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PERSPECTIVE

Perspectives on the age and distribution of large wood in riparian carbon pools

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Abstract: Most knowledge of carbon budgets is derived from the productivity and sequestration of carbon in terrestrial and marine ecosystems. Less is known of carbon stored in riparian areas associated with lakes and rivers. Case studies of the age distribution of carbon in aquatic large wood (C_{lw}) from two different landscapes with different drainage patterns were established using tree-ring and ^{14}C dating. Cumulative negative exponential distributions of the age of C_{lw} ranged over periods from 1000 to 9485 years. Large woody debris had mean residence times of 261 years in small oligotrophic lakes and 350–800 years in a stream reach. Large wood can reside for an order of magnitude longer in freshwater–riparian ecosystems than in comparable above-ground terrestrial ecosystems. Although riparian areas make up only a small fraction of most landscapes, they may account for a relatively larger proportion of aged C_{lw} than is stored above ground in terrestrial ecosystems.

Résumé :
La connaissance des budgets de carbone provient en très grande partie des études sur la productivité et la séquestration de carbone dans les écosystèmes terrestres et marins. On possède moins de données sur le carbone emmagasiné dans les zones ripariennes des lacs et des rivières. Nous avons procédé à deux études de cas de la répartition du carbone dans du bois de grande taille (C_{lw}) en milieu aquatique, dans deux paysages différents à structures de drainage distinctes, à l'aide de datations basées sur les anneaux de croissance et sur le ^{14}C. La distribution cumulative exponentielle négative des âges du C_{lw} s'étend sur des périodes de 1000 à 9485 années. Les débris ligneux de grande taille ont un temps de séjour moyen de 261 ans dans les petits lacs oligotrophes et de 350 à 800 ans dans une section de cours d'eau. Le bois de grande taille peut demeurer 10 fois plus longtemps dans les écosystèmes d'eau douce et les écosystèmes ripariens que dans les écosystèmes terrestres épigées comparables. Bien que les zones ripariennes ne représentent qu'une faible fraction de la plupart des paysages, elles peuvent contribuer une proportion relativement plus importante du C_{lw} que celle qui s'accumule au-dessus du sol dans les écosystèmes terrestres.

[Traduit par la Rédaction]

Introduction

Despite considerable knowledge of carbon (C) storage in forests and soils (Dixon et al. 1994; Turner et al. 1995; Trumbore et al. 1996), few if any studies have quantitatively addressed the age distribution of C and its storage in the dead, large wood (>25 cm in diameter) associated with aquatic–terrestrial ecotones. While C storage in forests is often limited by the relatively rapid decay of wood after the death of a tree, C assimilated in trees that enter aquatic systems as large wood (LW) often decays very slowly in submerged or buried environments. This wood may represent a distinct type of carbon sink and can be an important source of aged particulate organic carbon in river systems (Becker 1993; Raymond and Bauer 2001), low-density substrate for invertebrates (Culp and Davies 1985; O'Conner 1991; Bowen et al. 1998), and aquatic structure and habitat (Mallory et al. 2000).

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We assessed the age distribution of carbon sequestered in LW by sampling aquatic LW (>25 cm diameter) in two types of riparian ecotones: freshwater lake littoral zones adjacent to *Pinus–Tsuga–Thuja* forests in the Michigan–Huron and Lower St. Lawrence ecoregions (Abell et al. 2000) and stream channels flowing through *Quercus–Carya–Acer* gallery forests and prairie vegetation in the Middle Missouri freshwater ecoregion. The objectives of this perspective are to explore means of characterizing the temporal distribution of LW in several stream and lake aquatic ecosystems, and to characterize the age, decay rates, and distribution of aquatic LW with case studies from lake and stream riparian areas. This objective is a first step toward understanding ecosystem level carbon sequestration in freshwater. Specifically, our hypotheses are (*i*) that the age of carbon in LW of streams and

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littoral zones can be characterized by negative exponential functions, and (*ii*) that LW is sequestered for much longer periods in riparian and littoral zones than is LW in terrestrial forest ecosystems.

Materials and methods

Four study lakes and a stream reach (Table 1) were chosen that were relatively free of recent anthropogenic disturbances (e.g., removal of aquatic wood, riparian structures) to best reflect the long-term temporal dynamics of aquatic LW. The location of the stream reach was chosen because of its availability as a research site, because the reach appeared to have LW that had recently entered the stream, and because it had LW of an unknown age in the water. The stream reach is in a floodplain of agricultural and forest lands and has been without recent logging. The stream channel is actively meandering in a broad floodplain, is composed of sediments of low hydrologic resistance (glacial till), is unconstrained by bedrock, and is low gradient. The LW of streams is potentially more mobile than that in lakes because it may move (Sickle and Gregory 1990) into a particular stream reach from an upstream source, be carried into a lower stream reach, be deposited on the floodplain as floodwaters recede, move into a downstream water body such as a lake, or be buried in fluvial sediments.

