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Banking carbon: a review of organic carbon storage and physical factors influencing retention in floodplains and riparian ecosystems

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ABSTRACT: Rivers are dynamic components of the terrestrial carbon cycle and provide important functions in ecosystem processes. Although rivers act as conveyers of carbon to the oceans, rivers also retain carbon within riparian ecosystems along floodplains, with potential for long-term (> 10^2 years) storage. Research in ecosystem processing emphasizes the importance of organic carbon (OC) in river systems, and estimates of OC fluxes in terrestrial freshwater systems indicate that a significant portion of terrestrial carbon is stored within river networks. Studies have examined soil OC on floodplains, but research that examines the potential mechanistic controls on OC storage in riparian ecosystems and floodplains is more limited. We emphasize three primary OC reservoirs within fluvial systems: (1) standing riparian biomass; (2) dead biomass as large wood (LW) in the stream and on the floodplain; (3) OC on and beneath the floodplain surface, including litter, humus, and soil organic carbon (SOC). This review focuses on studies that have framed research questions and results in the context of OC retention, accumulation and storage within the three primary pools along riparian ecosystems. In this paper, we (i) discuss the various reservoirs for OC storage in riparian ecosystems, (ii) discuss physical conditions that facilitate carbon retention and storage in riparian ecosystems, (iii) provide a synthesis of published OC storage in riparian ecosystems, (iv) present a conceptual model of the conditions that favor OC storage in riparian ecosystems, (v) briefly discuss human impacts on OC storage in riparian ecosystems, and (vi) highlight current knowledge gaps. Copyright © 2015 John Wiley & Sons, Ltd.

KEYWORDS: carbon; river; floodplain; riparian ecosystem; organic matter

Introduction: Why Does River Organic Matter (OM) Matter?

Rivers distribute and deliver sediment and organic carbon (OC) through the landscape. Spatial distribution of carbon within riparian ecosystems regulates delivery to the ocean and atmosphere, retention and storage within the geosphere, and ecosystem processing for the foundation of foodwebs (Vannote *et al.*, 1980; Allan and Castillo, 2007; Aufdenkampe *et al.*, 2011). We frame this discussion regarding distribution and retention of OC in rivers around floodplains and riparian ecosystems.

We refer to floodplains as the relatively flat topographic surfaces adjacent to rivers that experience inundation on annual to decadal timescales, to be distinguished from adjacent uplands that are not regularly inundated. Floodplains are estimated to cover between 0.8×10^6 and 2×10^6 km^2 globally (Leopold *et al.*, 1964; Tockner and Stanford, 2002; Mitsch and Gosselink, 2015). We refer to riparian ecosystems as the biota and biogeochemical processes occurring at the interface of terrestrial and freshwater ecosystems along floodplains (Gregory *et al.*, 1991; Naiman *et al.*, 2005). Riparian ecosystems provide ecological and societal benefits such as flood attenuation and denitrification, which is largely dependent on carbon content (Devito *et al.*, 2000; Hill *et al.*, 2000; Wohl, 2000a, 2000b; Craig *et al.*, 2008), but this discussion focuses on the physical attributes of rivers and factors that regulate retention of OC as influenced by climate, geology, hydrology, and geomorphology. First, we briefly review relevant aspects of riparian ecosystems and the services they provide to create the context for more detailed discussion of OC dynamics in rivers including ecosystem processing of OC and terrestrial carbon budgets.

Physical complexity and river ecosystem processing of OC

Position along river networks and resulting channel and floodplain characteristics regulate components of riparian ecosystems, the local source of OC inputs, distribution and transport (Tank *et al.*, 2010) of OC, biogeochemical processing (Battin *et al.*, 2008), and resulting ecosystem services.

We adopt the river-centric convention of stream ecologists when referring to allochthonous organic matter (OM) as that which is derived from outside of the channel including riparian vegetation (e.g. leaves, needles, wood), and autochthonous OM as that which is produced through primary production in the stream (e.g. algae, periphyton). Allochthonous and autochthonous OM provide the trophic foundation for river ecosystems (Vannote *et al.*, 1980; Allan and Castillo, 2007). Organic matter is the primary source for OC within rivers when compared with fossilized carbon (kerogen; Allan and Castillo, 2007). Approximately 45–50% of OM by mass, depending on species, is OC (Allan and Castillo, 2007). Usage of OM and OC throughout this manuscript is not interchangeable, but instead specifically refers to one or the other.

Terrestrial allochthonous detrital material entering headwater streams is the primary source of OM input to river systems (Vannote *et al.*, 1980; Gomi *et al.*, 2002; Allan and Castillo, 2007; Hilton *et al.*, 2008; Chapin *et al.*, 2011). These OM inputs are a major source of OC and provide the foundation for biogeochemical processing and foodwebs in aquatic and terrestrial environments (Allan and Castillo, 2007). Narrow headwater channels receive high inputs of plant debris as coarse particulate organic matter (CPOM; > 1 mm) from riparian ecosystems and uplands, which is broken down into fine particulate organic matter ($0.5\ \mu m < FPOM < 1$ mm) by aquatic invertebrates and microbes within the channel, on the floodplain, and within the subsurface (Wagener *et al.*, 1998; Allan and Castillo, 2007; Chapin et al., 2011). Dissolved organic carbon (DOC; $< 0.5\ \mu m$) can be derived from living biomass or leached from particulate organic matter (POM), and can remain in channel and floodplain sediment through adsorption to mineral grains, constituting a significant amount of OC in sediment and soil (Allan and Castillo, 2007). Downed large wood (LW; >10 cm in diameter and 1 m in length) also provides a significant source of POM (including CPOM and FPOM) to river systems (Ward and Aumen, 1986). In larger rivers that receive more abundant sunlight, autochthonous primary production is a more significant source of OM present in the channel.

The degree of physical channel complexity along a river segment influences the distribution and concentration of POM and OC. We refer to channel complexity qualitatively as the (1) magnitude of channel boundary irregularities, (2) sinuosity, radius of curvature and wave length of channel meanders and bends, (3) number of channels across the valley bottom, (4) number and spacing of flow obstructions, (5) variation in bed slope and bedforms, (6) size and variation in bed material, (7) type, abundance, and density of aquatic and riparian vegetation, and (8) number and spacing of steps, pools and riffles for any stream or river segment. Many factors of channel complexity are analogous to Manning's channel roughness coefficient (Arcement and Schneider, 1989), which incorporates roughness components as well as slope, planform, and bedforms. Thus, a highly incised, straight channel lined by concrete would have a very low complexity. In contrast, a sinuous headwater stream of the same size with channel spanning logjams approximately every few meters, 4–5 threads of channelized flow across the valley bottom, abundant steps and backwater pools, channel substrate alternating from boulders to cobbles, and lined with abundant willows and trees would have a very high degree of channel complexity.

Rivers with a high degree of channel complexity (1) increase the residence time of water, sediment, LW, and POM within sites of flow separation and off-channel areas such as the floodplain and hyporheic zone, (2) maintain biological hotspots that facilitate breakdown of OM, and (3) effectively filter excess nutrients and DOC from surface and shallow subsurface waters (Bilby, 1981; Stallard, 1998; Kasahara and Wondzell, 2003; Battin *et al.*, 2008, 2009; Hilton *et al.*, 2008). Riparian ecosystems, particularly those with high degrees of channel complexity, facilitate retention and complex biogeochemical processing of pollutants and excess nutrients (Devito *et al.*, 2000; Battin *et al.*, 2008; Tank *et al.*, 2010), which can be present in high concentrations in highly impacted watersheds (Devito *et al.*, 2000; Allan and Castillo, 2007; Craig *et al.*, 2008). High DOC concentrations in surface waters create potential risks for human consumption because carcinogenic disinfectant byproducts are produced when DOC is combined with chlorine at water treatment plants (Trussell and Umphres, 1978; Coffin *et al.*, 2000; Sapkal and Valunjkar, 2013). In watersheds with a substantial proportion of agricultural land use, carbon content of riparian soils is an important factor for water quality and amelioration of high nitrate concentrations because denitrification can be carbon limited (Hill, 1996; Hill *et al.*, 2000) and is largely dependent on availability of OM in riparian soils (Devito *et al.*, 2000).

River fluxes of OM and thus OC exert an important control on freshwater and nearshore ecosystems and the ecosystem services they provide. Physical and biological processes in rivers influence OC retention over varying timescales (Battin *et al.*, 2008, 2009; Aufdenkampe *et al.*, 2011; Wohl *et al.*, 2012a), and understanding these processes is crucial for determining potential impacts of global climate change, land-use, and land-cover changes on OC dynamics within river systems. Improved understanding of the distribution and retention of OC in river systems can inform river management practices and foster opportunities for ecosystem processing of excess nutrients.

Rivers and the global carbon cycle

Global carbon budgets, which estimate the annual exchange of carbon between short-term reservoirs (i.e. atmosphere, vegetation, soil, near-surface sea water), do not fully account for carbon dioxide (CO_2) released to the atmosphere annually. A significant portion of OC (~2 Pg C yr^{-1}) is assumed to be taken up by terrestrial sources (Le Quéré *et al.*, 2009; Ballantyne *et al.*, 2012). However, current estimates of oceanic and terrestrial carbon sinks do not fully account for the total carbon released annually to the atmosphere through burning of fossil fuels.

The terrestrial carbon component contains the largest uncertainty of all aspects of the global carbon cycle (Gregory *et al.*, 2009), yet appears to be able to absorb an increasing amount of CO_2 (Ballantyne *et al.*, 2012). Battin *et al.* (2009) and Aufdenkampe *et al.* (2011) estimate that a significant portion (~22%) of carbon entering headwater streams is unaccounted for by delivery to the oceans or CO_2 outgassing from metabolism by aquatic biota. This suggests that carbon is being stored somewhere within the terrestrial environment along river systems (Fig. 1; Stallard, 1998; Battin *et al.*, 2009; Aufdenkampe *et al.*, 2011; Hoffmann *et al.*, 2013). This represents a potential carbon reservoir previously unaccounted for in carbon stock estimates, which may help to close the missing terrestrial carbon sink (Cole *et al.*, 2007). Wetlands have been identified as significant carbon reservoirs (Kayranli *et al.*, 2010) and the largest source of net ecosystem productivity among land surface types (Schulze *et al.*, 2005), but forest inventories of vegetation and soil organic carbon (SOC) have not examined surfaces adjacent to rivers as distinct landforms with different SOC content

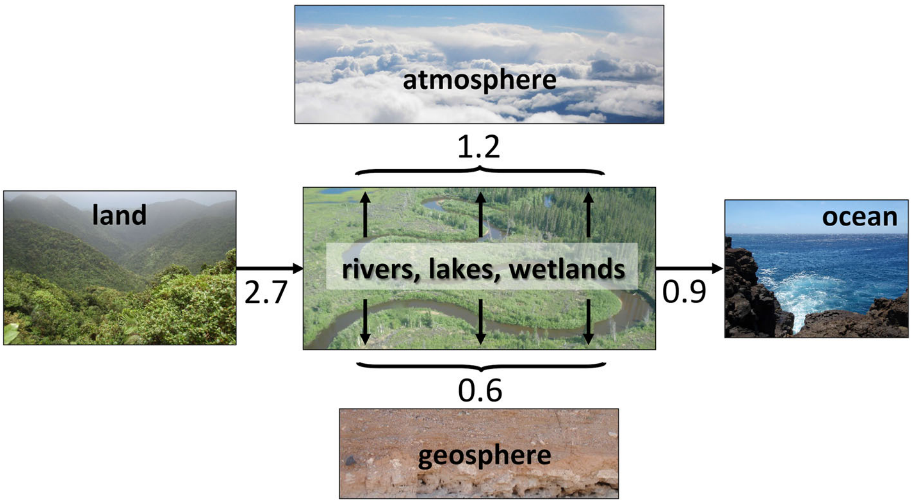

Figure 1. Modified from Aufdenkampe *et al.* (2011; Fig. 3). Values represent carbon fluxes in petagrams of carbon per year (Pg C yr^{-1}) based on calculations from Battin *et al.* (2009). Surface water facilitates fluxes between terrestrial carbon reservoirs, delivering carbon to the atmosphere and the ocean. Recent research has shown that only a relatively small proportion of carbon reaches the ocean makes it to the ocean after (i) outgassing to the atmosphere following metabolism by biota and (ii) sinks to the geosphere. This suggests that rivers facilitate terrestrial carbon storage. This figure is available in colour online at wileyonlinelibrary.com/journal/espl

than those of the adjacent uplands. Despite being a dynamic component of the terrestrial carbon cycle, river systems are among the least investigated freshwater landscape features as potential long-term carbon reservoirs (Cole *et al.*, 2007). Limited research conducted to date, however, suggests that river networks might store a significant proportion of terrestrial carbon (Jaramillo *et al.*, 2003; Walter and Merritts, 2008; Cierjacks *et al.*, 2010; Wohl *et al.*, 2012b; Hoffmann *et al.*, 2013, Hoffmann *et al.*, 2014a).

