to the atmosphere	Storage in sediments	Export to the ocean
Streams	Inorganic C	NA	NA	
	Organic C	NA	NA	
Lakes	Inorganic C	0.11 (0.07–0.15)	NA	
	Organic C	0	0.05 (0.03–0.07)	
Reservoirs	Inorganic C	0.28	NA	
	Organic C	0	0.18 (0.16–0.2)	
Wetlands[a]	Inorganic C	NA	0	
	Organic C	0	0.1	
Rivers	Inorganic C	0.23 (0.15–0.3)	NA	0.26 (0.21–0.3)
	Organic C	0	NA	0.45 (0.38–0.53)
Estuaries		0.12 (see text)	NA	NA
Ground water	Inorganic C	0.01 (0.003–0.03)	0	0.19 (0.13–0.25)
	Organic C	0	<0.016	
Total		0.75	0.23	0.9

Sources and derivation of these values are explained in the text. Import from land is calculated as the sum of export to the ocean and losses en route through the inland waters from land to sea. The CO_2 efflux from rivers does not include the net effect of inundated floodplains, which could increase the estimate here three-fold (see text).
NA no estimate was made.
[a] *Wetlands efflux and storage values are excluded from the mass balance of the aquatic ecosystems because a significant fraction of the carbon they fix is atmospheric and thus functionally behave like terrestrial systems.*

Small streams

These headwater systems tend to be net sources of the CO_2 to the atmosphere (Jones and others 2003) but we do not have an estimate that covers these at a global scale. Although we can estimate, albeit crudely, an average pCO_2 in headwater streams, we do not know the area, globally, that such streams cover, nor a good way to estimate the gas piston velocity across stream types and sizes.

Wetlands

Wetlands are ecosystems that are intermediate between terrestrial and aquatic systems and as such are difficult to integrate in our attempt to clarify their respective roles. This is especially so with respect to CO_2 gas exchange because their highly supersaturated waters do not necessarily constitute a net efflux from the system as it can be offset by direct atmospheric CO_2 uptake of the emergent vegetation (Wilcock and others 1999; Caraco and Cole 2002). Only whole-system approaches such as eddy-covariance flux measurements can potentially provide a measure of the net balance for these ecosystems. The prevailing view is that wetlands worldwide still constitute a significant net sink for carbon dioxide (Roulet 2000; Roehm 2005). Although most of this excess carbon fixation will likely be buried (see section below), a portion will be exported downstream as dissolved organic carbon (DOC) where it may eventually support some heterotrophic respiration in lakes and rivers. However, because CO_2 uptake in these land-water transitional systems is largely done by the emergent part of the vegetation, it is more akin in function to that of a forest. Thus, in our model of carbon flow, wetland gas flux is considered a component of the terrestrial influx of carbon from the atmosphere and is not separately quantified.

Summing these estimates for lakes, rivers and estuaries, we arrive at a global estimate of at least 0.75 Pg C y^{-1} that is net transferred from inland aquatic systems to the atmosphere. The inclusion of the net effect of inundated floodplains could raise this to possibly 1.65 Pg C y^{-1} and we are still missing significant types of aquatic systems. Even our conservative global value of 0.75 Pg C y^{-1} represents nearly twice the organic fraction of the carbon annually delivered to the oceans (Schlesinger and Melack 1981; Meybeck 1993; Harrison and others 2005), and is much larger than the rate at which carbon is buried in these systems (see below). As this CO_2 loss comes largely as the result of the decomposition of organic matter, its large magnitude suggests that inland waters oxidize a substantial fraction of the organic load they receive from land.

Methane

Although the mass of methane emitted from aquatic systems is small compared to CO_2, CH_4 has a disproportionately larger effect on climate warming, so we include it here. Because aquatic environments are frequently anoxic, some of the carbon gas efflux occurs as CH_4. The global annual efflux of CH_4 from lakes has recently been estimated as between 6 and 36 Tg carbon (Bastviken and others 2004). The riverine wetlands of the Amazon basin contribute an additional 22 Tg C y^{-1} (Melack and others 2004). Our most conservative estimate of the relative importance of methane emission suggests that the carbon gas efflux as methane is 4% of CO_2–C efflux (Table 1).