The forests bordering two of the study lakes were not logged, whereas the forests were selectively logged for *Pinus strobus* (eastern white pine) circa 1900 around the other two lakes. The aquatic–forest interface of the lake study sites is relatively stable and constrained by bedrock. Our study lakes represent relatively closed systems with respect to LW owing to the limited movement of LW between lakes.

We obtained samples and measurements for analysis from 67 specimens of aquatic LW (*Quercus* spp., *Juglans nigra*, *Acer* spp., *Betula* spp., *Populus* spp., *Salix* spp.) in a 0.5-km stream reach of Medicine Creek, Mo., U.S.A. We collected data and cross-sections from 256 specimens of LW (*Pinus strobus*) in the littoral zones of Scott, Dividing, and Swan lakes in Algonquin Provincial Park, and from McCulloch Lake in Lady Evelyn Smooth Water Provincial Park in Southern Ontario, Canada. Sampling of LW for age distributions was exhaustive at four sites and random at one lake site. Volume, mass, and C were calculated for each piece of LW. We sorted LW by age and summed the C mass beginning with the oldest dates. We divided cumulative values by the sum of all C to construct cumulative relative distributions.

We used both dendrochronology and radiocarbon dating to determine the age of LW. Wood and ring-width plots were visually matched for ring-width signatures and latewood characteristics (Baillie 1982; Stokes and Smiley 1996). Statistical verification of the ring-width dating was done using the computer program COFECHA (Grissino-Mayer et al. 1996) and Student's *t* tests as well as tree-ring chronologies derived from living, old trees (*Pinus strobus*, *Quercus alba*) in Ontario and Iowa (Duvick 1996; Guyette 1996*a*, 1996*b*). Carbon isotope measurements and radiocarbon age determinations for the samples in this project were conducted by Geochron Laboratories, Cambridge, Mass., U.S.A. The dates are based upon the Libby half-life (5570 years) for ^{14}C. All dates are corrected for ^{13}C. Wood samples of 20–30 g were treated with hot, dilute HCl to remove carbonates; with 0.1 N dilute NaOH to remove humic acids and organic contaminants, and a second time with dilute HCl. After washing and drying, the samples were combusted to recover carbon dioxide. We calibrated the radiocarbon ages using a calibration program (Stuiver et al. 1998). These ages are referenced to the year AD 2000 to be comparable with tree-ring dates. LW in the stream channel that was not tree-ring dateable and had intact leaves, bark, terminal growth rings, or small branches (<2 cm) was classed as "modern". Ten random samples from this category all ^{14}C-dated less than 100 years before present (BP) and verified this categorization. We randomly assigned modern dates (<100 years BP) to members of this class.

Results and discussion

The sequestration of C is a function of the time C is stored in both the living and dead components of the tree. Here we examined the age distribution of dead LW in lakes and streams and compared these with the decay of wood in terrestrial forest ecosystems. The age distribution of C_{lw} at all study sites took the form of negative exponential distributions (Figs. 1 and 2) such as has been hypothesized for LW (Harmon et al. 1986; MacMillian 1988). Equations 1 and 2 were fit to these cumulative distributions of mean ring dates as empirically derived probability density functions to determine the remaining proportion of C assimilated at a given age in the aquatic and riparian LW carbon pools. The equations describe the probabilistic fate of C assimilated in the boles of trees that are eventually incorporated into aquatic–forest ecotones as follows:

$$(1) \qquad C_{lw} = 100\ e^{-kt}\ \text{(stream)}$$

$$(2) \qquad C_{lw} = 100\ (1 - e^{-kt})^{l}\ \text{(lakes)}$$

where C_{lw} is carbon in LW, k represents decay constants (0.0065 for the lakes; 0.0015 for the stream), t is time (years BP), and $l = 5$ (a dimensionless exponent for C stored in living trees before entering the water).