The objectives of this paper are to (i) summarize the primary reservoirs for OC in river systems, (ii) discuss differences in fluvial environments that can influence OC storage with respect to landscape- and local-scale controls, (iii) summarize published data of OC stocks in riparian ecosystems, and (iv) discuss gaps in existing knowledge of OC in fluvial systems. Although human activities are likely to affect OC dynamics in fluvial environments, we address these potential effects only briefly in this review.

Organic Carbon (OC) Reservoirs in Riparian Ecosystems

Organic carbon is stored along river networks in four primary reservoirs: (1) standing riparian biomass; (2) large downed wood; (3) sediment, including OM, litter and humus on or beneath the surface within the channel and across the floodplain; and (4) in-stream biomass (Fig. 2). Work to quantify and compare autochthonous net primary production in stream and allochthonous litter inputs indicates wide differences among

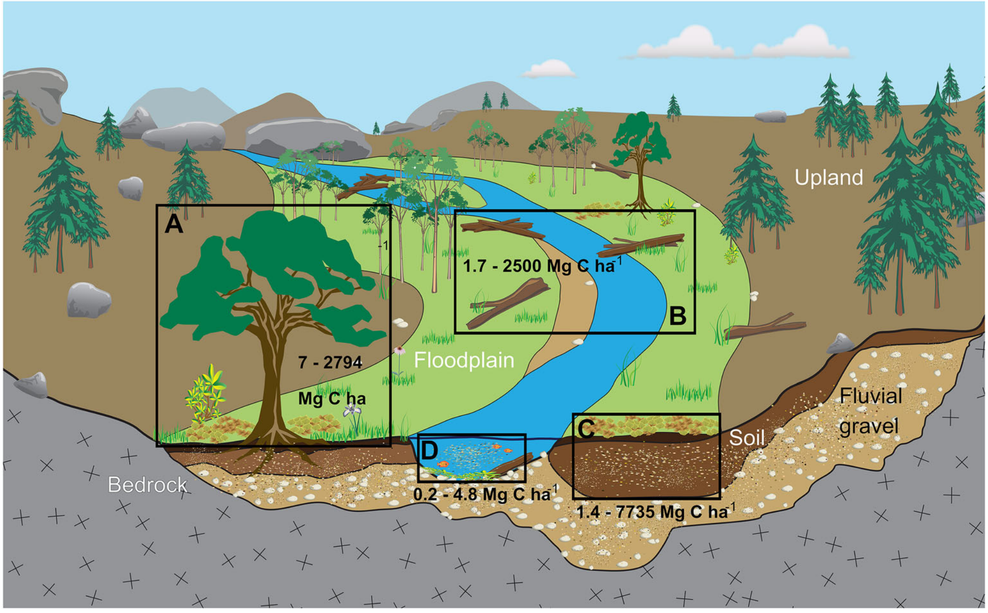

Figure 2. Organic carbon is stored within four primary reservoirs in river systems: above- and below-ground standing biomass as riparian vegetation (A), large in-stream and downed wood on the floodplain (B), sediment on the floodplain surface and in the shallow subsurface, including soil organic carbon, litter and humus (C), and in-stream biomass including filamentous algae, periphyton, benthic invertebrates, fish, and particulate organic matter (D). Values indicate the estimated range of organic carbon per area (Mg C ha^{-1}) from studies cited in this review. Values from Naiman *et al.* (1987) and Findlay *et al.* (2002) show that in-stream biomass (D) accounts for a relatively small portion of carbon stored in river systems per area when compared to the other three reservoirs. This figure is available in colour online at wileyonlinelibrary.com/journal/espl

climatic regions, such that OC values per area are dominated by primary productivity in warmer climates and allochthonous OM in cooler climates (Allan and Castillo, 2007). Comparison of values from sediment, wood, and above-ground biomass with those of in-stream biomass (i.e. benthic invertebrates, filamentous algae, fine benthic OM, and fish) of boreal streams from Naiman *et al.* (1987) shows that storage within in-stream OC stocks per area is relatively insignificant (Fig. 2; 0.8–4.8 Mg C ha^{-1}). Comparison with values from work by Findlay *et al.* (2002) in arid, temperate, and tropical streams indicates similar low values for in-stream biomass (0.21–1.9 Mg C ha^{-1}). Organic carbon delivered by streams can contribute to riparian ecosystems during high flows (Pinay *et al.*, 1992; Hall *et al.*, 2009; Tank *et al.*, 2010) and when physically removed from the channel by biotic activities. However, because OC fluxes from the channel to the floodplain are incorporated into surface and subsurface sediment and in-stream biomass values are small compared to the other three reservoirs, we do not focus on OC within active channels as a major reservoir for OC in river ecosystems. Additionally, in-stream biomass and OC fluxes are variable spatially and temporally, making in-stream OC reservoirs extremely transient. Standing biomass in riparian ecosystems, however, is much larger (7–2794 Mg C ha^{-1}) and can include trees that store carbon for 10^2–10^4 years. For these reasons, we focus in this paper on the largest and most persistent OC reservoirs in riparian ecosystems: (1) standing riparian biomass; (2) large downed wood; and (3) floodplain sediment and OM.

River valleys, floodplains, and riparian ecosystems funnel water, sediment, and associated OC through the landscape. Geologic, climatic, hydrologic, and geomorphic characteristics of the landscape influence the travel time and retention of water, sediment, and OC along this journey and provide opportunities for storage. Riparian ecosystems tend to contain more moisture than adjacent uplands, and commonly exhibit distinct vegetation types. This means that riparian ecosystems may store more OC per area than other, more thoroughly examined components of the landscape such as upland forests, grasslands, and agricultural plots. Work in tropical regions, for example, indicates that floodplains store more OC than drier, adjacent uplands (Jaramillo *et al.*, 2003).

Quantitative comparisons among sites will be discussed later, following a review of OC storage in riparian ecosystems. First, we discuss potential controls on OC retention along river systems (Fig. 3). We discuss factors that dictate OC storage in a variety of settings, which can result in widely different magnitude or direction of influence, depending on the region.

Landscape-scale Controls on OC in Riparian Ecosystems

The distribution of OC at the landscape scale (10^2–10^6 km^2) depends largely upon factors that influence gross primary production and the decay, transport, and accumulation of OM (Dodds *et al.*, 2015). These large-scale drivers include geologic setting and ecoregion (Fig. 3). Geologic setting refers to tectonic history, lithology, and geologic structure. Ecoregions or biomes characterize biogeographic regions by climate, soil type, and biotic communities. Differences in climate influence physical and chemical weathering of rocks and sediment, available moisture, vegetation communities within a given biome, soil development, and decomposition of OM.

Ecoregions are characterized by distinct vegetation on regional scales, but they do not differentiate vegetation in riparian ecosystems from adjacent uplands. Riparian vegetation communities, however, vary in association with each ecoregion and differ in rates of gross primary production (Naiman *et al.*, 2010). Vegetation type regulates the form, quality, and seasonality of OM inputs available for breakdown or storage in riparian ecosystems (Schulze *et al.*, 2005; Chapin et al., 2011). Decomposition of OM is highly dependent on temperature and moisture, which also control the rate of chemical and physical weathering of soil and rock. Grain size distributions in rivers affect the availability of mineral facies for adsorption of OC, and thus influence relative differences in rates of OC mineralization by microbes and aquatic invertebrates (Schulze *et al.*, 2005; Allan and Castillo, 2007).

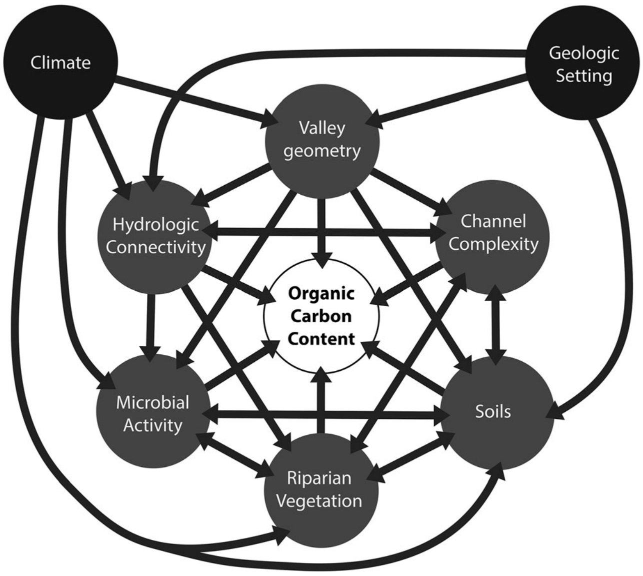

Figure 3. A conceptual diagram of regional and local controls on organic carbon (OC) reservoirs in riverine systems. Potential influences are highlighted here, but the mechanism, direction, and magnitude of each influence varies greatly across different geologic settings and climatic regions.

Together with climate, geologic setting controls topography, elevation, and drainage basin and valley characteristics. These factors in turn influence local climate, hydrologic disturbance regime, aqueous and soil chemistry, soil type, and rates of primary production (Fig. 3). Thus, the direction and magnitude of the influences on OC sources, retention, and fluxes in riparian ecosystems vary greatly across Earth's surface depending on both regional and local characteristics.

Climatic influences of OC in riparian ecosystems

As a source of energy and water, regional climate plays a crucial role in regulating primary productivity, decomposition, and disturbance, thus determining sources, transport, accumulation, and breakdown of OM. Globally, the major control of climate is solar energy, and thermally defined zones can be broadly delineated by latitude (Bailey, 2009). We define hydroclimatic differences in river systems across broad climatic regions including (1) boreal or subarctic, (2) temperate, (3) arid, and (4) tropical. It becomes apparent when classifying published values of OC in riparian ecosystems using even these generalized climatic regions that large gaps are present in all but the temperate regions. Using data from temperate regions, Woodall and Liknes (2008) identified the highest OC stocks as occurring in areas with cool summers, suggesting temperature-limited decay rates, whereas the lowest OC stocks are found in semi-arid areas, suggesting water-limited primary productivity and OM inputs. Carbon reservoirs are positively correlated with available moisture and negatively correlated with maximum temperature (Woodall and Liknes, 2008). Flow variability of rivers influences riparian plant community structure and the sources and distribution of OM along floodplains (Camporeale and Ridolfi, 2006). For these reasons, we briefly cover climatic controls on OC accumulation and mobilization, including general trends in regional flow regimes. Flow regimes specific to each climatic region regulate (i) riparian vegetation recruitment and survival, (ii) aggradation and degradation of floodplain sediment, and (iii) transport and recruitment of LW to the stream and on the floodplain.

Tropical regions

Relatively constant annual temperatures characterize tropical regions, with seasonal variations dominated by precipitation. The year-round growing season results in high productivity and abundant vegetation in uplands and riparian areas, with high POM inputs to streams (Lyons *et al.*, 2002; Alin *et al.*, 2008; Hilton *et al.*, 2008; West *et al.*, 2011; Wohl and Ogden, 2013). Low variability in temperatures is accompanied by low monthly and inter-annual variability of discharge in tropical rivers (Wohl, 2007), providing a regulated environment for primary production, OM inputs, and exports of OC. Variations in precipitation, however, may create distinct seasons of increased moisture and peak discharge in some rivers (Wohl *et al.*, 2012a), which likely influence OC storage along extensive floodplains and riparian ecosystems in lowland, tropical river systems. Flood pulses deliver sediment and OM to the floodplain and riparian wetland ecosystems, creating potential for high OC reservoirs. Abundant moisture and warm temperatures in tropical regions, however, facilitate rapid decomposition of OM. In addition to high decomposition rates, monsoons and heavy precipitation leach soils of nutrients and OM in tropical environments, resulting in little-to-no organic O- and A-horizons in soils, which commonly have a litter layer atop B-horizons (Birkeland, 1999).