Aquatic Gas Flux in Regional Balances

The quantification of the net efflux of CO_2 derived from land-derived carbon in freshwater ecosystems to the atmosphere is also necessary to understand regional carbon budgets. Striking examples come from both the arctic tundra and the humid tropics. The Amazon example shows that the inclusion of the net flux of CO_2 from the aquatic parts (including the seasonal floodplain) changed the assessment of this enormous humid tropical forest from a net sink of atmospheric CO_2 to a system that may not sequester C (Richey and others 2002). Kling and others (1991) calculate that about 20% of the NEP of the arctic tundra is returned to the atmosphere as gas flux from lakes and rivers. Similar results were recently reported for Finland. Lakes, which cover 10% of the total area, evade annually 20% of the annual C accumulation in forest plus soils (Kortelainen and others 2006). Similarly, for the boreal zone, Algesten and others (2003) showed that about half of the organic C exported from the watershed was respired and released to the atmosphere as CO_2 in aquatic habitats (lakes and rivers). For the watershed of the Gulf of Bothnia, part of the Baltic Sea, the remaining half of the C that is fluvially transported subsidizes aquatic respiration in the Gulf of Bothnia such that R exceeds GPP by some 7–10 mmol C m^{-2} d^{-1}. The negative NEP of the Gulf of Bothnia is about equal to measurements of CO_2 efflux from the Baltic to the atmosphere (Algesten and others 2004).

STORAGE

For aquatic systems storage is estimated from dated sediment cores. The best studies include spatial sampling to correct for sediment focusing in the deepest part of the basins. For most systems the measurable storage integrates decades at least, and sometimes millennia. Published estimates at the global scale come from several sources and represent a large number of lakes and reservoirs with a reasonably global distribution. We have no information on sediment storage in rivers or streams and assume that these are likely small over decadal or longer time steps.

Lakes

Einsele and others (2001) compiled C burial estimates for very large inland water bodies with striking results. Although there are not many lakes with areas greater than 10,000 km^2 these few lakes alone are estimated to have accumulated some 27 Pg C during the Holocene. Small and medium sized lakes, because of their larger numbers and faster sediment accumulation rates store even more C (Mulholland and Elwood 1982). The data compiled by Einsele and others (2001) suggest that the global, Holocene, storage of C in the sediments of all lakes is on the order of 820 Pg; lakes with areas less than 500 km^2 contain about 70% of this total. These data suggest that small lakes may be disproportionately important in sediment C storage. It is also highly likely that Einsele and others have underestimated the importance of small lakes. The average size of world lakes is about tenfold smaller than the smallest lake size considered by Einsele and others (see Downing and others 2006). Thus, some unknown portion of lake C burial in the smallest lakes is missing in this account. Using a different approach, Stallard (1998) estimated the storage in lakes that have not been impacted by agriculture and by those that have. If we assume that the annual rates reported by Stallard (1998) for un-impacted lakes endured for 10,000 years, the total storage would be 420 Pg, smaller than the estimate of Einsele and others (2001) but still appreciable. If the time horizon for the agricultural impact is the past 100 years, the additional accumulation would be 8 Pg (see Stallard 1998).

C storage in lakes is large in part because lake sediments are preserved for considerably longer (10,000 years or more) than forest biomass or soil (decades to centuries). The annual rates of C storage in lakes have been estimated on a global-basis by several authors using different approaches (Mulholland and Elwood 1982; Meybeck 1993; Dean and Gorham 1998; Stallard 1998; Einsele and others 2001). The estimates range from 0.03 to 0.07 Pg C y^{-1} (mid-range 0.05; Table 1). These rates are trivial in comparison to contemporary C sequestration by terrestrial vegetation and soils (about 1.3 Pg y^{-1}) or the oceanic physical-chemical sink of inorganic C of at about 1.9 Pg y^{-1} (Sundquist 1993). On the other hand, if we compare the storage of organic C in marine sediments (about 0.12 Pg y^{-1}; Sarmiento and Sundquist 1993) we see that lakes store about 30–60% as much organic C per year as does the ocean and do this in less than 2% of the area of the sea. Globally, on an areal basis, Dean and Gorham (1998) derived average long-term carbon burial rates in lakes of the order of 14 g C m^{-2} y^{-1}. Using a more extensive data set Stallard (1998) suggests a lower average rate of 4.5 g m^{-2} y^{-1}. As a comparison, net carbon accumulation in forest soils in southeastern Canada averaged over Holocene time has been estimated at 1.2 g C m^{-2} y^{-1} (Harden and others 1992; Tremblay and others 2002). It thus appears that the intensity (that is, the rate of storage per unit area) of C burial in lakes is greater than either the ocean or in terrestrial systems, especially when we consider the millennium time scale. Obviously, terrestrial systems are highly patchy and the net storage at a global scale is a complex mosaic of gains and losses in both time and space. Here we are comparing only very broad averages.