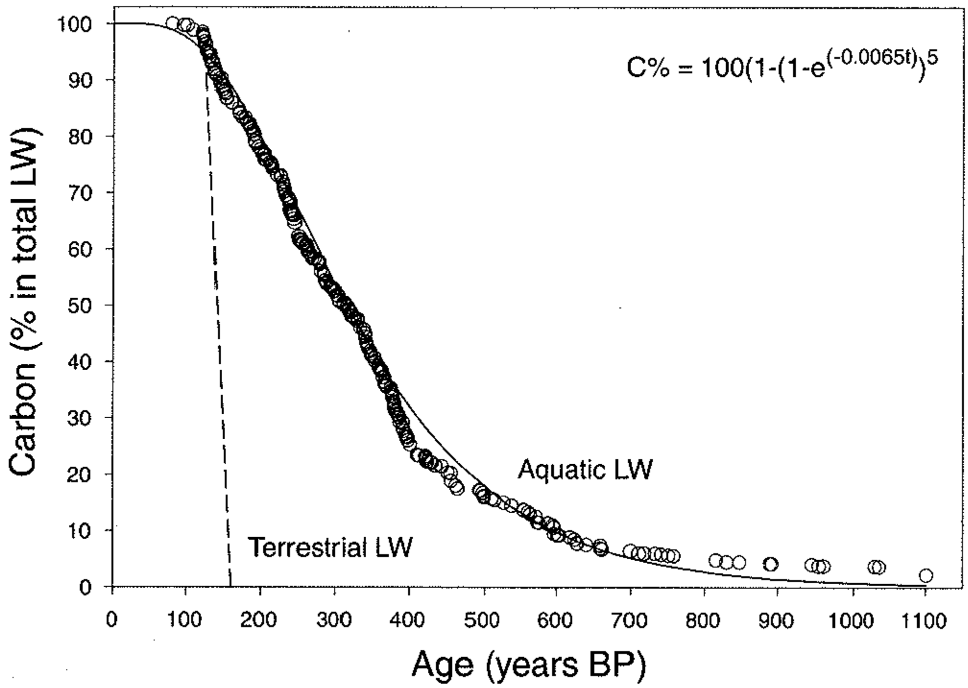
The exponents ($-kt$) describe the release of carbon from aquatic LW. Additionally, where the duration of C storage is long in living trees relative to aquatic LW, an exponent (l) defines the time that C is held in living trees (Harmon et al. 1986). In eq. 2 we used half of the average life of a tree that falls into the lake (100 years) as a rough estimate of the average time that C is stored in living tree boles (Guyette and Cole 1999). The value of k for eq. 1 (used in Fig. 2) is based on the in-stream volume of wood only and does not include sections of wood buried in sediments (these are not measurable). In addition, there may be an "age shadow" effect in the age distribution of LW. An "age shadow" is defined as the unexpected absence of wood in the temporal distribution of wood possibly caused by the migration and return of a meander belt within the floodplain. An "age shadow" is created as the meander belt of a stream moves away from recently buried wood and into older buried wood. Thus, wood collected in natural stream channels may not be unbiased with respect to the age of wood stored in a flood plain. A much smaller value of k may more accurately reflect the age

Table 1. Site and temporal characteristics for large wood (LW), dated samples, and carbon. Water area is total lake or stream reach surface area.

Site name	Medicine	Swan	Scott	Dividing	McCulloch
Water body	Stream	Lake	Lake	Lake	Lake
Latitude	40°22′N	45°30′N	45°29′N	45°24′N	47°19′N
Longitude	93°18′W	78°43′W	78°43′W	78°36′W	80°45′W
Water area (ha)	0.1	87	27	53	42
Number LW dated	67	82	29	105	40
Mean length, diameter LW (m)	4.4, 0.36	10.7, 0.36	10.4, 0.35	15, 0.39	12.1, 0.32
Range of age C_{lw} (years BP)	<10 to 9485	107–1070	128–877	4–1050	2–1134
LW mean residence time by piece (years)	2212	333	271	196	279
Mean assimilation–release period for C_{lw} by mass (years)	389	443	368	295	341

Note: Mean LW residence time by piece is the mean age of all dated LW without respect to their mass, thus the stream reach had smaller, older pieces that account for the much longer residence time. The mean assimilation–release period for carbon in LW (C_{lw}) includes the time carbon is stored in living trees that enter aquatic systems. Time is in years before present (BP).

Fig. 1. The cumulative age distribution of carbon from the large wood (LW) of eastern white pine (*Pinus strobus*) in the littoral zones of four small oligotrophic lakes and the C remaining in terrestrial LW (Mattson et al. 1987; Turner et al. 1995). Goodness-of-fit for aquatic LW data (O) and the equation is 98%. Age corresponds to *t* in the equation. BP, before present.



distribution of wood in the stream–floodplain–subterranean system of carbon storage.

Mean residence time for LW in the study lakes was 261 years and ranged from means of 350 years to 800 years in the study stream depending on the value of *k* used. These residence times are about 9–80 times greater than the mean residence time of wood in adjacent terrestrial forests (Table 2) (Nabuurs and Mohren et al. 1995; Jenkins and Parker 1997; Spetich et al. 1999). We found mean C assimilation–release periods (C in living and dead phases of LW) of 362 years in four Ontario lakes and 389–839 years for LW in the study stream.

Reductions in the specific gravity (G_b, the basic specific gravity based on the volume of wet wood) of wood with age reflect differences in decay processes, decay rates in terrestrial versus aquatic and subterranean–riparian ecosystems, and the effect of time on C storage and quality. LW on the ground in terrestrial ecosystems decays in an oxygen-rich and moist environment in eastern North America, where precipitation is abundant and well distributed throughout the year. Oxygen is more limiting to decay of LW when it is submerged in lake or stream waters, but wave action, currents, and lake turnover can deliver oxygen by mass flow to LW. In contrast, decay of LW is most limited when LW is subterranean, buried in water-saturated soils in floodplains and bogs, where anaerobic conditions prevail because the diffusion of oxygen is so slow.