Processes in steep tropical uplands deliver OC to lowland environments (Ramos Scharrón *et al.*, 2012). Slope failures in steep uplands of tropical regions likely flush OM through riparian ecosystems relatively rapidly compared to other regions (Lyons *et al.*, 2002; Hilton *et al.*, 2008, 2010; Ramos Scharrón *et al.*, 2012), perhaps simply supplying flatter lowlands with OC inputs. Climatic patterns such as the El Niño Southern Oscillation can be responsible for rapid deposition of 20 to 80 cm of sediment in a single event on the floodplains of the Amazon River (Aalto *et al.*, 2003) and aggradation of 2.8 to 3.7 mm yr^{-1} has been calculated for the Amazon River floodplains during 9500–3000 yr BP (Mertes and Dunne, 2007). Although conditions exist for rapid decomposition of carbon along floodplains in the tropics, work by Alin *et al.* (2008) and Goni *et al.* (2008) suggest that recalcitrant terrigenous OC and aged soil OM can persist along floodplains for 10^2 to 10^3 years without being metabolized. Their work along floodplains of the Fly and Strickland Rivers in Papua New Guinea used radiogenic carbon isotopes in surface water and floodplain and delta sediment to determine that OC from headwaters does consist of highly processed OM, but the majority is very old and dominated by terrigenous sources in streams and on floodplains (Alin *et al.*, 2008) and on the subaqueous Fly River delta, where marine sources of carbon were not detected (Goni *et al.*, 2008).

Temperate regions

Distinct seasonality in temperature and discharge within temperate regions is responsible for consistent annual patterns of productivity, OM inputs, and OC retention in riparian ecosystems. Temperate regions encompass a range of dominant vegetation types, including evergreen and deciduous forests, shrublands, and grasslands. Consistent seasonal trends in OM inputs and temperature regulate biogeochemical processing of OM, such that OC accumulates more rapidly in soils compared to tropical regions. Moderate inter-annual variability and low monthly variability in discharge of temperate rivers (Wohl, 2007) likely dampen variability in the aggradation and degradation of floodplain sediment and LW. However, local climate – and carbon processing – can be highly variable depending on topography, latitude, and location relative to the oceans. Temperate regions encompass the most variability in temperature, precipitation, discharge and floodplain disturbance regime among the climatic regions covered here. Consequently, we distinguish arid regions within the temperate latitudes as a separate category.

Arid regions

Riparian ecosystems typically have increased moisture and greater vegetation density compared to adjacent uplands, and this trend is generally more pronounced in arid regions (Friedman and Lee, 2002). Limited primary production, as a result of potential evaporation exceeding precipitation, limits OM inputs to riparian ecosystems in arid regions. Although a large portion of vegetation in arid regions includes cacti, succulents, and woody perennial plants and trees with photosynthetic stems that appear to create limited plant litter, riparian ecosystems receive a significant amount of OM from seasonal flowers, grasses, seed casings, small leaves, and wood (Sponseller and Fisher, 2006). Low moisture availability in arid regions limits productivity, but also hinders decomposition of OM and thus increases opportunities for OC storage in riparian ecosystems (Harms and Grimm, 2008).

Reservoirs of OC in arid-region riparian ecosystems are highly influenced by timing of precipitation and flooding, which can occur sporadically throughout the year. Subtropical deserts, however, typically receive the majority of their moisture as monsoons. This strong seasonality in precipitation affects productivity, decay rates, local transport and redistribution of OM more greatly than in temperate regions (Merritt and Wohl, 2003; Stromberg *et al.*, 2010). High spatial and temporal (i.e. daily, monthly, and annual) variability of discharge in many arid rivers (Wohl, 2007) is likely to provide little predictability of mobility and aggradation of sediment, wood, and OM. Flash floods, common in arid regions, redistribute OC in sediment among channels and floodplains (Valett *et al.*, 2005). Thus, storage of OC is likely highly variable, spatially and temporally, in arid-region riparian ecosystems.

Boreal regions

Boreal or subarctic regions experience large temperature variation between seasons. The short summers are generally warm and humid, with very long days, resulting in high levels of seasonal productivity of forest and wetland vegetation in the summer and significant OM inputs in the autumn months. Rivers in subarctic and boreal regions experience low inter-annual variability and large monthly variability in hydrograph peaks as a result of snowmelt and ice breakup during the spring and early summer months (Wohl, 2007), However, lower snowpack and earlier snowmelt as a result of increased warming may alter the magnitude of annual peaks (Costard and Gautier, 2007). Timing of peak flows remains relatively consistent, with the potential for secondary peaks as ice breakup migrates downstream (Costard and Gautier, 2007). This seasonal hydrologic disturbance regime is responsible for consistent transport of OC onto and from floodplains.

Subarctic soils may contain significant amounts of OC in peatlands, permafrost, and from terrestrial OM inputs (Schuur *et al.*, 2008; Tarnocai *et al.*, 2009). Long, cold winters and shallow water tables perched above permafrost facilitate saturated conditions that limit aerobic microbial activity and metabolism of OC pools, contributing to extensive OC storage in soils. Throughflow in the active layer of periglacial environments, however, causes seasonal flushing during snowmelt (Koch *et al.*, 2013), which may mobilize shallow SOC in subarctic regions (Striegl *et al.*, 2005), particularly in floodplains. This mobilization promotes a distinct seasonality of OC flushing from the active layer, which may limit OC storage. Icejams and logjams, however, are common and promote overbank flow, sometimes increasing flow stage by 8–10 m on major rivers such as the Lena in Russia (Costard and Gautier, 2007).

Permafrost serves as a significant reservoir and source of OC from soils in boreal river networks, and may include LW frozen into floodplain deposits (Wohl, 2013a). Bank erosion and collapse, which are increasingly common with climate change and melting of permafrost (Costard and Gautier, 2007), may transport OC that has been stored for significant periods of time (i.e. $>10^3$ years). Because (1) permafrost constitutes the highest observed values of SOC in upland soils (Schuur *et al.*, 2008; Tarnocai *et al.*, 2009), (2) seasonal melt flushes OC from the active layer (Striegl *et al.*, 2005; Koch *et al.*, 2013), and (3) riparian soils experience increased depth of melting, abundant hyporheic exchange, and higher magnitude and longer duration of throughflow, boreal environments may exhibit a reversal of SOC trends in riparian areas, such that riparian soils have lower OC content compared to surrounding upland soils.

Highlands and mountainous regions

Mountainous terrain within all climatic zones can assume characteristics of other climatic regions. Topographic influences can alter precipitation regimes, create meso-climates, and change hydrologic disturbance regimes (Jong *et al.*, 2005). Increased elevation can induce orographic precipitation such that highlands receive more rain than surrounding lowland regions (Loukas *et al.*, 2000; Jong *et al.*, 2005). Lower temperatures at higher elevations may result in seasonal snowpack and limit microbial activity. In general, mountainous environments tend to change the hydroclimatic regime by decreasing temperature and increasing precipitation, thus shifting toward a wetter and cooler climate, providing more consistency in hydrologic response and disturbance regime (Jong *et al.*, 2005), slowing decomposition of OC, and potentially increasing retention of OC. Exceptions exist, including steep mountainous environments which experience rapid denudation, hillslope erosion, and channel incision (Hilton *et al.*, 2008). These characteristics are regulated by and discussed further in the context of geologic setting.

Geologic setting

Geologic setting includes tectonic setting, rock type, weathering rates, sediment production, and ultimately the availability of minerals and nutrients, which can all influence OC retention along riparian ecosystems. Tectonic setting broadly includes active and passive tectonic plate boundaries in continental interiors and along continental margins. Active uplift, whether within the interior or along the margins of continents, encourages steep hillslopes and streams, more frequent mass wasting, and potential mobilization and subsequent breakdown/mineralization of OC downslope, with less opportunity for storage along headwater streams (Hilton *et al.*, 2008; Wohl and Ogden, 2013). Transport of sediment by rivers toward lower gradient interiors of continents, as in the Amazon and Mississippi River basins, may result in significant aggradation and storage of sediment (Meade, 2007) and associated OC. Mountain ranges with steep rivers along continental margins are more likely to transport sediment and OC to the ocean more rapidly (Hilton *et al.*, 2008, 2010; Leithold *et al.*, 2006).

The tectonic nature of continental margins plays an important role in determining the duration of storage of OC. Tectonically passive continental margins create potential to store OC in sediment of deltaic deposits or within estuaries. Riverine environments along low-elevation coasts constitute potential storage for 10^2 to 10^4 years, but are subject to tides, changes in sea level rise, and storm surges (Mertes and Dunne, 2007). Tectonically active margins provide potential for much longer storage periods of 10^5 to 10^9 years, particularly those that occur where subduction of oceanic tectonic plates beneath continental plates moves sediment and OC into the mantle to be recycled through volcanic processes (Dasgupta and Hirschmann, 2010). Although it is important to note differences in potential storage between continental interiors and active and passive continental margins, we do not cover additional details regarding the fate or storage of OC once it reaches the ocean.

Geologic setting controls topography and influences local climate and hydroclimatic disturbance regime. Topography influences potential transport and storage of sediment, soil, and OM. In rivers flowing through low-lying, relatively flat regions, floodplains are likely to retain OM for longer periods of time (Noe and Hupp, 2009) compared to steep, mountainous terrain with more rapid downstream movement of OM (Benda *et al.*, 2005; Hilton *et al.*, 2010). Similarly, geologic setting dictates the energy gradient between any given point along a river and base level, which influences channel slope and the balance between water and sediment inputs, and thus channel incision and floodplain and channel aggradation (Lane, 1955; Schumm, 1977; Leopold and Bull, 1979; Schumm, 1993).

Geologic and climatic controls on base level play a major role in whether rivers aggrade or incise the landscape through which they flow and thus potential for OC storage along floodplains. Local base level of rivers and streams associated with knickpoints, lakes, inland seas, reservoirs, and sea level influences stream gradients, erosion, and aggradation. Changes in local base level and sea level have the ability to influence OC storage in riparian ecosystems because active uplift and steep slopes facilitate hillslope mass wasting and floodplain erosion (Hilton *et al.*, 2010). Limited research suggests that floodplains in low-relief environments within the interior United States (Guyette *et al.*, 2008), and even smaller, steep streams in the tectonically passive interior US Rocky Mountains (Wohl *et al.*, 2012a), are more likely to retain OM within the terrestrial environment for a longer period than streams in regions of active tectonic uplift. Thus, tectonic, topographic, and climatic setting creates the template for local characteristics and factors such as channel form and complexity, which influence distribution and fluxes of OM within river systems.

Localized Controls on the Distribution of OM in Riparian Ecosystems

As with the landscape scale, the distribution of OC at the local scale of individual valley segments 10^1–10^3 m in length depends on factors that influence gross primary production and the decay, transport, and accumulation of OM. At the local scale, these factors include valley and channel geometry as well as biotic influences.

Valley and channel geometry

Climate interacts with geology to create the topography that influences fluxes of water, sediment, and OM through the landscape (Schumm, 1977; Benda *et al.*, 2005). Channel form changes downstream along an idealized progression from primarily erosive, steep, coarse-grained headwater streams toward lower-gradient channels with finer-grained substrate (Schumm, 1977; Montgomery and Buffington, 1997). However, this downstream progression may take the form of spatially discrete zones, with distinctly different hillslope processes, degrees of sediment and water connectivity between hillslope and channels, and channel characteristics that influence OM dynamics, so that downstream changes in OC reservoirs can be characterized via geomorphic process domains (Montgomery, 1999). Process domains help to identify the relative degree of connectivity between hillslopes and channels and categorize spatially distinct regions by the dominant geomorphic processes responsible for sediment dynamics and ecosystem disturbances (Wohl, 2010a; Polvi *et al.*, 2011; Bellmore and Baxter, 2014).

Hillslope–river connectivity, valley confinement and channel geometry (i.e. cross-sectional geometry, planform, bedforms, bank irregularities) influence fluxes of water, sediment, living biomass, POM, and OC (Schumm, 1977; Montgomery, 1999; Gomi *et al.*, 2002; Benda *et al.*, 2005; Hilton *et al.*, 2008). Although river and hillslope coupling of water and sediment may be expected to decrease with increasing distance downstream (Montgomery, 1999; Brierley and Fryirs, 2005), spatial heterogeneity of lithology and geomorphic processes interrupt this idealized progression (Benda *et al.*, 2005). Spatial heterogeneity in bedrock jointing, for example, facilitates longitudinal heterogeneity in valley geometry (Ehlen and Wohl, 2002; Wohl, 2008), as does glaciation (Amerson *et al.*, 2008).