In lakes, organic carbon storage is much more important than the deposition of inorganic carbon in the form of carbonates, except perhaps in saline environments. The cause of the higher areal rates of organic carbon storage in lakes compared to oceans reflects not only the generally greater productivity of freshwater systems but also the compounding influence of a rapid lacustrine sediment accumulation rate with a high preservation rate (Dean and Gorham 1998). Although DOC is the largest pool of organic carbon in lake water, POC is the dominant form of organic carbon in the sediments. Carbon storage rates in lakes commonly increase with lake productivity, and are inversely proportional to lake size (Mulholland and Elwood 1982; Paterson and others 1998; Kortelainen and others 2004). Agriculture and other intensive land-use change tend to increase sedimentation rates (Einsele and others 2001), and small man-made agricultural ponds have been identified as major sites for carbon burial (Smith and others 2002).

The major storages of terrestrial C on land are reported to be in soils (1,395 Pg) and in biomass (~460 Pg; Post and others 1982; Raich and Schlesinger 1992). The sediments of natural lakes contain a significant portion of terrestrial organic matter that is not explicitly included in most terrestrial inventories. The most appropriate comparison would be between soil C and Holocene C accumulation in lake sediments (400–800 Pg). Soil C turns over more rapidly than does lake sediment C and is thus more likely to influence the atmosphere than are lake sediments. Despite considerable uncertainties then, the global estimates suggest that Holocene lake sediments contain as much as or up to perhaps twice the C in terrestrial biomass, or from about 25–50% as much C in terrestrial soils plus biomass.

Lake carbon burial can represent an important part of the total carbon stored in the watershed at the regional scale. A large-scale assessment of the standing stock and sedimentation rate for a representative set of lakes in Finland shows that lake sediments covering 10% of the total surface area of Finland contain 0.6 Pg of carbon (Kortelainen and others 2004), co-equal with forest biomass, (0.65 Pg C; Kauppi and others 1997) and about one-half the C in forest soils (1–1.3 Pg; Liski and Westman 1997). Scaling up from the Finnish data, Kortelainen and others (2004) estimate boreal lake sediments to contain 19–27 Pg. Molot and Dillon (1996), extrapolating from Canadian data, estimate a much larger boreal storage in lakes. These authors suggest that boreal lakes contain at least 120 Pg, about twice the C in boreal plant biomass (64 Pg) and nearly 30% as much as is stored in boreal peatlands (419 Pg).

Some of the world's largest and deepest lakes have existed for much longer than Holocene time and have accumulated even more sediment. Lake Malawi, for example, which has a depositional area of about 23,800 km^2 and 2.5 km of sediment contains, conservatively, about 300 Pg C (Filippi and Talbot 2005; T. Johnson and S. Alin, Personal Communication). Over Holocene time the estimate for Malawi is only 5 Pg (Einsele and others 2001). It is likely that other similarly old lake systems (Tanganykia, Baikal and others) will have very large C inventories once cores that reach the bottom of the sediment stratigraphy are analyzed. Of course these large old inventories are not part of an active C pool on even millennial time scales but are interesting for comparison.

