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AUTOCHTHONOUS VERSUS ALLOCHTHONOUS ORGANIC MATTER IN RECENT SOIL C ACCUMULATION ALONG A FLOODPLAIN BIOGEOMORPHIC GRADIENT: AN EXPLORATORY STUDY

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Abstract

The mechanisms controlling soil succession in floodplains remain much less studied than in uplands due to the complexity that flood-driven erosion and sedimentation bring into soil development processes. The amount of organic matter and C generally grows with soil ageing and is controlled by multiple and interacting allogenic and autogenic factors, but to what extent the production of organic matter by *in situ* vegetation contributes to soil formation in floodplains remains unknown. The objective of this work was to explore the importance of autochthonous organic matter versus allochthonous organic matter in organic C accumulation of floodplain forest soils along a vegetation succession and hydrogeomorphic connectivity gradient. Physicochemical analyses of sediment collected after one single flood event in a large Mediterranean floodplain (Middle Ebro, a 9th order regulated river reach in NE Spain) were used to estimate the proportion of organic C found in the topsoil (first 10 cm) samples of young (<25 yr), mature (25-50 yr) and old (>50 yr) floodplain forests that had an allochthonous (i.e., % of organic C deposited by floods) or autochthonous (i.e., % of organic C produced *in situ* by vegetation) source. Results of this exploratory study showed that the accumulation of autochthonous organic C in the floodplain topsoil only occurred in floodplain forests older than 50 year-old, but even then, it was more than six-fold less abundant than that with an allochthonous origin. Moreover, a linear mixed effect model showed that, although autochthonous organic C accumulation was mainly explained by the forest structure, a small proportion of it was also controlled by an allogenic factor, the groundwater table depth. Then, groundwater table depth variations could be partly controlling autochthonous organic matter production and decomposition in this Mediterranean floodplain. Although flow regulation and embankment has dramatically limited the hydrogeomorphic dynamics of the river, allogenic overbank sedimentation during flood events still controls floodplain soil succession and organic C accumulation in the floodplain.

Keywords: floodplain soils, sediment texture, soil organic carbon, overbank sedimentation

INTRODUCTION

Organic matter accumulation within floodplains is an ecosystem function that provides important benefits such as water quality enhancement or mitigation of greenhouse effect (Johnston, 1991; Day et al., 2004; Verhoeven et al., 2006; IPCC, 2007). Soil organic matter is especially relevant since it forms a larger and more lasting pool than living biomass. However, soil successional patterns have been much less studied in floodplains than in upland forests (Wigginton et al., 2000). The main reason is that successional trajectories in floodplains are recurrently brought to a starting point by destructive floods (Hughes et al., 1997; Geerling et al., 2006; Cabezas et al., 2009a), thus making the forest floor development much more unpredictable than in the more stable uplands.

The role of floodplain soils as sink or source of organic C varies along the longitudinal river axis, with downstream river sections importing the suspended sediment and a part of organic matter of the upstream sections of the catchment (Steiger and Gurnell, 2003; Noe and Hupp, 2005). Along the transversal river axis, from the water channel to the floodplain, flood events determine the role of a given ecotope as sink or source of organic matter as well as its source (allochtonous *vs*. autochthonous) for a given study period. Organic matter produced by biotic assemblages is incorporated into surface soils during the intervals between overbank flooding. During floods, low-organic fluvial sediments may be deposited on floodplain landforms, and the organic matter that had been stored in different compartments such as the soil or standing vegetation is either exported or buried (Cabezas and Comín, 2010), maintaining the soil in a continuous immature state (Drouin et al., 2011). As vegetation develops in the absence of destructive floods, the floodplain surface roughness increases and enhances sediment deposition, which in turn causes its elevation in relation to the river channel to rise (Hupp, 2000; Bendix and Hupp, 2000; Steiger et al., 2001). Sandy sediment trapping by young and

dense thickets of vegetation predominates in the most exposed zones, while organic matter produced *in situ* may be more easily retained in less exposed zones such as the hydrologically disconnected floodplain.

Overbank sedimentation of fine sediment especially favors the accumulation of organic C in the soil as organic matter forms easily complexes with fine sediment (silt and clay <63 μm) (Asselman and Middelkoop, 1995; Steiger and Gurnell, 2003), silt and clay fraction and organic carbon being positively correlated (Pinay et al., 1992; Bechtold and Naiman, 2006). However, accretion is also negatively feedbacked by hydrological disconnection (Bendix and Hupp, 2000). Both increasing distance to and elevation above the main channel generally contribute to the decrease in duration and frequency of flooding (Corenblit et al., 2007), eventually leading to a decrease in the input of sediment and organic matter bounded to sediment particles (i.e., allochthonous organic matter) (Asselman and Middlekoop, 1995; Walling and He, 1997; Piégay et al., 2008; Cabezas et al., 2010). In other words, the input of organic C in a given forest patch via sedimentation is limited to areas that are hydrogeomorphologically connected to the main channel. On the other hand, as floodplain forest succession and hydrogeomorphic disconnection develop, litter (i.e., authochthonous organic matter) accumulates in the topsoil because it is less likely to be intensively and frequently removed by floods (Friedman et al., 1996). It follows that similar to floodplain vegetation dynamics (Corenblit et al., 2007), the soil development and organic C accumulation is driven mainly by abiotic factors at the early stages of soil succession, implicating that during the allogenic vegetation succession stage allochthonous organic matter dominates. But if these hydrogeomorphic drivers are gradually replaced by biotic factors in later stages of succession, i.e. late-seral stages, it is expected that during autogenic succession stages autochthonous organic matter dominates. This theoretical framework of soil succession would fit with classic succession theory (Clements, 1916). However, studies devoted to quantify these processes within floodplain zones have not been frequent, and the relative roles of abiotic (hydrology, topography and sediment dynamics) and biotic (forest structure) factors as drivers of organic C dynamics in floodplain soil development remain largely unknown (but see Cierjacks et al., 2011). More particularly, although it is widely recognized that floodplains are highly productive ecosystems (Naiman et al., 2005), little is known about how much autochthonous sources contribute to organic C accumulation locally. In fact, the efforts done to understand patterns of organic C accumulation in floodplain soils have rarely considered autochthonous and allochthonous sources separately (but see Daniels, 2003; Cabezas and Comín, 2010).