Valley confinement regulates the distribution of hydraulic forces responsible for sediment transport and resulting channel form (Dunne and Leopold, 1978; Leopold *et al.*, 1964; Montgomery, 1999; Wohl *et al.*, 2012b). Narrowly confined valleys concentrate flow and promote rapid increases in hydraulic force with increasing discharge, which limits deposition of sediment and OM. Broad, unconfined valleys dissipate transport energy during flood flows, facilitate deposition and storage of OM, and promote the development of multithread channel planforms (Wohl, 2000a; Naiman *et al.*, 2005; Wohl, 2013a). Multithread channels increase channel complexity and create positive feedbacks as flow diverges around channel obstructions, islands and bars, resulting in accumulation of OM (Bilby, 1981; Montgomery *et al.*, 2003; Quinn *et al.*, 2007; Richardson *et al.*, 2009; Wohl and Cadol, 2011; Camporeale *et al.*, 2013; Polvi and Wohl, 2013; Wohl, 2013a; Beckman and Wohl, 2014; Wohl and Beckman, 2014). Hydraulic backwaters and pools immediately downstream of obstructions delay downstream transport of OM and provide the physical complexity that facilitates biological hotspots in which microbes and aquatic biota mineralize OC and nutrients (Battin *et al.*, 2008). These types of channel structures are particularly important in headwater streams with high inputs of OM (Conners and Naiman, 1984; Baron *et al.*, 1991; Richardson *et al.*, 2009; Tank *et al.*, 2010).

Characteristics of riparian soils and plant communities correlate strongly with valley form, the catchment hydrologic regime, hillslope and floodplain geomorphic processes, and distribution of geomorphic surfaces (e.g. floodplains, berms, banks) across the valley bottom (Sollins *et al.*, 1985; Gregory *et al.*, 1991). Heterogeneity in riparian vegetation and soils is closely linked to connectivity of water on and beneath the stream bed and floodplain, which is influenced by valley geometry, channel planform, gradients in soil moisture, and redox potential in the riparian corridor (Tabacchi *et al.*, 1998; Polvi *et al.*, 2011). Thus, the amount of OC stored, and the relative contribution of different OC pools, may vary considerably in different portions of a given watershed. Heterogeneity of drainage networks, the natural disturbance regime, process domain, and land management activities affect channel form and influence the variability of riparian plant community structure (National Council for Air and Stream Improvement, 2005). Riparian vegetation plays a key role in the distribution of OM throughout a watershed by contributing OM to riparian ecosystems as in-stream and floodplain wood, leaf litter, and decaying roots, and by influencing flow characteristics and channel geometry.

For the purpose of our discussion, we define hydrologic connectivity as fluxes of water (i) longitudinally within channels, (ii) laterally between floodplains and channels, and (iii) vertically between surface water, hyporheic flow, and groundwater (Wainwright *et al.*, 2011; Bracken *et al.*, 2013). While hydrologic connectivity influences the connectivity of sediment, we refer to these concepts separately and refer to sediment connectivity primarily as the downstream transport of sediment and lateral exchange and potential storage on the floodplain (Fryirs, 2013; Hoffmann *et al.*, 2009). Each of these facets of connectivity influences the distribution and biogeochemical processing of OM in river systems (Stanford and Ward, 1993; Pringle, 2003; Wohl, 2010b, 2014b). Lateral and longitudinal hydrologic connectivity, for example, facilitate the transport, accumulation, retention, and breakdown of OM (Bilby, 1981; Montgomery *et al.*, 2003; Battin *et al.*, 2008; Wohl, 2013a). Increased lateral and vertical connectivity facilitate saturated conditions in floodplains, thus increasing vegetative production but limiting decomposition of OM. Saturated conditions limit microbial metabolism and mineralization of SOC (Falloon *et al.*, 2011; Moyano *et al.*, 2012) and foster the accumulation and long-term storage of OC (Polvi and Wohl, 2012; Wohl, 2013b). Hyporheic exchange promotes aeration, microbial metabolism of OC (Edwards, 1998; Zarnetske *et al.*, 2011), and adsorption of DOC onto soil mineral facies (Schulze *et al.*, 2005).

Precipitation and flow regimes influence all forms of hydrologic connectivity, as does the topography that governs water routing through a catchment (Dunne and Leopold, 1978; Benda *et al.*, 2005). Hydrologically flashy systems that respond quickly to rainfall flush OM and OC through the catchment quickly (Dunne and Leopold, 1978), limiting opportunities for decomposition (Battin *et al.*, 2008) and potential for long-term storage (Aufdenkampe *et al.*, 2011; Wohl *et al.*, 2012b). Conversely, catchments with significant interception, high infiltration, and high channel complexity, produce longer flow paths and increase lag times for hydrograph response (Dunne and Leopold, 1978). This delay in downstream conveyance of water facilitates accumulation of fine sediment and POM (Montgomery *et al.*, 2003; Sear *et al.*, 2010; Wohl, 2013a; Wohl and Beckman, 2014), hyporheic exchange, mineral adsorption of DOC (Schulze *et al.*, 2005), and fosters hotspots for decomposition of OM (Battin *et al.*, 2008).

Biotic influences on channel geometry

Biotic influences on channel geometry include: (1) riparian vegetation (Tabacchi *et al.*, 1998; Camporeale *et al.*, 2013; Merritt, 2013); (2) riparian grazing and browsing (Kauffman *et al.*, 1983; Clary, 1999); (3) LW (Abbe and Montgomery, 2003; Collins *et al.*, 2012; Wohl, 2013a); (4) beavers (Ives, 1942; Persico and Meyer, 2013; Polvi and Wohl, 2013; Westbrook *et al.*, 2013; Wohl, 2013b); and (5) aquatic biota

(Butler, 1995; Montgomery *et al.*, 1996; Statzner *et al.*, 2000, 2003; Jones, 2012). In this discussion, we focus on major changes to channel form that influence the major reservoirs of OC by biotic drivers including riparian vegetation, LW, and beavers. Although fauna can influence channel geometry through grazing, major changes to channel form are typically a function of intensive grazing associated with livestock and thus are related to land use, which is discussed later.

Interactions between channel geometry and riparian vegetation affect channel cross-sectional form, planform, spatial variations in flow velocity (Trimble, 2004; Nepf and Ghisalberti, 2008; Camporeale *et al.*, 2013; Merritt, 2013), and therefore the distribution and fluxes of OM. Lateral connectivity to the floodplain, for example, partly reflects channel geometry and significantly influences germination, establishment, and survival of many riparian species (Cooper *et al.*, 1999; Merritt and Poff, 2010; Camporeale *et al.*, 2013). Some riparian plant species are adapted to tolerate high shear stress during high flows (Camporeale *et al.*, 2013) and provide stability to channel banks by increasing soil cohesion through root tensile strength (Abernethy and Rutherfurd, 2001). This resistance to bank erosion creates a positive feedback: flow velocity decreases along banks and vegetated islands, and this facilitates sediment deposition immediately downstream and creates new germination sites for riparian plants, which then contribute to bank stability and continued aggradation (Tabacchi *et al.*, 1998; Naiman *et al.*, 2005; Camporeale *et al.*, 2013; Merritt, 2013).

In forested environments of the northern hemisphere, beavers can play an important role in storage of OM along riparian ecosystems (Naiman *et al.*, 1986; Correll *et al.*, 2000; Wohl, 2013b). Alligators and hippopotamuses can also influence channel form by constructing canals and small water holes or ponds to aid their travel, predation, and foraging, but these effects are still relatively insignificant compared to the extensive geomorphic engineering of the beaver (Butler, 1995). Beavers greatly alter channel geometry and valley bottoms in what has been termed the beaver meadow complex (Ives, 1942). Beavers engineer an extensive series of terraced dams, ponds, and canals, which greatly increase channel complexity, promote lateral connectivity to the floodplain, encourage floodplain aggradation, raise riparian water tables, and thus contribute to the rapid colonization and growth of wetland riparian plant species (Westbrook *et al.*, 2006; Polvi and Wohl, 2013; Westbrook *et al.*, 2013; Wohl, 2013b). In Rocky Mountain National Park, USA, valleys with beaver meadows (Morgan, 1868) contain deeper accumulations of fine sediment and higher OC content than valleys without beaver activity (Kramer *et al.*, 2012; Wohl *et al.*, 2012b). These beaver-influenced sediments can persist for thousands of years (Persico and Meyer, 2009, 2013; Polvi and Wohl, 2012). The geomorphic effects of beaver activities on the distribution of OM and associated OC storage are similar to those created by in-stream wood and logjams.

Channel planform, disturbance regime, and riparian vegetation dynamics impact the wood load in channels and floodplains, and the resulting OC dynamics. Feedbacks between hydraulics and vegetation mentioned earlier also apply to wood with regard to the dissipation of energy and accumulation of sediment (Montgomery *et al.*, 2003; Sear *et al.*, 2010; Wohl, 2013a; Beckman and Wohl, 2014; Wohl and Beckman, 2014). In-stream wood not only facilitates channel complexity and flow divergence, but also provides refugia for aquatic invertebrates and microbes that break down and metabolize CPOM and FPOM (Allan and Castillo, 2007). Channel-spanning logjams create pools and trap sediment and POM for time periods of 10^0 to 10^1 years (Montgomery *et al.*, 2003; Sear *et al.*, 2010; Wohl, 2013a; Beckman and Wohl, 2014; Wohl and Beckman, 2014). Large pieces of wood and abundant wood associated with old-growth forests, in particular, can form persistent channel-spanning logjams that facilitate the development of multithread channels (Brummer *et al.*, 2006; Collins *et al.*, 2012; Wohl *et al.*, 2012b). Continuous avulsion and shifting of channels occur partly as a response to undercutting of standing trees during high flows, which ensures continued recruitment of in-stream wood (Collins *et al.*, 2012; Wohl, 2013a). Increased channel complexity as a result of riparian vegetation, beaver dams, and persistent logjams increases sediment deposition, accumulation and retention of OM (Polvi and Wohl, 2012, 2013; Wohl *et al.*, 2012b; Wohl, 2013a, 2013b; Wohl and Beckman, 2014).

A Review of OC Stocks in Riparian Ecosystems

In this section, we discuss influential factors and relative differences in three primary pools for OC storage in river systems: (1) standing riparian biomass; (2) dead biomass as LW in the stream and on the floodplain; and (3) floodplain surface (i.e. litter) and subsurface (i.e. humus and soil) sediment and OM. In this context, we summarize existing knowledge of floodplain and riparian components of river systems. We do not include specific discussion of other wetland environments, lakes, reservoirs, alluvial fans, estuaries, and deltas, even though these depositional environments are likely substantial storage areas for OC (Chmura *et al.*, 2003; Cole *et al.*, 2007; Bianchi and Allison, 2009; Kayranli *et al.*, 2010). Reported values of OC specific to riparian ecosystems and floodplains are published in journals of diverse disciplines and do not necessarily frame findings as carbon storage in riparian ecosystems or floodplains. We gather this information and present it in a way that highlights the primary reservoirs and influential factors for potential long-term (10^2–10^4 years) storage.

Riparian vegetation

Vegetation constitutes a significant OC reservoir in riparian ecosystems and provides the source for much of the LW and CPOM that is stored on the floodplain. A limited number of studies have examined OC pools in riparian biomass (Table I; Fig. 4), each with specific objectives that influenced the biomass components measured (e.g. Fierke and Kauffman, 2005). Reported values for total riparian biomass OC, which includes vegetation and LW in some studies, are wide-ranging (<1 to 2794 Mg C ha^{-1}), and directly reflect the vegetation structure and successional stage (Table I). Published research has largely focused on temperate regions (Table I; Fig. 4), including several studies that examined streams impacted by disturbance (Giese *et al.*, 2000, Giese et al., 2003; Fierke and Kauffman, 2005; Ruffing *et al.*, in press). Highest values were observed for mesic, old growth, conifer-dominated riparian forests in the southern Rocky Mountains (Fig. 4; Wohl *et al.*, 2012b), while lowest values occurred in early successional cottonwood stands (Fierke and Kauffman, 2005), herbaceous-dominated meadows (Dwire *et al.*, 2004; Cierjacks *et al.*, 2010; Wohl *et al.*, 2012b), and willow shrub stands (Wohl *et al.* 2012b). At disturbed temperate sites, alteration or removal of riparian vegetation resulted in notably lower OC pools (Giese *et al.*, 2000, Giese *et al.*, 2003; Fierke and Kauffman, 2005; Ruffing *et al.*, in press). Mature temperate hardwood forests include a wide diversity of tree and understory species, yet total OC storage in riparian biomass consistently ranges from ~100 to 300 Mg C ha^{-1} (Table I).