The mean specific gravity of *Quercus* spp. (oak species) is reduced by half during about 6500 years of aquatic and subterranean storage (Fig. 3), whereas mean G_b of *Quercus* spp. LW on forest floors is reduced by half in approximately 40 years (Harmon et al. 1986; MacMillian 1988). In the lit-

Fig. 2. The cumulative age distribution of carbon in the aquatic large wood (LW) of a stream reach and C remaining in terrestrial coarse wood (Harmon et al. 1986; MacMillan 1988). Age data for LW are from calibrated radiocarbon dates and tree-ring dating (13). Goodness-of-fit for aquatic LW data (O) and the equations are 85% for $k = 0.0015$. The smaller value of k is based on the existence of an age shadow (see text). Age corresponds to t in the equation given for aquatic LW. BP, before present.

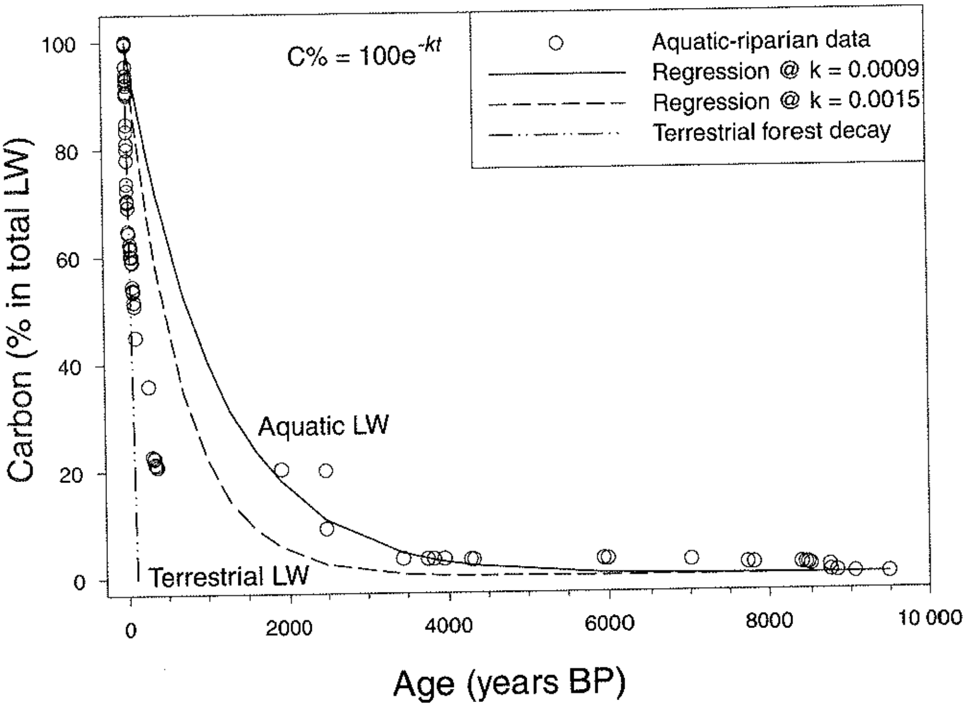


Table 2. Characteristics of large wood (LW) in the littoral zones of lakes and in a stream channel (with subterranean storage) compared with LW in terrestrial forest ecosystems.

Characteristics	Lake littoral	Stream channel	Forests
Mean C_{lw} residence time (years)	261	350	10–40[a,b]
C assimilation–release (years)	362	389	49–140
G_b half life (years)	334	6500	35–40[c,d]
Decay constants	0.0065	0.0015	0.024–0.086[e,f,g,h,i]
Maximum ages dead LW (years)	1097	9485	60–160
LW volume / area ($m^3 \cdot m^{-2}$)	0.0212[j]	0.0045	0.0019–0.011[b,k,l,m]

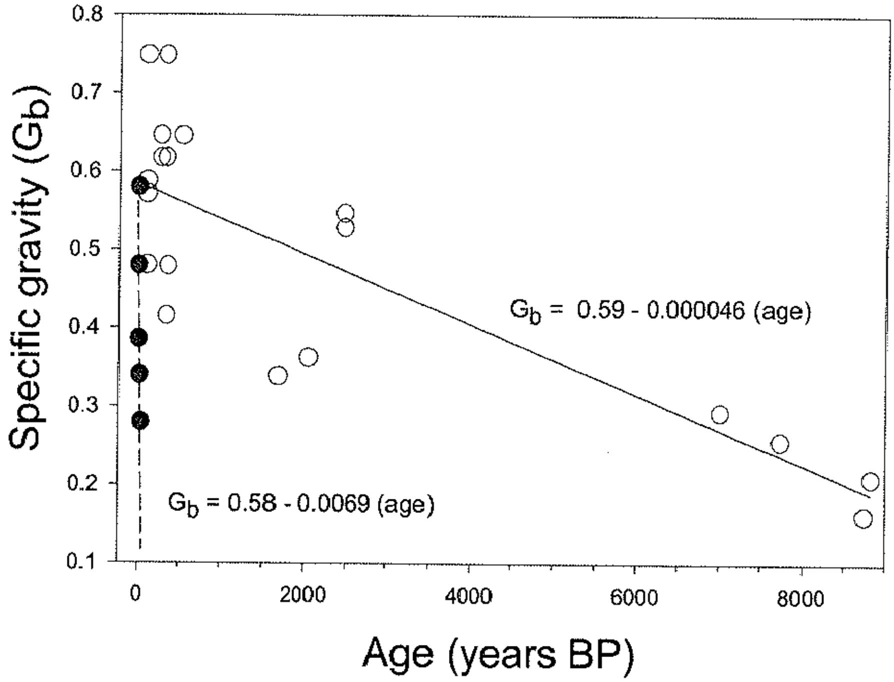
Note: Data for terrestrial ecosystems are for forest tree species and ecosystems comparable to the study regions. The C assimilation–release period is the mean time from carbon fixation to its release from LW (years in living tree + years as dead wood). The specific gravity (G_b) half-life is for *Pinus* in lakes and *Quercus* in a stream reach. Maximum ages for forest are derived from decay constants. Data citations: a, Nabuurs and Mohren (1995); b, Spetich et al. (1999), c, MacMillian (1988); d, Mattson et al. (1987); e, Harmon et al. (1986); f, Turner et al. (1995); g, Chambers et al. (2000); h, Alban and Pastor (1993); i, Onega and Eickmeier (1991); j, Mallory et al. (2000); k, Jenkins and Parker (1997); l, Shifley et al. (1997); m, Muller and Liu (1991).