Reservoirs

Man-made impoundments store large amounts of C in their sediments. Unlike the situation in lakes, C storage in reservoirs is mostly recent and likely short lived because dams are short lived. On the other hand, the fate of reservoir sediments following impoundment failure or removal is not known so we do not know how long this C might be sequestered beyond the life of the impoundment. The global surface area of reservoirs most often cited is about 400,000 km^2 (for example, Dean and Gorham 1998) and estimates of C burial range from about 0.16–0.2 Pg C y^{-1} (mid-range of 0.18 Pg C y^{-1}; Table 1). The global area for reservoirs is likely an underestimate as it misses most small reservoirs and farm ponds (Smith and others 2002). St. Louis and others (2000) estimate reservoir area at 1,500,000 km^2. Steadily increasing in numbers, reservoirs bury more organic carbon than all natural lake basins combined and globally exceed organic C burial in the ocean by more than 1.5-fold. The first years or decades in the life of artificial impoundments are usually marked by exceptionally high rates of carbon burial due to enhanced particle trapping. Dean and Gorham (1998) estimated that, at an average sedimentation rate of 2 cm y^{-1}, an average bulk density of 1 g cm^{-3}, and an average organic carbon content of 2%, world reservoirs bury organic carbon at a total annual rate of 0.16 Pg y^{-1} or 400 g C m^{-2} y^{-1} (Table 1). This is close to the previous estimate of 0.2 Pg y^{-1} from Mulholland and Elwood (1982) and we therefore used the midpoint value of 0.18 Pg C y^{-1} in Table 1. This value is conservative. Applying the same areal rate to the larger total reservoir area estimated by St. Louis and others (2000) would increase the total burial of carbon in reservoirs to 0.6 Pg y^{-1}. This storage is of recent anthropogenic origin and could appropriately be compared to the modern net C sink on land of about 1–2 Pg y^{-1} (Schimel and others 2001).

TRANSPORT IN RIVERS AND GROUNDWATER

The most obvious source of export of C from the continental margins (*E*, equation 1) occurs through riverine flux. These fluxes are large, fairly well quantified, and have been derived from estimates of water discharge (for example, Dai and Trenberth 2002) and measurements of aqueous carbon concentrations. River export of organic carbon to the sea has thus been estimated as ranging from 0.38 (Degens and others 1991) to 0.53 Pg C y^{-1} (Stallard 1998) with several other estimates falling within this range (for example, Schlesinger and Melack 1981; Meybeck 1982; Ludwig and others 1996; Aitkenhead and McDowell 2000; Table 1). Riverine export of dissolved inorganic carbon resulting from the fixation of atmospheric carbon through rock weathering is likely to be between 0.21 and 0.3 Pg C y^{-1} (Suchet and Probst 1995; Stallard 1998, Table 1). Globally about half of the bicarbonate transported by rivers originates from silicate weathering (in which case 100% of the bicarbonate came from CO_2 sequestration) and half from carbonate weathering (in which case only half the bicarbonate came from CO_2 sequestration; Stallard 1998; Meybeck 1993). Thus, in total about 75% of the inorganic C that rivers deliver to the ocean represents terrestrial respiration that is never measured as CO_2 evolution from the soil. It is hidden soil respiration masquerading as the bicarbonate ion.

Groundwater export to the sea has not been considered as yet in global C budgets. Groundwater comprises 97% of the world's liquid freshwater (van der Leeden and others 1990; IUCN 2000) and can contain substantial quantities of organic and inorganic carbon (Cai and others 2003; Hem 1985). Some groundwater discharges as the base flow of rivers and is included in river carbon export. However, estimates of submarine groundwater discharge (SGD; groundwater injected directly to the sea without entering a river) span a broad range (Church 1996; Cai and others 2003). Imbalances in the world water budget (van der Leeden and others 1990; Dai and Trenberth 2002; Shiklomanov and Rodda 2003) and groundwater residence times from 3 to 25 ka suggest SGD equal to 1.4–12% of river influx, with the most accepted values between 5 and 10% (Taniguchi and others 2002; Slomp and Van Cappellen 2004). Estimates of groundwater alkalinity of around 60 mg l^{-1} (Cai and others 2003) and a minimum DOC concentration of 1 mg l^{-1} (Simpkins and Parkin 1993) suggest SGD of carbon of 0.13–0.25 Pg C y^{-1} (Table 1).

Collectively, using mid-range values for the river and groundwater components, inland waters thus deliver about 0.9 Pg C y^{-1} to the oceans, roughly equally as inorganic and organic carbon (Table 1).

TOWARD A COMPREHENSIVE ACCOUNT OF THE ROLE OF FRESHWATER ECOSYSTEMS IN THE GLOBAL CARBON CYCLE

In an eloquent passage describing the role of rivers in continental-scale geomorphology, Leopold and others (1964) described rivers as "the gutters down which flow the ruins of continents". This conclusion, based on geomorphologic considerations, pervades much of the global-scale descriptions of the carbon cycle, at least where freshwater ecosystems are concerned. However, the present synthesis of current estimates of carbon fluxes in freshwater ecosystems (Figure 1, Table 1) strongly indicates that continental hydrologic networks, spanning from river mouths to the smallest tributaries far upstream, do not act as neutral pipes or gutters, but instead are active players in the C cycle despite their modest size. Leopold's continental ruins do not merely flow; they are actively processed within inland waters.