Table I. Published values of organic carbon pools from biomass and carbon inputs via litterfall in alluvial riparian ecosystems

Location	Climate	Drainage area (km^2)	Biomass components measured	Riparian vegetation type	Total biomass carbon	Reference
Chamela Biological Station, Jalisco, Mexico	Tropical	—	Trees (live), vines, seedlings, roots	Tropical floodplain forest (combination of evergreen and deciduous species)	119 –188[a]	Jaramillo *et al.*, 2003
Pen Branch Fourmile Branch Meyer's Branch (third order tributaries to Savannah River, South Carolina, USA)	Temperate	—	Trees, shrubs, herbaceous, litterfall, forest floor, fine roots, submerged aquatic vegetation	Bottomland hardwood forest (different seral stages; deciduous species)	7.5 –108.8	Giese *et al.*, 2000, Giese *et al.*, 2003
Meyer's Branch Savannah River South Carolina, USA	Temperate	—	Trees, shrubs, herbaceous	Cypress-tupelo forest	174 –192[a]	Muzika *et al.*, 1987
Danube River, Austria	Temperate	—	Trees, shrubs	Mature hardwood, conifer and cottonwood forests;	160 –280	Cierjacks *et al.*, 2010
				Young reforestations	35	
Williamette River, Oregon, USA	Temperate	—	Trees (live and dead)	Black cottonwood (chronosequence of five successional stages)	<1–218[a]	Fierke and Kauffman, 2005
Six streams, southeast Wyoming, USA (first and second order)	Temperate (mountains)	2.7–14.2	Trees, shrubs, herbaceous, forest floor	Conifer-dominated	53 –166	Ruffing *et al.*, in press
North St Vrain and Big Thompson Rivers, Colorado, USA	Temperate (mountains)	20–36	Trees, shrubs, herbaceous, forest floor	Conifer-dominated; willow-dominated; herbaceous meadow	194 –360 57 42	Wohl *et al.*, 2012b
West Chicken Creek Limber Jim Creek, northeast Oregon, USA	Temperate (mountains)	—	Herbaceous (above- and below- ground)	Herbaceous meadow	7– 21.5[a]	Dwire *et al.*, 2004

[a] Estimated from reported biomass values using a conversion factor of 0.5 (assuming 50% carbon content).

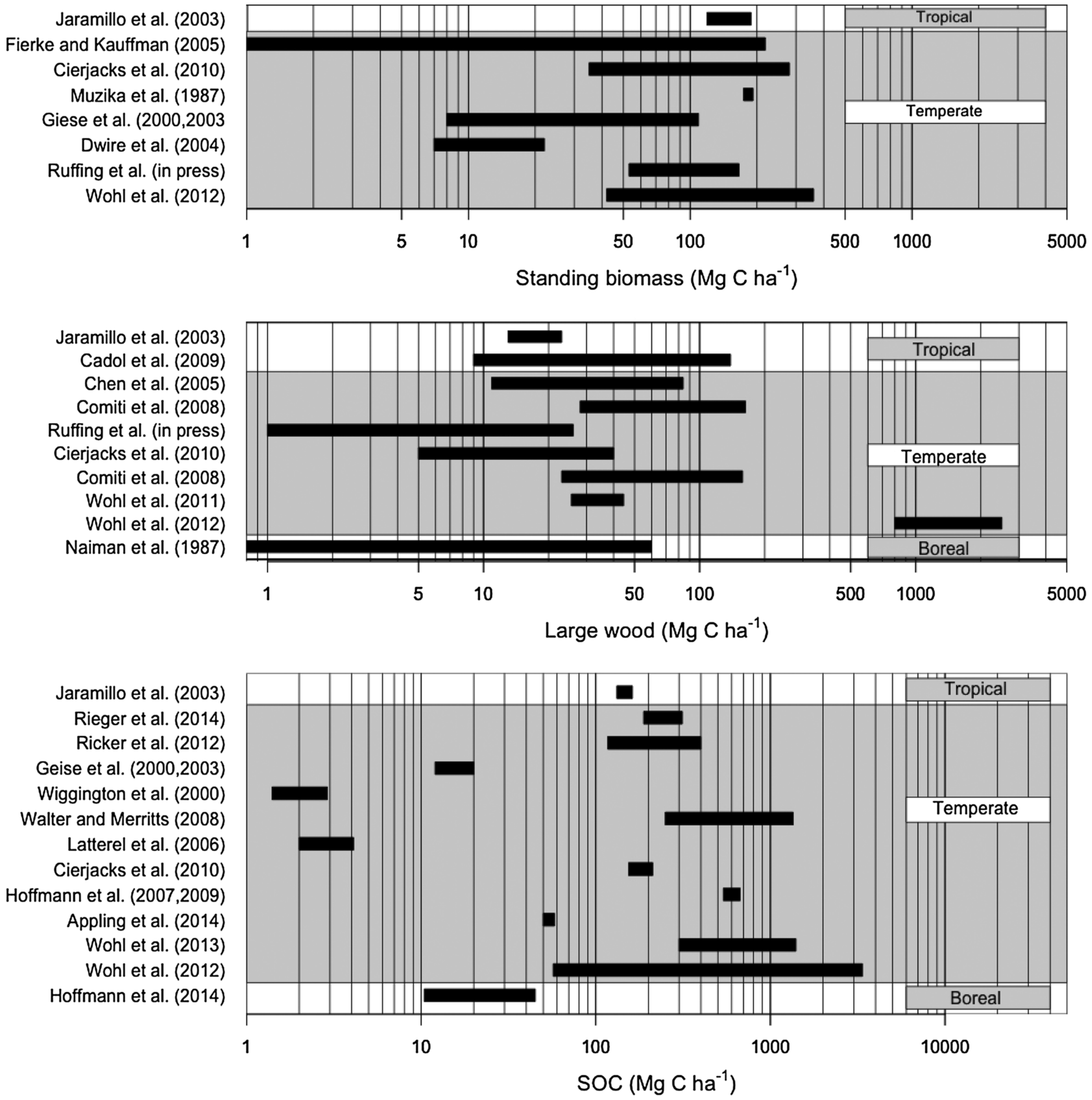

Figure 4. Studies cited here that quantify carbon reservoirs in riparian ecosystems and floodplains. Black bars indicate ranges of values reported by each study of organic carbon (OC) storage in biomass, large downed wood, and soil organic carbon (SOC). Note the different scale on *x*-axis of SOC figure. More details described in Tables I–III.

Studies of estimated riparian biomass were limited primarily to temperate regions, with few data for other climatic regions. No published estimates of riparian biomass OC were found for arid regions. However, pioneer species of willow and cottonwood are common in the floodplains of many desert rivers in North America (Stromberg *et al.*, 2013), and values may be comparable to those reported for mature cottonwood forests in Oregon (190–218 Mg C ha^{-1}; Fierke and Kauffman, 2005). In tropical floodplain forests, total biomass OC values appear at the higher end of those in temperate riparian ecosystems (Fig. 4; Jaramillo *et al.*, 2003). To improve understanding of riverine OC storage, more riparian vegetation types in different ecoregions need to be sampled for a complete suite of biomass components.

Field-based estimation of OC pools in riparian vegetation involves intensive sample collection and processing (Fig. 4). To facilitate more rapid assessment of riverine biomass and OC stocks, different remote sensing techniques have been applied (Filippi *et al.*, 2014). Suchenwirth *et al.* (2012, 2014) distinguished riparian vegetation types and used high spatial resolution remote sensing data to estimate carbon stocks along the Danube River, Austria, which proved comparable to field-based estimates (Fig. 4; Cierjacks *et al.*, 2010). With increased focus on regional carbon budgets, development of remote sensing tools holds promise for estimating OC stocks for different vegetation types globally, including riparian floodplains.

Large downed wood

Large downed wood provides an important source of OM to river systems and floodplains. In a tropical Costa Rican forest, large dead wood accounted for a third of the OC in above-ground woody biomass within the entire watershed (Clark *et al.*, 2002). Dead wood in subalpine forests in the Colorado and Wyoming Rocky Mountains ranged from 2.8 to 60% (1.3–34.3 Mg ha^{-1}; Kueppers *et al.*, 2004) and 12.9 to 56% (Bradford *et al.*, 2008) of that in above-ground woody biomass. Long residence times of LW in streams and on the floodplain provide potential for long-term storage of OC and sources of POM. Numerous factors influence the volume and residence time of stored wood in river systems, including characteristics of the riparian forest stand age, stem density, species, wood decay rate, hydroclimatic disturbance regime and floods, and wood recruitment mechanisms, which include individual tree topple, disturbance-related mortality, bank and floodplain erosion, and transport from adjacent uplands and channels (Benda and Sias, 2003; Collins *et al.*, 2012). Thus, the recruitment, residence time, and stored volume of floodplain and in-stream wood are largely dictated by climate, geologic setting, and local controls on channel form.

The amount of OC stored on the floodplain and in the channel as wood varies with drainage area, ecoregion, forest stand characteristics, and valley and channel characteristics. Limited research suggests that in smaller rivers (i.e. drainage areas < 1000 km^2) downed in-stream and floodplain wood can constitute the primary reservoir of stored OC (Naiman *et al.*, 1987), particularly in unconfined valley segments wider than 10 times the bankfull channel width (Wohl *et al.*, 2012a). Larger rivers (i.e. > 1000 km^2), in which channel width typically exceeds the length of individual pieces of wood, historically had substantial wood accumulations in the form of wood rafts (Triska, 1984; Wohl, 2014a), although wood rafts are now rare because of systematic wood removal from rivers.

Volumes of in-stream wood tend to be greatest in temperate environments, which have larger trees than boreal regions, but longer decay times than tropical regions (Table II, Fig. 4; Cadol *et al.*, 2009; Wohl, 2013a). Although studies of decay rates within rivers are almost non-existent, decay rates for logs on a forest floor vary from 50 to 100 years in dry climates (O'Connell, 1997; Ellis *et al.*, 1999), 10 to 100 years in humid temperate climates (Boyce, 1961; Harmon, 1982), and less than 10 years in the tropics (Delaney *et al.*, 1998; Clark *et al.*, 2002; Lewis *et al.*, 2004). These differences between regions correspond to the potential for long residence times of LW in temperate rivers and the relative mass of OC stored in living vegetation. Hyatt and Naiman (2001) documented LW that had been in the Queets River of Washington for up to 1400 years, although most pieces were < 50 years old. In the redwood forests of north-western California, LW residence times can exceed 200 years (Keller *et al.*, 1995). In old growth, conifer-dominated riparian forests of the southern Rocky Mountains, standing trees account for only 7–22% of the total stored OC, whereas downed wood accounts for 77 to 93% (Fig. 4; Wohl *et al.*, 2012b). Although tropical floodplain forests also store notable amounts of OC (Fig. 4), over 90% comes from standing riparian biomass (trees and vines), whereas downed wood contributes only about 8%, presumably due to rapid decay rates (Jaramillo *et al.*, 2003).

Forest stand characteristics that influence the storage of OC as LW include species composition and stand age. Species composition and stand age influence susceptibility to disturbances such as wildfire, blowdowns, and insects (Turner, 2010). Species composition and stand age also influence piece size and shape of LW, and therefore mobility and residence time of LW on floodplains and in channels (Montgomery *et al.*, 2003; Wohl *et al.*, 2011). Finally, species composition and stand age influence mortality rate and rates of LW decay and abrasion (Keim *et al.*, 2000; Hyatt and Naiman, 2001; Latterell and Naiman, 2007; Wohl and Goode, 2008).

Channel geometry and in-stream wood play an important role in the retention and ecosystem processing of OC because wood obstructing channelized flow can facilitate complex flow paths and hydrologic connectivity to the floodplain and floodplain retention of OM (Sear *et al.*, 2010; Wohl *et al.*, 2011; Collins *et al.*, 2012; Polvi and Wohl, 2013; Wohl, 2013a; Beckman and Wohl, 2014), delay the downstream transport of POM (Bilby, 1981; Montgomery *et al.*, 2003; Quinn *et al.*,

Table II. Published values of ages and carbon storage as downed wood on floodplains and in active channels

Location	Climate	Ages of wood (yr)	Organic carbon content (Mg C ha^{-1})	Organic carbon content (Mg C 100 m^{-1})	Reference
Floodplains					
South-eastern Australia	Temperate	240 ± 40			Webb and Erskine, 2003
Ontario, Canada	Temperate	350 – 800			Guyette *et al.*, 2002
Missouri, USA	Temperate	3515[a]			Guyette *et al.*, 2008
Colorado, USA	Temperate		800–2500		Wohl *et al.*, 2012b
South Carolina, USA	Temperate		25.5– 44.5[b]		Wohl *et al.*, 2011
Quebec, Canada	Temperate		57.3		Naiman *et al.*, 1987
Central Chile	Temperate		23–158[b]		Comiti *et al.*, 2008
Tierra del Fuego, Argentina	Temperate		30[b]		Comiti *et al.*, 2008
Danube River, Austria	Temperate		5– 40		Cierjacks *et al.*, 2010
Southeast Wyoming, USA (first and second order)	Temperate		1–26		Ruffing *et al.*, in press
Chamela Biological Station, Jalisco, Mexico	Tropical		13–23[e]		Jaramillo *et al.*, 2003
Active channels					
Quebec, Canada	Boreal		0.8–60, 23.2[f]		Naiman *et al.*, 1987
British Columbia, Canada	Temperate		10.9– 83.9[c]		Chen *et al.*, 2005
Washington, USA	Temperate	19[c], >1400[d]			Hyatt and Naiman, 2001
Washington, USA	Temperate			0.75–35.5[b] 0 –21.8[b]	Fox and Bolton, 2007
Italy	Temperate			0.1– 0.7[b]	Comiti *et al.*, 2006
Central Chile	Temperate		28 –163[b]		Comiti *et al.*, 2008
Tierra del Fuego, Argentina			28[b]		
La Selva, Costa Rica	Tropical		9 –139[b]	1.4 –15.8[b]	Cadol *et al.*, 2009

[a] Wood buried by floodplain aggradation.