toral zones, in one of the study lakes the G_b of *Pinus strobus* (eastern white pine) decreased by half in 334 years (Guyette and Cole 1999). The cellulose–lignin ratio in wood is known to decline with time in water-saturated wood and may account for the recalcitrant nature of some particulate organic carbon in rivers as water further erodes structurally weakened old wood (Hedges 1990; Raymond and Bauer 2001).

The piece size of LW and the quantity of carbon per piece of LW are a function of time. Large wood becomes smaller with time from weathering, erosion of the exterior surface, and breakage. Consequently, the quantity of carbon decreases with decreasing piece size. The amount of carbon per piece was significantly ($p < 0.01$) reduced with time (Fig. 4) because of reductions in the volume of LW pieces. Time, however, explains less than 30% of variance (Fig. 4) in the quantity of carbon per piece. This relationship is weak at our study sites and may be weak in many freshwater ecosystems because of the great variability in tree size, the portion of the tree entering the water, and the integrity of the tree stem upon entry into the stream or lake.

Piece size may also have an effect on the movement of LW (Braudrick and Grant 2000) and carbon within aquatic systems. Small pieces of LW will be moved much more readily in streams, especially smaller streams. Wood may move into environments (e.g., subterranean, fluvial, and benthic sediments) where the rates of decay may be much different than those in the waters of streams and lakes. As LW in lakes becomes smaller, it may be incorporated into lake-

Fig. 3. A comparison of the specific gravity (G_b) of *Quercus* spp. that occurs with time in the aquatic–subterranean ecotones (○) of the study stream and large wood (LW) on a terrestrial forest floor (●) (MacMillian 1988). BP, before present.



shore bogs or washed ashore by wave action. In streams, small wood may be incorporated into fluvial deposits or be deposited on the soils of floodplain forests. The movement and fate of LW in streams has been of particular interest in northwestern North America (Maser and Sedell 1994; McHenry et al. 1998; Wing et al. 1999) because of its contribution to aquatic habitat.