The processes in aquatic systems that we have reviewed are true net fluxes and need to be compared to other net fluxes for perspective. Because they are subsidized by terrestrial inputs, aquatic systems can simultaneously be net accumulators of sedimentary organic matter and net sources of CO_2 to the atmosphere. This concept is often confusing to those more familiar with terrestrial systems. Our conservative estimates (Table 1) indicate that the net CO_2 efflux from inland water ecosystems (0.75 Pg C y^{-1}) is about three-fold greater than our conservative estimate of organic carbon storage for all inland aquatic ecosystems (0.23 Pg C y^{-1}). The two C net ''reactions'' along the flow path summed, (burial plus efflux of CO_2 to the atmosphere) are slightly larger than the export to the ocean in the riverine ''pipe'' (0.9 Pg C y^{-1}). Inland waters, then, receive at least 1.9 Pg C y^{-1} from land, which is a considerable portion of terrestrial NEP (below); return 40% of this C atmosphere as CO_2; sequester about 12% in sediments; and transport the remaining 48% to the ocean. The estimate of riverine gas flux includes only the main river channel and not the inundated floodplains because floodplains alternate between pseudo-terrestrial and aquatic. Accepting the idea from Richey and others (2002) that floodplains are a net source of CO_2 to the atmosphere, the major effect of including these floodplains would be to increase aquatic CO_2 efflux to 1.65 Pg C y^{-1} and the export of C from land from 1.9 to 2.8 Pg C y^{-1}.

Referring back to equation (1), the import (I) to aquatic systems is much larger (by between 1 and 1.6 Pg C y^{-1}) than riverine export to the sea (E). Either way, the aquatic pipe appears to be highly active and should not be looked at as a neutral transport system.

In what contexts do these C fluxes matter? Clearly, these fluxes are a combination of background ambient processes and anthropogenically altered ones. The four aquatic fluxes we have considered, net gas exchange with the atmosphere (G), burial or storage in sediments (S), export to the ocean (E) and importation of C from land to inland waters (I) are all on the order of 1 Pg each. These fluxes have different impacts on the assessments of both regional and global C balances.

Storage and export

The net burial of C in the sediments of inland aquatic systems and the fluvial plus ground water export to the ocean can be significant components of both regional and the global C balance. These aquatic fluxes are quite small in comparison to the major gross inputs and outputs of C on land, terrestrial GPP and respiration (R), each of which are about 100 Pg y^{-1} (Raich and Schlesinger 1992; Zhao and others 2005). On the other hand, these net aquatic fluxes are of comparable magnitude to key net fluxes at a global scale. The present day net ecosystem productivity (NEP = GPP−R) of the terrestrial biosphere has been estimated by various approaches to range from about 1–4 Pg y^{-1} (Randerson and others 2002). These approaches include remote sensing of vegetation changes with coupled models (for example, Potter and others 1993); inverse modeling of spatial and temporal changes in atmospheric CO_2 (for example, Schimel and others 2001) or comparisons and hybrids or extensions of both (for example, Pacala and others 2001; see Randerson and others 2002). Although the value of terrestrial NEP is not perfectly constrained, it has only two possible fates: export and storage (in these large scale analyses fires are treated as CO_2 losses like R). Inland aquatic systems transport about 0.9 Pg y^{-1} and store an additional 0.23 Pg y^{-1} in the sediments of lakes plus reservoirs. If we subtract from export the moiety of inorganic C that came ultimately from carbonate rock (about 0.1 Pg y^{-1}; Stallard 1998; Berner 1993) the remaining 1.03 Pg y^{-1} is still a significant fraction of contemporaneous terrestrial NEP that is either stored or exported by aquatic systems.