[b] Estimated from reported values and wood density for reported species assuming 50% of mass as carbon.

[c] Reported median value.

[d] Maximum age reported.

[e] Estimated range from reported wood volumes, reported mean wood densities, and reported error.

[f] Calculated mean from published values.

2007; Battin *et al.*, 2008), and create biological hotspots that provide opportunities for biota to metabolize OC (Gomi *et al.*, 2002; Allan and Castillo, 2007; Hilton *et al.*, 2008; Tank *et al.*, 2010).

Large in-stream and floodplain wood can persist for thousands of years (Guyette *et al.*, 2002, 2008; Webb and Erskine, 2003), and can constitute the majority of the OC stored on floodplains (Wohl *et al.*, 2012b). Persistent large downed wood can also serve as a continued source of POM for riparian and aquatic ecosystems (Ward and Aumen, 1986; Guyette *et al.*, 2002, 2008; Webb and Erskine, 2003). Accurate estimates of the natural range of variability in contribution of wood to OC reservoirs are impractical because a long history of human modification has resulted in substantial reductions in wood loads (Wohl, 2014a).

Litter, POM, humus, and SOC

The floodplain surface and shallow subsurface host a large reservoir for OC, including surface organic layers and SOC. Surface organic layers, frequently termed the forest floor, consist of plant litter in various stages of decay (Perry *et al.*, 2008). Litter is the OM that comprises the top layer of the forest floor, and is composed of small branches, twigs, and recently fallen needles and leaves that are still identifiable and little altered by decomposition (Naiman *et al.*, 2005; Lutes *et al.*, 2006). The litter layer may also include OM from shrubs, grasses, and forbs that have recently died. Litterfall is the OM that falls to the floodplain forest floor or the allochthonous material that enters streams from riparian vegetation. On the forest floor, the humus layer underlies the litter layer and is comprised of partially decomposed OM and litter, which is no longer recognizable as discrete plant parts.

Floodplain litter and humus layers reflect riparian vegetation type, successional stage, local productivity of vegetation, and the climatic and edaphic factors that regulate decomposition (Benfield, 1997). In uplands, the highest litterfall rates are found in tropical equatorial forests (~5.3 Mg C ha^{-1} yr^{-1}; Vitousek, 1984; Vitousek and Sanford, 1986), followed by tropical montane (~3.1 Mg C ha^{-1} yr^{-1}; Veneklaas, 1991) and warm temperate forests (Table III; ~2.5 Mg C ha^{-1} yr^{-1}; Bray and Gorham, 1964; Naiman *et al.*, 2005). The lowest litterfall rates have been observed in boreal and cool temperate forests (<1 to ~1.5 Mg C ha^{-1} yr^{-1}; Bray and Gorham, 1964; Naiman *et al.*, 2005). Reviews of allochthonous litterfall to rivers show the same geographical trends as litterfall to the forest floor and reveal an inverse relationship between riparian litter production and latitude (Xiong and Nilsson, 1997) and a positive relationship between litterfall and annual precipitation (Benfield, 1997). Riparian vegetation is generally characterized by higher plant diversity, biomass, and higher rates of litter production than adjacent upland vegetation (Xiong and Nilsson, 1997). The majority of published information on litterfall by riparian vegetation is limited to warm, temperate forest floodplains in North America, where annual litter inputs range from approximately 2.8 to 4 Mg C ha^{-1} (Table III), indicating higher productivity in riparian forests relative to uplands.

In most riparian areas, however, the forest floor organic layers, especially the litter layer, are much more dynamic than in upland environments. During high flows, OM from upstream riparian sources and in-stream primary productivity can be deposited and local floodplain OM redistributed (Pinay *et al.*, 1992; Hall *et al.*, 2009). Hillslope erosion and debris flows can deliver OM from upslope and bury riparian OM under mineral sediment (Ramos Scharrón *et al.*, 2012). Erosional and depositional disturbances contribute to the mosaic of OC distribution in riparian areas and the creation of biogeochemical hotspots (McClain *et al.*, 2003), partly through the redistribution of litter and POM by fluvial processes.

Riparian vegetation litter is a major source for POM for lotic foodwebs, particularly along headwater streams where channels are narrow and allochthonous inputs are high (Vannote *et al.*, 1980; Conners and Naiman, 1984; Ward and Aumen, 1986; Gomi *et al.*, 2002; Allan and Castillo, 2007; Hilton *et al.*, 2008; Richardson *et al.*, 2009; Tank *et al.*, 2010). Discontinuities due to tributary variation in valley form, and anthropogenic and natural disturbances, disrupt an idealized downstream pattern in which autochthonous C inputs grow progressively more important than allochthonous inputs (Tabacchi *et al.*, 1998; Allan and Castillo, 2007).

The distribution, accumulation, and type of POM influence the rate of decomposition and mineralization of nutrients (Vannote *et al.*, 1980; Gomi *et al.*, 2002; Allan and Castillo, 2007; Hilton *et al.*, 2008; Tank *et al.*, 2010). Allochthonous carbon inputs in headwater streams are composed primarily of CPOM in the form of wood, litter, and humus (Vannote *et al.*, 1980; Ward and Aumen, 1986; Allan and Castillo, 2007; Richardson *et al.*, 2009; Tank *et al.*, 2010). Microbes and aquatic invertebrates break down CPOM to FPOM, contributing OC and nutrients to aquatic and terrestrial foodwebs that include numerous vertebrate, invertebrate, and microbial taxa (Vannote *et al.*, 1980; Wagener *et al.*, 1998; Allan and Castillo, 2007). Litter and redistributed POM pools can be dynamic by means of hydraulic redistribution, but continued aggradation can facilitate decomposition and storage as humus and SOC.

Soils are the third largest reservoir in the global carbon cycle after the deep ocean and geologic storage, and store more carbon than living biomass and the atmosphere combined (Ruddiman, 2001). Abundant research has examined SOC content in various landscapes, but work focusing on river systems is limited (Fig. 4). The majority of research has occurred in temperate and subtropical regions, whereas boreal, arid, and tropical regions have received considerably less attention. Although OC studies in floodplain sediment are very limited in tropical regions, Moreira-Turcq *et al.* (2004) and Jaramillo *et al.* (2003) suggest that tropical riparian ecosystems contain SOC values comparable to the lower end of values in temperate regions (Table III). Cabezas *et al.* (2009) indicate that Mediterranean temperate climates may have similar trends, whereas temperate and subtropical climates appear to have much variability in SOC storage.

Hydrologic disturbance, particle sorting and potential accumulation of fine sediment make riparian ecosystems a dynamic component of the terrestrial carbon cycle, with implications for SOC processing and potential long-term storage. Soil moisture and percent clay content are positively correlated with SOC content (Pinay *et al.*, 1992; Jobbágy and Jackson, 2000; Wigginton *et al.*, 2000; Hoffmann *et al.*, 2009; Moyano *et al.*, 2012), so that dry, coarser textured soils typically contain less OC. Dissolved organic carbon transported through riparian soils may be adsorbed to clay mineral surfaces (Schulze *et al.*, 2005). Typical soil chronosequences exhibit a decrease in SOC content with depth (Birkeland, 1999; Jobbágy and Jackson, 2000). This relationship does not appear as strong in floodplain soils (Cole *et al.*, 2007; Gurwick *et al.*, 2008b), although it can be present (Walling, 2006).

Soil organic carbon distribution in riparian ecosystems can be complex because surface and subsurface microbial activity and mineralization of OC can be disconnected. Much OC can be stored as roots and in buried A-horizons (Blazejewski *et al.*, 2009) and SOC content may become more stable with burial (Cole *et al.*, 2007) because it is farther from intense

Table III. Published values for carbon accumulation rates and total storage on floodplains

Location	Climate	Drainage area (km^2)	Accumulation rate (Mg C ha^{-1} yr^{-1})	Sediment organic carbon content (Mg C ha^{-1})[a]	Reference
Alberta, Canada	Boreal	—	—	10.4–45, 23.6[g]	Hoffmann, Hoffmann, Johnson and Kuhn, 2014a
Ichauwaynochaway Creek, Georgia, USA	Temperate	2600	0.18 (over 30 years)[b] 1.07 (over 100 years)	—	Craft and Casey, 2000
Headwaters in southern New England, USA	Temperate	<600 ha	0.03 0.007 pre-colonial	262 (117–400)	Ricker *et al.*, 2012
Rhine River, Germany	Temperate	185,000	0.034–0.254	538–671	Hoffmann *et al.*, 2007, 2009
Chickahominy, Virginia, USA	Temperate	1210	1.4	—	Noe and Hupp, 2009
Choptank		290	0.7		
Dragon Run		360	0.9		
Mattaponi		2360	1.4		
Pamunkey		2800	0.7		
Patuxent		900	0.7		
Pocomoke		970	0.3		
Atchafalaya River, Louisiana, USA	Temperate	5670	8	—	Hupp *et al.*, 2008
Tar River, North Carolina, USA	Temperate	8056	2.8	—	Brinson *et al.*, 1980
North St. Vrain & Big Thompson Rivers, Colorado, USA	Temperate	20–36	—	57–622[c] 224–3365[d] 1014[e]	Wohl *et al.*, 2012b
Beaver Brook and Upper Poudre River, Colorado, USA	Temperate	3.8–110		300–400[f] 1150–1400[e]	Wohl, 2013b
6 rivers southwestern England	Temperate	276–1124	0.7–1.1	—	Walling, 2006
20 streams, mid-Atlantic Piedmont, USA	Temperate	11–1230	—	250–1350	Walter and Merritts, 2008
Savannah River, South Carolina, USA	Temperate	51–57	—	1.4–2.9	Wigginton *et al.*, 2000
Middle Fork Flathead River, MT, USA	Temperate	2300	—	7735	Appling, 2012
Queets River, WA, USA	Temperate	1153	—	2–4.1	Latterell *et al.*, 2006
Danube River, Austria	Temperate	104,000	2.9	—	Tockner *et al.*, 1999
Ebro River, Spain	Temperate	40,434	1.4–3	—	Cabezas *et al.*, 2009
Kankakee River, Illinois, USA	Temperate	—	0.6	—	Mitsch *et al.*, 1979
Cache River, Illinois, USA	Temperate	—	0.6	—	Mitsch *et al.*, 1977
Appalachicola River, Florida, USA	Temperate	—	0.2	—	Mulholland, 1981
Danube River, Austria	Temperate	—	—	154–186 176 212	Cierjacks *et al.* 2010
Pen Branch Fourmile Branch Meyer's Branch (third order tributaries to Savannah River, South Carolina, USA)	Temperate	—	—	12–20[d]	Giese *et al.*, 2000, 2003
Danube, Austria	Temperate	—	—	188–313	Rieger *et al.*, 2014
Jalisco, Mexico	Tropical	—	—	132–162[c]	Jaramillo *et al.*, 2003
Amazon River, Brazil	Tropical	3660	1–2.5	—	Moreira-Turcq *et al.*, 2004

[a] Mean (range in parentheses, when available).

[b] Greater historical rates are interpreted to reflect land use and lack of soil conservation practices in the past.

[c] Floodplain sediment; forested site.

[d] Floodplain sediment and downed, dead wood; forested site.

[e] Active beaver meadow.

[f] Relict/abandoned beaver meadow.

[g] Calculated mean of reported means.

microbial activity at the surface (Gurwick *et al.*, 2008a; Ricker *et al.*, 2012). Because microbial activity is regulated by temperature, seasonal and diurnal variations influence microbial metabolism of OC. The moist conditions of riparian soils facilitate increased metabolism of SOC by microbes (Billings *et al.*, 1998), whereas saturated conditions associated with shallow water tables decrease metabolism and increase potential for long-term storage (Falloon *et al.*, 2011). Continued aggradation and burial of floodplain soils may contribute to high rates of OC sequestration (Gurwick *et al.*, 2008a).