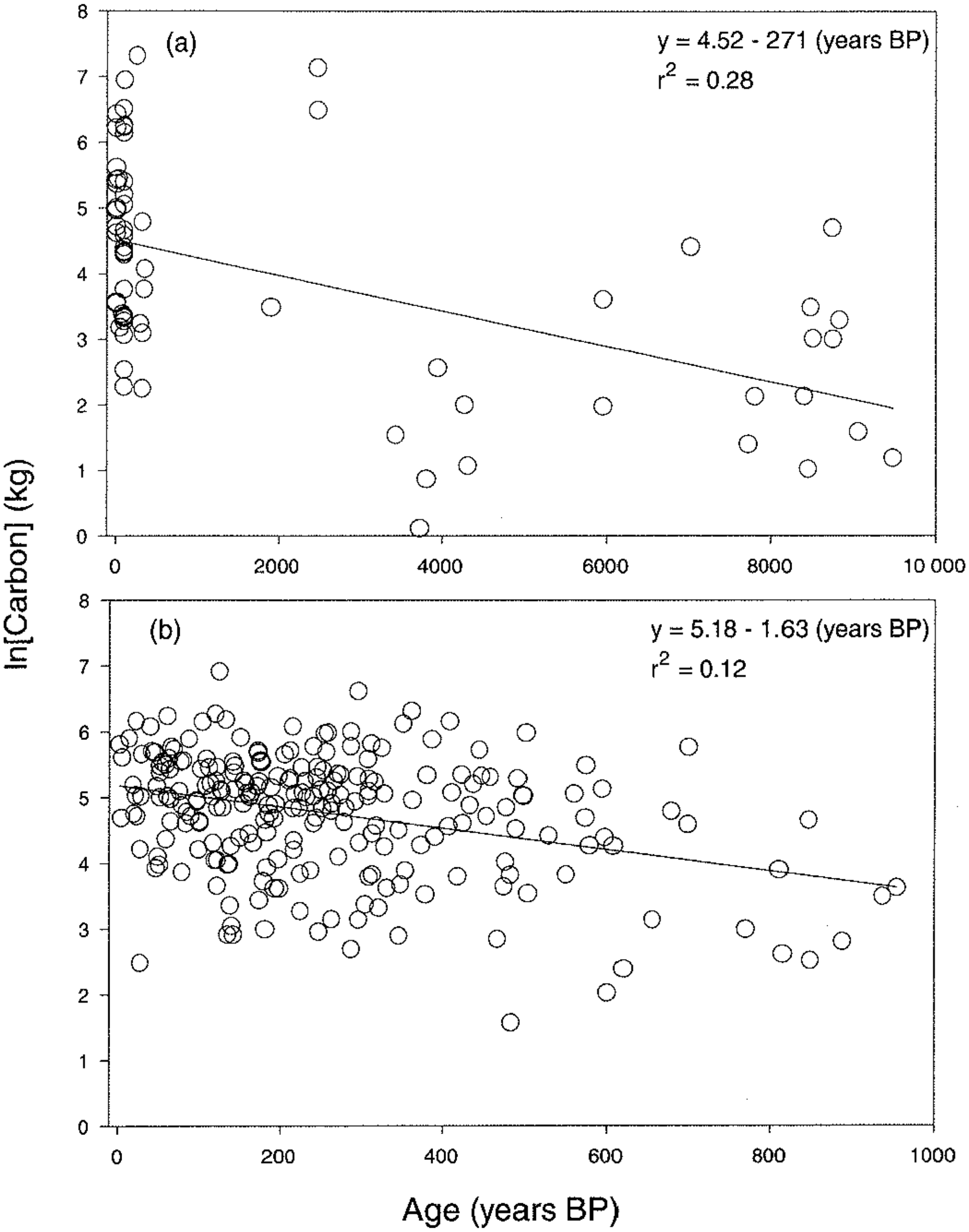
The age and distribution of C_{lw} illustrates the importance of riparian dynamics for the storage of C. Although we aged only wood in water, subterranean storage in both flood plains and along lakeshores may be important in long-term C storage. Wood in streams flowing through sediments of low hydrologic resistance is constantly being excavated, buried, reburied, and only slowly exported to downstream waters. About 65 percent of the LW mass was involved (partially buried) in fluvial sediments, and thus had reduced downstream mobility and a high probability of having been or being totally buried before contemporary export downstream. In lake systems, some species like *P. strobus* are potentially highly mobile because they may float for centuries.

Relative to terrestrial forests, carbon sequestration by LW in freshwater–forest ecotones may constitute only a small portion of carbon input because of the limited spatial dimensions of riparian ecotones, but may represent a large carbon sink because of the temporal duration of carbon storage. For example, there are about 1.1 million hectares of flood plain in a total area of about 7.5 million hectares in North Missouri, the region of our stream study site. Thus, riparian areas, including floodplains, represent about 15% of the landscape but may sequester carbon in LW 10 times longer (Table 2) than the landscape as a whole. There are about 250 000 lakes in Ontario, the location of our study lakes. Lakes in the vicinity of our study area averaged 8.6% of the area of the landscape and lake littoral zones were 1.3% of the total area of the landscape. However, this 1.3% may sequester carbon more than six times longer than the landscape as a whole. These estimates do not include areas with wood buried in lake bogs, rivers, lake bottoms, and wood in deep water. Thus, the role of carbon sequestration in aquatic environments may be large in proportion to area because the duration of carbon storage is greater in aquatic than in terrestrial environments.

The long-term storage of wood submerged or buried in streams and lakes has been noted elsewhere. Thousands of pieces of ancient LW (*Quercus* spp.) have been tree-ring dated from aquatic and riparian ecosystems in Germany and Western Europe (Pilcher et al. 1984; Becker 1993). Ancient (<4763 years BP) particulate organic matter has been reported in the waters of major rivers (Raymond and Bauer 2001). *Pinus sylvestris* (Scots pine) LW from lakes in Fennoscandia have been tree-ring dated and used to construct a continuous tree-ring chronology dating to 7500 years BP (Zetterberg et al. 1996). In addition to our case study sites, we found wood over 2000 years in age in 0.5-km survey reaches of 9 of 10 rivers in Missouri. Rarely, however, are sampling or collections of LW in aquatic systems conducted in a manner consistent with construction of statistical distributions (i.e., random or exhaustive) at the study or ecosystem level. Although we used random, stratified random, and exhaustive sampling in our case studies, these studies only allude to potential differences in residence times of C_{lw} in terrestrial and riparian areas.

Changes in the dynamics of C storage in lakes and streams may result from global climate change (King et al. 1999; Magnuson et al. 2000) and increases in human population density. Changes in temperature may result in changes in bacterial activity (Vaque et al. 1994; Trumbore et al. 1996) and degradation of LW in lake littoral zones stream waters.