Terrestrial NEP is conceptually distinct from the apparent ''missing anthropogenic CO_2 sink''. This ''missing sink'' is the difference between anthropogenic inputs of CO_2 to the atmosphere, the measured increase of CO_2 in the atmosphere and fairly well constrained estimates of the net uptake of CO_2 by the world's oceans. The recent (past decade) ''missing sink'' computed by difference which averages about 1.9 Pg y^{-1} (with large inter-annual and inter-investigator variability; Houghton 2003) is a change in sink strength (sometime called a ''delta sink'') on top of some unknown, but likely small, pre-industrial value of terrestrial NEP (Schlesinger 2005). We do not know to what extent inland aquatic systems matter to the ''missing sink''. To impact the missing sink, there would have to be a change in either storage or export for aquatic systems over the past 100–150 years. However, both fluvial export and to a lesser extent sediment storage are potentially large enough that increases or decreases in these rates could be significant to the anthropogenic CO_2 sink. It has been argued, for example, that the imbalance in the contemporary C budget of Europe is, in fact, balanced by the losses in rivers and storage in sediments (Siemens 2003; Janssens 2003).

Sediment storage may be enhanced by eutrophication, reservoir and small pond construction, and the building of small dams that change the rate at which erosion occurs and the ultimate fate of eroded sediments (Smith and others 2001, 2002). In our budget we have included only a conservative estimate for reservoir C burial of 0.18 Pg (Table 1). Stallard (1998) argues much of the anthropogenic missing C sink (0.6–1.5 Pg y^{-1}) may be largely in man-made aquatic and semi-aquatic habitats such as rice paddies, which we did not include. Smith and others (2001, 2002) suggest that small farm ponds may be quantitatively significant as well. These are areas that require more research at the global scale.

Fluvial and ground water exports of C may be affected by climate change-induced (or land-use-induced) changes in hydrology, as well as indirectly by the anthropogenic rise in atmospheric CO_2, and we have not included these effects. Increased water output of large rivers has had a concomitant increase in the export of inorganic C (Raymond and Cole 2003) and dissolved organic C (Claire and Ehrman 1996; Freeman and others 2004). Some of the CO_2 fertilization studies have found that elevated CO_2 leads to increases in CO_2 removal from the atmosphere without the expected increases in plant or soil C (Jones and others 1998). These results could suggest that C sequestered by photosynthesis at elevated CO_2 is exiting the system as either bicarbonate or DOC, which are known to be increasing in many regions (for example, Jones and Mulholland 1998; Freeman and others 2004; Evans and others 2005). In summary, although we can say that mechanisms exist that could link anthropogenic forcing functions to increases in riverine C exports, there is no evidence yet that the magnitudes are significant at a global scale.

Inland aquatic systems, by our assessment, make a net contribution of 0.75 to perhaps 1.65 Pg C y^{-1} to the atmosphere as CO_2. These small fluxes are included as part of the approximately 100 Pg y^{-1} of "terrestrial" respiration when this respiration is assessed by inverse modeling of the atmosphere at large spatial scales (for example, Raich and Schlesinger 1992). On the other hand, when terrestrial NEP is assessed from changes in vegetation and soil C inventories, or from eddy covariance towers with relatively small footprints, this aquatic loss of terrestrially derived C is not necessarily included and is rarely explicitly considered. Similarly, the importation of DIC and DOC into lakes and streams from water that percolates through land and exits the system represent parts of the terrestrial balance that is lost laterally without being measured. In the case of exported DIC, a portion of terrestrial respiration is missed. In the case of DOC, a portion of terrestrial NEP is moved so that it is no longer stored on land. Working in Scottish peatland, Billett and others (2004) found that the fluvial exports of DIC plus DOC plus CO_2 net efflux from the stream surface accounted for about 350 kg C ha^{-1} y^{-1} (of watershed). The aquatic losses of exported DIC plus outgassed CO_2 were larger than net ecosystem CO_2 exchange (NEE) between the terrestrial watershed and the atmosphere measured with flux towers [uptake 278 kg C ha^{-1} y^{-1} (of watershed)]. Thus the NEE tower would have assessed the peatland ecosystem to be a net sink for atmospheric CO_2 but the integrated terrestrial-aquatic balance shows it to be a net source of CO_2 to the atmosphere. At present there are only a handful of studies that have tried to comprehensively integrate the C balance of terrestrial watersheds with their aquatic components. These lateral aquatic losses are not always so significant. Shibata and others (2005), working in small forested watersheds in Japan, found that DIC plus DOC export were only about 2% of measured NEP. They did not estimate CO_2 efflux from the stream, which can be much larger than the export of DIC in some systems (Richey and others 2002; Fahey and others 2005).