Potential for long-term storage of SOC depends on the source and form of the OC (Gurwick *et al.*, 2008b) and the residence time of floodplain sediment (Oost *et al.*, 2012). Dissolved organic carbon may travel through river networks in ~10 to 10^2 years, whereas POM may take much longer (i.e. > 10^3 years; Raymond and Bauer, 2001), presumably being stored within floodplain sediment. Residence time of SOC is influenced by biologic and physical factors. Our discussion is framed primarily within the context of physical drivers that influence residence time of sediment and organic debris on floodplains in riparian ecosystems, with only limited mention of the biogeochemical factors that influence metabolism. The biologically-driven residence times typically of interest to ecologists and biogeochemists, however, are dependent on other factors discussed earlier, including moisture content, temperature, and characteristics of riparian vegetation communities.

Although researchers have examined OC storage and dynamics in river systems, work investigating mechanistic and geomorphic controls on OC storage in riparian ecosystems is limited. Pinay *et al.* (1992) were among the first to examine carbon storage in riparian soils, with explicit distinction of geomorphic influence on sediment size distributions and associated SOC. Examination of three segments of the Garonne River in France indicated that confined, erosional segments dominated by sandy soils contained less SOC than less confined, depositional segments dominated by silty clay soils (Pinay *et al.*, 1992). However, a much larger fraction of the OC in the erosional, sandy soil reach was available for biological uptake. Fine–grained sediments can serve as nutrient and OC sinks, whereas sandy soils readily release available carbon during high flows (Pinay *et al.*, 1992).

Channel geometry and the degree of valley confinement and relative width of the floodplain to the channel can play a crucial role in the aggradation of sediment and accumulation of POM and SOC (Fryirs *et al.*, 2007). Several studies indicate that wider valley bottoms and lower-gradient channels store more fine sediment, POM, and SOC compared to steeper and more laterally confined valley segments (Blazejewski *et al.*, 2009; Noe and Hupp, 2009; Wohl *et al.*, 2012b).

Reach characteristics associated with hydroclimate, flow regime, and valley geometry, including riparian valley width, duration of inundation, sediment sources, distance from the active channel, and flow velocity, may also account for significant differences in POM and SOC storage (Hupp *et al.*, 2008). Although floodplains have received some attention as sites of OC accumulation, less frequently inundated surfaces such as terraces should also be evaluated for OC content (Latterell *et al.*, 2006). Spatial differences in OC content among geomorphic surfaces in various landscapes will likely depend on climate, vegetation type, distance from the channel, and land use before, during, and after the time of aggradation and abandonment. Gurwick *et al.* (2008a) emphasize the importance of the abundance of OC at the time of deposition, rather than the time since deposition, with regard to controls on current OC content.

Regional Comparisons of Floodplain OC Storage and a First-order Estimate of Global Floodplain OC Storage

Reported accumulation rates and mass of OC calculated per area within riparian ecosystems (Fig. 4) reveal that OC reservoirs in riparian ecosystems are highly variable across and within particular climatic regions. This indicates that other factors such as geologic setting and local-scale variables play an important role in OC storage within riparian ecosystems. Temperate regions exhibit the most variability, but this could reflect the fact that most of the work done to quantify OC storage in riparian ecosystems comes from temperate regions, as well as the diversity of temperature, moisture, and meso-climate conditions within temperate latitudes. Highlands in various climatic regions, for example, suggest the potential for large OC reservoirs along small mountainous streams (Aguado and Burt, 2007), which might have OC storage per unit area at least an order of magnitude higher than most lowland rivers (Wohl *et al.*, 2012b; Wohl, 2013b; Hoffmann *et al.*, 2014a; Hoffmann *et al.*, 2014b), except for those highly impacted by land use and legacy sedimentation (Walter and Merritts, 2008).

Drawing on the literature cited in Tables I–III and Fig. 4, we propose a conceptual model of the conditions under which OC retention is maximized in riparian ecosystems (Fig. 5). Although these conditions encompass the regional and local characteristics discussed earlier and in Fig. 3, and their influence on the three primary reservoirs for moderate-to-long-term OC retention and storage, Fig. 5 does not capture the full complexity of OC dynamics associated with all potential factors. The most notable of these complexities are moisture and temperature. As discussed earlier, an intermediate level of moisture provides optimal conditions for the decomposition of OC, such that saturation or limited moisture hinders decomposition (Jobbágy and Jackson, 2000; Falloon *et al.*, 2011). Rivers in tropical forests provide an example. Although higher

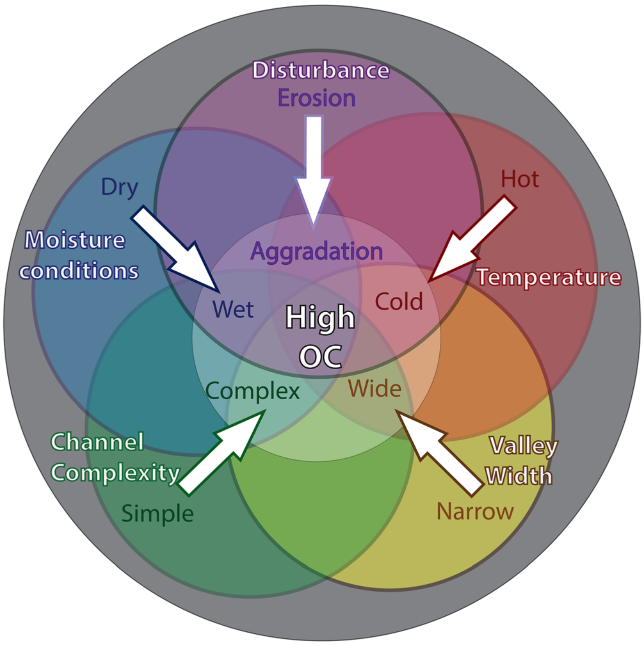

Figure 5. Optimal conditions for high organic carbon (OC) retention (in the center of the diagram) in river systems based on relationships between regional and local controls in Fig. 3. Arrows denote the gradient toward optimal conditions with regard to valley width, channel complexity, moisture, temperature, and disturbance. Fig. 3 illustrates the inter-relations between other factors that influence these optimal conditions. Channel complexity, for example, is influenced by biotic drivers such as vegetation, beavers, and large downed wood; whereas moisture conditions are influenced by ecoregion, valley characteristics, channel complexity, and soil type. This model indicates that optimal conditions for OC retention are low gradient river segments in broad unconfined valleys with high levels of channel complexity – which facilitates hydrologic connectivity, saturated conditions, and sediment aggradation – in cooler climates. Each component in this conceptual model can be influenced by various factors in Fig. 3. For example, moisture conditions can be influences by climate, valley geometry, channel form, and hydrologic connectivity.

temperatures facilitate increased growth of riparian vegetation in the tropics, they also increase decomposition rates, which lowers OC storage as indicated in Fig. 3 and the optimal conditions captured in Fig. 5. This is why we suggest that colder environments store more carbon. Cold and wet environments provide another example of the complexity of influences on OC storage: wet conditions are required to produce vegetation, but cold conditions regulate decomposition. The combined factors of wet and cold environments increase OC storage. The schematic illustration in Fig. 5 is not meant to imply linear relationships between OC storage and temperature, moisture, or other factors, but rather to illustrate the directional trends in these relationships and the optimal conditions for OC storage.

Currently, limited data in most climatic regions constrain our ability to examine potential differences across Earth's surface. From the studies cited here, it appears that large primary productivity in tropical regions results in large reservoirs of standing biomass, but high rates of decomposition limit LW and SOC reservoirs compared to temperate regions (Fig. 4; Jaramillo *et al.*, 2003). Although work indicates large SOC reserves in boreal regions outside of riparian areas (Tarnocai *et al.*, 2009), the limited work cited here (Hoffmann *et al.*, 2014a) does not indicate these difference along boreal floodplains. We emphasize that inferences are constrained by currently published work, but we draw on this work to discuss potential conditions for optimal OC storage.

Warmer temperatures and increased moisture increase decomposition rates and metabolism of OC (Trumbore and Czimczik, 2008; Falloon *et al.*, 2011). Although warm, moist, tropical climates have high primary productivity and standing biomass, high decomposition rates and the lack of distinct seasonal fluxes of litter timed with redistribution from seasonal flow regimes likely limit total carbon storage in soil, litter, and LW (Clark *et al.*, 2002; Cadol *et al.*, 2009). Conversely, metabolism of riparian ecosystems in boreal regions is temperature limited. Moisture controls are more complicated because microbial respiration increases with increasing moisture content, but saturated conditions limit aerobic respiration and metabolism of OC. Abundant moisture and saturated conditions from snowmelt and shallow water tables overlying permafrost in alpine and boreal regions also limit metabolism. Low primary productivity in boreal regions, however, limits potential uptake of OC to soils and storage within large trees and LW. Limited work along boreal and alpine floodplains indicates a relatively small range of SOC storage in riparian ecosystems (1.8–234.6 Mg C ha^{-1}: Hoffmann *et al.*, 2014a; Hoffmann *et al.*, 2014b), but very high SOC contents in boreal peatlands and permafrost (322–696 Mg C ha^{-1}; Tarnocai *et al.*, 2009) suggest that the limited work on boreal floodplains (Table III; Fig. 4) may not capture the true range of variability in subarctic rivers.

Valley geometry influences available space for energy dissipation and the aggradation of alluvial sediment, which can influence primary productivity, abundance of riparian vegetation, and complexity of channel geometry. With room to move in relatively wide valleys and atop alluvial plains, channels can adjust their bedforms, width:depth ratio and cross-sectional form, slope, channel planform, and grain size distribution (Leopold *et al.*, 1964; Knighton, 1998; Wohl, 2014b) to develop complex geometries and floodplains that help to slow the movement of water, and facilitate moist conditions and deposition of sediment, OM, and OC.

Increased lateral and vertical hydrologic connectivity should ensure increased OC storage, as reflected in the highest SOC contents listed in this review (Wohl *et al.*, 2012b; Wohl, 2013b), but this is dependent on the magnitude and frequency of hydrologic and geomorphic disturbances and the variability of moisture conditions. As long as connectivity between the floodplain and the channel facilitates aggradation, continued accumulation and storage of OC is ensured. Erosion of the floodplain during high magnitude floods can displace OC stored in floodplain sediment and remove riparian vegetation, hence the significance of wide valleys and open plains, which can dissipate energy and limit erosion of the floodplain.

We expect that low gradient, wide floodplains in old-growth forests with complex channel geometry, a high degree of lateral hydrologic connectivity between channels and floodplains, saturated soil conditions, and slow rates of organic decay associated with relatively cold temperatures will have the greatest per unit area storage of OC. Although the data presented in this review do not necessarily support this, we hypothesize that boreal, alpine, and cool temperate regions that exhibit the earlier-mentioned physical attributes are likely to store more OC per unit area compared to other regions, primarily because of low temperatures and rates of decomposition. Additional, field-based quantifications of OC storage are needed to examine the validity of this conceptual model and our proposed optimal conditions of OC storage in riparian ecosystems.

An accurate approximation of global carbon storage in riparian ecosystems requires additional information in underrepresented regions, the use of common metrics for sampling and reporting values, and utilization of advanced computational resources capable of analyzing large quantities of remotely sensed data and modeling the various influential factors discussed here. Because temperate regions have received the most attention with regard to OC in riparian ecosystems, the ability to extrapolate values across Earth's surface is limited. Despite the paucity of data and shortcomings in the state of reported OC values, a first-order approximation can be made. Floodplains are estimated to cover approximately 0.8×10^6 to 2×10^6 km^2 globally (Leopold *et al.*, 1964; Tockner and Stanford, 2002; Mitsch and Gosselink, 2015). As a conservative estimate across all climatic regions, and using the median for both the minimum and maximum values of organic carbon stored in riparian ecosystems (i.e. 202–386 Mg C ha^{-1}) from each study cited earlier, riverine ecosystems could store as much as 16–125 Pg C globally. Because SOC is the largest reservoir of OC in riparian ecosystems (Fig. 4), we use the same method to estimate that floodplain SOC may account for 12 to 80 Pg C globally. When compared with modeled estimates of potential OC in soils globally (991–2469 Pg C; Hiederer and Kochy, 2011), our rough estimate suggests that riparian ecosystems could account for 0.5 to 8% of global SOC storage, even though they cover only 0.5–1% of the land surface. We emphasize that this is a first-order approximation that must be refined with additional quantification from less represented climatic regions, as well as better use of remote sensing data to quantify total floodplain area and proportions of that total area associated with differing sizes of rivers and differing valley geometry and flow regime.