Fig. 4. Two scatter plots illustrating a weak but significant relationship between age and the mass of carbon per piece of large wood (LW) (*a*) in a stream and (*b*) in lakes. The quantity of carbon in each piece of LW (*y* axis) is plotted against the duration (*x* axis) of carbon sequestering in LW. Note the order of magnitude of difference in the *x* axes for (*a*) stream and (*b*) lake wood. BP, before present.



Biological activity, even under anoxic conditions, may be governed by temperature-dependent reaction rates as quantified by the Arrhenius equation (Vollhardt 1987). The long-term storage of C_{lw} in the subterranean components of riparian floodplains, however, may be less affected by increases in atmospheric temperature like those found in soils (Trumbore et al. 1996) because of the insulation provided by 3–6 m of floodplain sediments that lie over LW in North Missouri streams. The effects of increasing human population may be equally important as, if not more important than the effects of climate change on aquatic–forest ecotones. Stream bank stabilization, river channelization, navigation improvements, river impoundment, and riparian and lakeshore development (Christensen et al. 1996) will all influence riparian forests and the dynamics of LW and C storage in freshwater ecosystems.

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References

Abell, R.A., Olson D.M., Dinerstein, E., Hurley, P.T., Diggs, J.T., Eichbaum, W. Walters, S., Wettengel, W., Allnutt, T., Loucks, C.J., and Hedao, P. 2000. Freshwater ecoregions of North America. Island Press, Washington, D.C.

Alban, D.H., and Pastor, J. 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Can. J. For. Res. **23**: 1744–1749.

Baillie, M.G.L. 1982. Tree-ring dating and archaeology. University of Chicago Press, Chicago.

Becker, B. 1993. An 11 000-year German oak and pine chronology for radiocarbon calibration. Radiocarbon, **35**: 201–213.

Bowen, K.L., Kaushik, N.K., and Gordon, A.M. 1998. Macroinvertebrate communities and biofilm chlorophyll on woody debris in two Canadian oligotrophic lakes. Arch. Hydrobiol. **141**: 257–281.

Braudrick, C.A., and Grant, G.E. 2000. When do logs move in rivers? Water Resour. Res. **36**: 571–583.

Chambers, J.Q., Higuchi, N., Schimel, J.P., Ferreira, L.V., and Melack, J.M. 2000. Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. Oecologia, **122**: 380–388.

Christensen, D.L., Herwig, B.R., Schindler, D.E., and Carpenter, S.R. 1996. Impacts of lakeshore residential development of coarse woody debris in north temperate lakes. Ecol. Appl. **6**: 1143–1149.

Culp, J.M., and Davies, R.W. 1985. Responses of benthic macroinvertbrate species to manipulation of interstitial detritus in Carnation Creek, British Columbia. Can. J. Fish. Aquat. Sci. **42**: 139–146.

Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C., and Wisniewski, J. 1994. Carbon pools and flux of global forest ecosystems. Science (Washington, D.C.), **263**: 185–190.

Duvick, D.N. 1996. Lake Ahquabi State Park. International Tree-Ring Data Bank. IGBP PAGES/World Data Center-A for Paleoclimatology Data Contribution No. IA025.CRN2-014. NOAA/NGDC Paleoclimatology Program, Boulder, Co., U.S.A.

Grissino-Mayer, H.D., Holmes, R.L., and Fritts, H.C. 1996. International Tree-Ring Data Bank program library version 2.0 users manual. International Tree-Ring Data Bank, Laboratory of tree-ring research, University of Arizona, Tucson.

Guyette, R. 1996*a*. Tree-ring data, Swan Lake, Ontario. International Tree-Ring Data Bank. IGBP PAGES/World Data Center-A for Paleoclimatology Data Contribution Series No. 96-013. NOAA/NGDC Paleoclimatology Program, Boulder, Co., U.S.A.

Guyette, R. 1996*b*. Tree-ring data, Ontario and Missouri. International Tree-Ring Data Bank. IGBP PAGES/World Data Center-A for Paleoclimatology Data Contribution Series No. 92-014. NOAA/NGDC Paleoclimatology Program, Boulder, Co., U.S.A.

Guyette, R.P., and Cole, W.G. 1999. Age characteristics of coarse woody debris (*Pinus strobus*) in a lake littoral zone. Can. J. Fish. Aquat. Sci. **56**: 496–505.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K, Jr., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. **15**: 133–302.

Hedges, J.I. 1990. The chemistry of archaeological wood. *In* Archaeological wood. *Edited by* R.M. Rowell and R.J. Barbour. American Chemical Society, Washington, D.C. Adv. Chem. Ser. 225. pp. 111–140.

Jenkins, M.A., and Parker, G.R. 1997. Changes in down dead wood volume across a chronosequence of silvicultural openings in southern Indiana forests. *In* Proceedings of the 11th Central Hardwood Forest Conference, 23–26 March 1997, University of Missouri, Columbia. *Edited by* S. Pallardy, R. Cecich, H. Garrett, and P. Johnson. GTR NC-188. pp. 162–169.