A PROSPECTIVE RESEARCH AGENDA

One of the prime objectives of global C budgets has been to accurately characterize (1) the identity and magnitude of the significant components and (2) the key exchanges among components of the global carbon cycle. We have integrated current estimates for several important aquatic components that have previously been assumed to be small and show that the plumbing of the carbon cycle through the aquatic conduit is more complex and interesting than represented by a simple neutral pipe. It is highly reactive. Many of the estimates we offer are only broadly constrained but several hold the potential for altering and improving our understanding of the global carbon budget and how humans have changed it. A research agenda is needed to further elucidate the relevant components and determine more exactly how aquatic, continental pathways connect them together.

A major unknown is the potential significance of very small streams and lakes in degassing CO_2 produced within the surrounding soils. Although not generated in situ, this highly localized carbon release is nevertheless important to regional carbon budgets and it may not be captured by the land-based instruments used to estimate terrestrial gas exchange (for example, flux towers). When streams are ignored, terrestrial respiration would be underestimated thereby overstating the land as a carbon sink. Similarly, the way carbon buried in reservoirs and lakes is integrated in the carbon budget depends ultimately on the origin of this carbon. For example, to assume that the carbon buried in impoundments is largely autochthonous would have very different implications to the budget than if it is construed mostly as translocated (that is, eroded) soil that would not have otherwise reached the aquatic environment (Stallard 1998; Smith and others 2001, 2002). More research is needed to elucidate where the carbon burial of lakes, reservoirs and particularly wetlands (that is, intermediate ecosystems with fuzzy boundaries) fit along this continuum. More effort is also required to circumscribe more narrowly how the average rates of carbon burial vary among different regions, what their main determinants are, and how they are affected by human activities (Duarte and others 2005).

We know very little about the role of groundwater in sequestering, transporting and releasing carbon. Because of its large volume and likely concentration of carbon, groundwater may contain hundreds of Pg of carbon. Groundwater pools have turnover times that may vary from days to millennia, but are under increasing pressure as a water source, and climate change has implications for past and future groundwater discharge and recharge. Therefore, research on its role in the global carbon budget may be critical. Similarly, we know little about the world's saline lakes. The endorheic watersheds feeding inland saline lakes can extend across a significant fraction of continental area. These saline lakes are terminal components of their watersheds and thus cannot export the carbon they receive from their watersheds, which can, consequently, only be stored in the sediments of these lakes or be emitted to the atmosphere. Yet, knowledge on the carbon budget of inland saline lakes is so sparse that, despite their potential global significance, they cannot be accurately incorporated into the tentative budgets depicted here.

Finally, at a more fundamental level, this synthesis shows that inland waters, like many other interfaces (McClain and others 2003), are disproportionately active sites for C cycling relative to the area they occupy in the landscape. However, it does not address the detailed processes and mechanisms that allow such higher activity to be sustained. This is most relevant if we are to use similar approaches to understand how the role of freshwaters must have changed from the start of the Holocene to the present, and how it is likely to be further modified by the continuing alterations of the planet by humans.

CONCLUSION

The synthesis presented here indicates that the carbon delivered from land to the freshwater components of terrestrial ecosystems must be at least 1.9 Pg C y^{-1} (Figure 1, Table 1). This figure accounts, conservatively, for all of the carbon transported fluvially to the ocean, buried in freshwater ecosystems or degassed as CO_2 therein, and exceeds the carbon finally delivered to the ocean by at least a factor of 2. All of our estimates are conservative and further revisions are likely to substantially increase the total amount of carbon processed by aquatic ecosystems. There is little doubt that the neutral pipe hypothesis is untenable, and that freshwater ecosystems represent an active component of the global carbon cycle that deserve attention. More broadly, the compartmentalization of the biosphere into reservoirs (land, atmosphere and oceans) may conveniently simplify depictions of carbon fluxes, but it also narrows our understanding of the functioning of the biosphere by downplaying the level of integration among all of these components. We submit that an accurate understanding of the carbon cycle in the biosphere requires a much more encompassing approach that considers the biosphere as a network of inter-connected metabolically active sites, rather than discrete boxes connected by neutral transport conduits.

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