Human Influences on OC Reservoirs in Riparian Ecosystems

In this section, we briefly review human alterations of OC dynamics in river systems. Although human-induced changes in process and form within uplands and river corridors have likely exerted a substantial influence on OC transport to, and processing and storage within, rivers, this topic has received minimal attention. This section is intended to highlight the major categories of human influence and emphasize the need for more focused research on this topic.

Land-use and land-cover changes are transforming landscapes at an accelerating rate throughout the world and are recognized as a critical gap in the current understanding of the terrestrial carbon cycle (Houghton, 1994; Tappeiner *et al.*, 2008). Land use can play a significant role in sediment and carbon supply to rivers, as well as accumulation rates within riparian ecosystems. Although largely undocumented, the conversion of fertile floodplains to other land uses, particularly agriculture, has likely caused significant carbon releases, reducing the amount of stored carbon (Mitra *et al.*, 2005). Land use can also influence biomass and SOC by altering the age of riparian forests (Giese *et al.*, 2000, 2003). Soil organic carbon increases with stage of forest succession (Wigginton *et al.*, 2000), although rates of OC accumulation can decline with time (Zehetner *et al.*, 2009).

Land use can increase floodplain accumulation of OC, particularly forest harvest and agricultural practices that accelerate erosion and downslope movement of sediment (Noe and Hupp, 2005; McCarty *et al.*, 2000). In a study of land-use trends in watersheds of southern New England, USA, Ricker *et al.* (2012) related patterns of riparian sedimentation and carbon sequestration rates to three major land-use periods: pre-colonial, colonial-agrarian, and modern. Although results varied across watersheds, they found that most of the stored sediment and SOC in riparian soils originated during the post-colonial period, and that net SOC sequestration rates have increased nearly 200-fold since pre-colonial times (pre-1800), likely due to regional deforestation and conversion to agricultural use. In contrast, Norton *et al.* (2011) found that degraded montane riparian meadows of the Sierra Nevada Mountains of California stored lower amounts of SOC than meadows in ‘proper functioning condition’. Degradation was attributed to logging, a legacy of heavy, unregulated livestock grazing, and more recently, recreational vehicle use. Loss of biodiversity in riparian ecosystems (Tockner and Stanford, 2002) can greatly influence OM inputs to riverine ecosystems and potential carbon stocks.

Flow regulation can also influence OC dynamics within riparian ecosystems. Structures such as dams and diversions interrupt downstream transport of OM and DOC. Walter and Merritts (2008) document legacy sediment and OC storage of 250 to 1350 Mg C ha^{-1} behind thousands of abandoned milldams in Pennsylvania and Maryland, USA. Bank erosion of this legacy sediment redistributes OC along downstream floodplains (Schenk *et al.*, 2013). Sediment aggradation in inland lentic waters including lakes and man-made reservoirs can store as much as 33% of the carbon moving through fluvial systems (Tranvik *et al.*, 2009). Flow diversion also alters flow characteristics that support riparian vegetation and entrain and transport OM. In an examination of temporal effects of hydrologic connectivity on nutrient dynamics along a floodplain in the Danube River within Austria, for example, Tockner *et al.* (1999) determined that accumulation of OM occurred primarily during large flood pulses, whereas export of DOC occurred primarily during moderate flood levels with limited connectivity to the floodplain.

Channel manipulation in the form of channelization, straightening, dredging, bank stabilization, and construction of levees can influence OC dynamics by encouraging incision and altering longitudinal and lateral fluxes of water and fine sediment, OM, and DOC. These types of channel manipulation are commonly done to reduce flooding and to more efficiently convey water. By increasing longitudinal connectivity, these types of channel manipulations increase downstream fluxes and decrease vertical connectivity between the channel and hyporheic zone, and lateral connectivity between the channel and floodplain. This alters fluxes of dissolved and particulate OC by reducing retention of water and sediment in riparian areas and entire watersheds. Decreased retention of water and sediment reduces biological uptake and storage of OC within riparian ecosystems (Naiman *et al.*, 1986). Current efforts in process-based channel restoration, however, aim to increase lateral connectivity of water and sediment to the floodplain and facilitate increased hyporheic exchange (Collins and Montgomery, 2002; Beechie *et al.*, 2010; Burchsted *et al.*, 2010).

Knowledge Gaps and Discussion

Although OC retention in floodplains and riparian areas is important for OC reservoirs and ecosystem processing, many gaps exist within our collective understanding of riparian OC pools. Gaps in knowledge include: (i) the magnitude of differences across regions and biomes; (ii) effects of a changing climate; (iii) residence time; and (v) human influences.

Data paucity

The most notable knowledge gap, apparent from this review, is the lack of global coverage of studies across diverse climates and geologic settings. Most studies, including surveys of OC in standing biomass, downed LW, and soil in riparian ecosystems, lie within temperate climates, and few to no studies have been conducted in boreal, tropical, and arid regions. Most studies have been conducted in North America and Europe, but it is difficult in these regions to study landscapes that have not been highly impacted by human activities. Examining the natural processes responsible for OC retention in river systems requires working in less human-altered regions before these natural processes become too highly impacted. Work in these areas may also provide a baseline for future restoration. Additionally, data are limited in: (i) more tectonically active landscapes, including the South American Andes and the Himalaya; (ii) areas which are difficult to study, such as large tropical rivers like the Amazon, and boreal rivers; (iii) mountainous environments, which are particularly sensitive to climate change; and (iv) arid and semi-arid regions, which may represent future conditions for many regions of the world following desertification and over-consumption of freshwater resources. Although we propose general patterns of climatic and landscape controls on OC retention in riparian ecosystems, more research is needed to examine these relationships, test proposed influences, understand relevant processes, and establish baseline conditions for OC retention along river networks. This is important not only for the terrestrial carbon cycle and storage, but also for ecosystem processing, foodwebs, ecosystem integrity, and ecosystem services.

A changing climate

As climate change alters precipitation regimes, changes in seasonal hydrologic connectivity will likely influence the ability of individual landscapes to retain OC. Rising mean annual temperatures, declining snowpack, and earlier snowmelt in mountainous regions (Bates *et al.*, 2008; Pederson *et al.*, 2011) are expected to decrease hydrologic connectivity (Allison *et al.*, 1990; Schulze and Walker, 1997; Alexander, 2014), and thus may impact ecosystem processing of OC and nutrients. Organic carbon with potential for long-term storage becomes more bioavailable as wetland soils dry completely or for longer periods throughout the year. This loss of moisture impacts soil microbial activity and the productivity of aquatic biota by altering connectivity, as well as changes in surface water temperature. Similarly, loss of connectivity causes shifts in riparian vegetation community structure and resulting leaf litter and POM. The directional shift caused by specific changes in processing of OC within riparian ecosystems is uncertain because of higher global average temperatures (Trumbore and Czimczik, 2008) and potential increase in the frequency of extreme storms (Bates *et al*., 2008). Increased intensity of feedbacks between riparian vegetation and channel planform impacts the natural ability of the landscape to delay, filter, and store POM, nutrients, and DOC from surface waters.

Projected sea level rise as a response to climate change has the potential to influence floodplain aggradation through changes in base level. Decline in the elevation of base level encourages channel incision, decreases lateral hydrologic connectivity, and may promote the decline of local water tables and abandonment of floodplain surfaces (Mertes and Dunne, 2007; Wohl, 2015). Periods of aggradation and degradation along the Mississippi River floodplain, for example, are closely tied to glacial cycles that regulate sea level (Knox, 2007). A rising sea level may mean less erosion of river channel beds, banks, and floodplains, and thus potentially more OC storage in riparian ecosystems.

Although disturbances such as insect infestations and wildfire occur naturally, their frequency and intensity are increasing with climate change (Westerling *et al*., 2006; Bentz *et al*., 2010). These factors influence the age, size, and abundance of wood available for recruitment and sources of CPOM (Amiro *et al*., 2010; Turner, 2010). Increased loss of old-growth forest as a result of increased frequency of these disturbances limits CPOM inputs, decreases standing biomass, and limits the size of large trees that can facilitate persistent, channel-spanning log jams (Wohl, 2013a).

Residence time

As mentioned earlier, residence time of OC in riparian ecosystems is regulated by the residence time of floodplain sediment and OM, as well as by microbial metabolism. Quantification of floodplain sediment turnover rates can help determine how long OM and associated OC remain in riparian ecosystems, but understanding rates of decomposition and mineralization of OC is required to fully quantify potential OC storage. The form in which OC is retained in riparian ecosystems influences potential for ecosystem processing or long-term storage. Recalcitrant and more stable forms of SOC may be retained for longer periods of time within the terrestrial carbon reservoir, whereas more labile and more easily processed forms of SOC serve as a source for metabolism by soil and aquatic biota (Blazejewski *et al*., 2005; Gurwick *et al*., 2008a). Hoffmann *et al*. (2013) identify three components of OC fluxes in sediment that warrant attention: (i) increases in bioavailable OC following disaggregation; (ii) adsorption of OC to mineral facies; and (iii) increased stability of OC following aggradation and burial. These topics beg the question: Which factor most limits OC storage in floodplains, residence time of floodplain sediment or rate of microbial metabolism? These topics may become increasingly important as riparian soils dry and sea levels rise. More research is also needed to understand how and when the composition of microbial communities changes and how shifts in microbial communities influence processing of OC. It is also important to emphasize the large-scale and local influences on potential aggradation, long-term storage, and fate of OC in river systems. What are the tradeoffs between OC storage along complex channels, for example, versus increased hotspots for microbial mineralization of OC?

Land use in the Anthropocene

Although geologic setting and a changing climate regulate conditions for OC retention in riparian ecosystems, human activities that decrease channel complexity and hydrologic connectivity have the ability to greatly decrease OC retention in river systems. However, the relative magnitude of these human-induced effects is undetermined for diverse regions and biomes. As we establish a baseline understanding the natural processes of OC storage along river networks, we can begin to examine the impacts of land use more thoroughly. Work in human-altered areas is needed to determine whether process-based river restoration (Collins and Montgomery, 2002; Wohl *et al*., 2005; Beechie *et al*., 2010; Wohl *et al*., 2015) and the use of green infrastructure in urban watersheds could mimic natural processes to increase carbon retention in riparian ecosystems.

The challenges facing freshwater sustainability under a warming climate are exacerbated by growing populations and increasing demand for freshwater as land-use managers continue to increase freshwater reservoirs and flow diversions. Flow alterations and unsustainable groundwater pumping may also lower the elevation of groundwater tables connected to rivers and streams and induce drying of riparian wetlands. Uncertainties regarding changes to the hydrologic regime, population growth, and land use leave many questions regarding the future of carbon in river systems.

Berhe *et al*. (2007) and Oost *et al*. (2012) suggest that erosion following disturbance increases the capacity of the landscape to take up carbon by removing vegetation and OC stored in soils. Uptake then increases as vegetation grows more rapidly and soils begin to develop. Thus, if human activities such as agriculture and urbanization increase erosion rates (Wolman, 1967) or severe storms and floods occur more frequently with the onset of climate change (Bates *et al*., 2008), more rapid terrestrial OC uptake may occur. If the transported sediment and associated OC is eventually delivered to a floodplain, delta, estuary, or subduction zone for longer-term storage, this provides space for more sediment and associated OC to accumulate, and therefore could provide a net increase in OC storage. If erosion simply makes the OC more available for decomposition and metabolism, storage capacity of OC would decrease following the disturbance.

Conclusion

Current research suggests that rivers play a significant, albeit currently poorly quantified, role in the global carbon cycle. Limited studies indicate that riparian ecosystems and floodplains can store a significantly larger amount of carbon per area compared to surrounding uplands. The primary reservoirs for OC in riparian ecosystems are: (i) above-ground standing biomass; (ii) large downed wood; and (iii) OM and sediment on and beneath the floodplain surface. The relative importance of these pools varies with scale, ecoregion, and geologic setting to the extent that no significant patterns have yet emerged. Land use, flow regulation, and channel manipulation greatly impact (i) water and sediment regime, (ii) hydrologic connectivity, (iii) channel complexity, and (iv) inputs and accumulation of OM that control retention of OC in riparian ecosystems. We propose that broad unconfined valleys with complex channel geometry and wet conditions in cool regions are optimal conditions for OC retention and storage in riparian ecosystems. Further investigation of a wide range of rivers across various scales and climates is necessary to determine global significance of river systems in the terrestrial carbon budget. Not all river systems are created equal – some types of rivers and some portions of each river are likely disproportionately important with respect to OC storage – but we need additional basic field data to begin to understand these differences. If research quantifies these differences, and particularly if we can identify hot spots of OC storage, such knowledge can be used to inform river management and restoration, not least because OC storage zones are also likely to be highly biologically productive for in-stream and riparian communities (Bellmore and Baxter, 2014).

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