King, J.R. Shuter, B.J., and Zimmerman, A.P. 1999. Signals of climate trends and extreme events in the thermal stratification pattern of multibasin Lake Opeongo, Ontario. Can. J. Fish. Aquat. Sci. **56**: 847–852.

MacMillian, P.C. 1988. Decomposition of coarse woody debris in an old-growth Indiana forest. Can. J. For. Res. **18**: 1353–1362.

Magnuson, J.J., Robertson, D.M., Benson, B.J., Wynne, R.H., Livingstone, D.M., Arai, T., Assel, R.A., Barry, R.G., Card, V., Kuusisto, E., Granin, N.G., Prowse, T.D., Stewart, K.M., and Vuglinshki, V.S. 2000. Historical trends in lake and river ice cover in the Northern Hemisphere. Science (Washington, D.C.), **289**: 1743–1746.

Mallory, E.C., Ridgway, M.S., Gordon, A.M., and Kaushik, N.K. 2000. Distribution of woody debris in a small headwater lake, central Ontario, Canada. Arch. Hydrobiol. **148**: 587–606.

Mattson, K.G., Swank, W.T., and Waide, J.B. 1987. Decomposition of woody debris in a regenerating, clear cut forest in the Southern Appalachians. Can. J. For. Res. **17**: 712–721.

Maser, C., and Sedell, J.R. 1994. From forest to sea: the ecology of wood in streams, rivers, estuaries, and oceans. St. Lucie Press, Delray Beach, Fla.

McHenry, M.L., Shott, E., Conrad, R.H., and Grette, G.B. 1998. Changes in the quantity and characteristics of large woody debris in streams of the Olympic Peninsula, Washington, U.S.A. (1982–1993). Can. J. Fish. Aquat. Sci. **55**: 1395–1407.

Muller, R.N., and Liu, Y. 1991. Coarse woody debris in an old-growth deciduous forest on the Cumberland Plateau, southern Kentucky. Can. J. For. Res. **21**: 1567–1572.

Nabuurs, G.J., and Mohren, G.M.J. 1995. Modeling analysis of potential carbon sequestration in selected forest types. Can. J. For. Res. **25**: 1157–1172.

O'Conner, N.A. 1991. The effects of habitat complexity on the macroinvertebrates colonizing wood substrates in a lowland. Oecologia, **85**: 504–512.

Onega, T.I., and Eickmeier, W.G. 1991. Woody detritus inputs and decomposition kinetics in a southern temperate deciduous forest. Bull. Torrey Bot. Club, **118**: 52–57.

Pilcher, J.R., Baillie, M.G.L., and Schmidt, B. 1984. A 7272 year tree-ring chronology for Western Europe. Nature (London), **312**: 150–152.

Raymond, P.A., and Bauer, J.E. 2001. Riverine export of aged terrestrial organic matter to the North Atlantic Ocean. Nature (London), **409**: 497–500.

Shifley, S.R., Brookshire, B.L., Larson, D.R., and Herbeck, L.A. 1997. Snags and down wood in Missouri old-growth and mature second-growth forests. North. J. Appl. For. **14**: 165–172.

Sickle, J.V., and Gregory, S.V. 1990. Modeling inputs of large woody debris to streams from falling trees. Can. J. For. Res. **20**: 1593–1601.

Spetich, M.A., Shifley, S.R., and Parker, G.R. 1999. Regional distribution and dynamics of coarse woody debris in Midwestern old-growth forests. Forest Sci. **45**: 302–313.

Stokes, M.A., and Smiley, T.L. 1996. An introduction to tree-ring dating. University of Arizona Press, Tucson.

Stuiver, M., Reimer, P.J., and Braziunas, T.F. 1998. High-precision radiocarbon age calibration for terrestrial and marine samples. Radiocarbon, **40**: 1127–1151.

Trumbore, S.E, Chadwick, O.A., and Amundson, R. 1996. Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. Science, **272**: 393–396.

Turner, D.P., Koerper, G.J., Harmon, M.E., and Lee, J.J. 1995. A carbon budget for forests of the conterminous United States. Ecol. Appl. **5**: 421–436.

Vaque, D., Gasol, J.M., and Marrase, C. 1994. Grazing rates on bacteria—the significance of methodology and ecological factors. Mar. Ecol. Prog. Ser. **109**: 263–274.

Vollhardt, P.C. 1987. Organic chemistry. W.H. Freeman Co., New York.

Wing, M.G., Keim, R.F., and Skaugset, A.F. 1999. Appling goestatistics to quantify distributions of large woody debris in streams. Comput. Geosci. **25**: 801–807.

Zetterberg, P., Eronen, M., and Lindholm, M. 1996. Construction of a 7500-year tree-ring record for Scots Pine (*Pinus sylvestris*, L.) in Northern Fennoscandia and its application to growth variation and paleoclimatic studies. *In* Growth trends in European Forests. *Edited by* H. Spiecker, K. Mielikainen, and M. Kohl. Springer-Verlag, Berlin. pp. 7–18.