The objective of this study was to evaluate the relative importance of autochthonous *vs.* allochthonous organic C (respectively AUTOC and ALLOC) along a vegetation succession and hydrogeomorphic connectivity gradient (a biogeomorphic gradient *sensu* Corenblit et al. 2007) in the soil of a large forested floodplain. ALLOC was expected to be more important at the more connected and younger sites, with abiotic factors driving succession (Corenblit et al., 2007) and AUTOC higher at disconnected and older forest patches, with biotic factors driving succession (Corenblit et al., 2007).

STUDY AREA

The study was carried out in an 8 km river segment in the Middle Ebro River. The segment was located 12 km downstream from the city of Zaragoza (41º36' N, 0º46' W, 175-185 m a.s.l., NE Spain). The Ebro River is one of the largest Mediterranean rivers in terms of length (~930 km), annual discharge (~12 000 hm^3 yr^{-1}) and drainage area (~86 000 km^2). The hydrological regime is pluvio-nival and the river is highly regulated by dams built for irrigation and flood control during the 1950's and 1960's. At the river gauge station of Zaragoza, the annual mean of the daily flow discharge between 1981 and 2003 is 230 m^3 s^{-1}. As a consequence of flow regulation, a decrease in bankfull discharge and in the duration and frequency of overbank flooding events throughout the second half of the 20th century was observed (Cabezas et al., 2009a). Both the selected river segment and the middle reach of the Ebro have a very limited channel migration rate since the 1970's and 1980's, due to two decades of intense bank protection works (Ollero, 2007; Magdaleno and Fernández, 2011).

However, the middle reach of the Ebro still maintains a sinuous shape (sinuosity = 1.39, mean longitudinal channel slope = 0.05 %, Ollero, 1995) as a relict of the former dynamic geomorphic regime before river training works. The average width of the submersible floodplain is 5 km but agriculture and human settlements have reduced the surface occupied by natural floodplain forest to ~4.5% of the floodplain surface (Ollero, 2007), usually occupying the inside of meander bends, which are not protected by bank protection works. Despite protection by levees, floodplain forests on both the convex and concave river banks are inundated by floods with recurrence intervals of <10 years (1981-2003). Tree communities are dominated by phreatophytic species (*Populus alba* L., *Populus nigra* L., *Salix alba* L., *Tamarix gallica* L., *T. africana* Poir. and *Tamarix canariensis* Willd.). Late-seral hardwood species (*Ulmus minor* auct. non P. Mill. and *Fraxinus angustifolia* Vahl) are commonly found, but usually with size stems smaller than 7.5 cm d.b.h. (González et al., 2010a).

METHODS

Plot selection along a vegetation succession and hydrogeomorphic gradient

Using a series of aerial photographs (1957, 1981 and 2003), 39 forest patches of different age: young (<25 years, 13 patches), mature (25-50 years, 13 patches)

and old (>50 years, 13 patches), all subjected to annual flooding along a hydrogeomorphic gradient, were selected for this study (*Fig. 1*).

One rectangular study plot was randomly placed within each forest patch to carry out a tree survey in 2006 and 2007, including the diameter and species record of every woody stem $\geq$ 0.3 m height (total = 6891 stems) (González et al., 2010a). Plot dimensions were scaled according to the dominant tree height and ranged from 25 to 1000 m^2. The collected information was used to calculate total and species-specific basal areas (BA, m^2 ha^{-1}) and stem densities (SD, stems ha^{-1}) following González et al. (2010a). Species-specific importance values (IV) were then calculated at each plot using a modification of the Gergel et al. (2002) formula, ranging from 0 (absence) to 1 (complete dominance): $IV_i = [(SD \text{ of species } i / \text{ total SD}) + (BA \text{ of species } i / \text{ total BA})] / 2$.

To describe the hydrogeomorphic regime at each plot, a network of 17 piezometers was installed in the floodplain (details in González et al., 2012). Water levels in the piezometers were continuously monitored from October 2008 to September 2010 (highest flood peak recorded at the gauging station of Zaragoza during the monitoring period: 1506 m^3 s^{-1}, February 2009, recurrence interval for the 1927-2003 period: 0.87 yrs) using integrated absolute pressure sensors and data loggers (van Essen DI502 TD Diver®), which permit the determination of groundwater table depths as well as water stages above piezometers during inundation and thus above the floodplain surface. Hereafter the synonym 'water table' was used for groundwater table and 'floodwater stage' for water stage above piezometers during inundation. The piezometer measurements were used to interpolate the water table levels and floodwater stages and, following González et al. (2012), to determine the deepest water

table level recorded (WT, m), flood duration (FD, % of the time) and flood frequency (FF, number of flood submersions) that represented the local hydrologic regime at each plot during the study period. The piezometer and plot elevations above sea level (ELEV, m) and the UTM coordinates necessary for all calculations had previously been recorded using a differential global positioning system (DGPS) Topcon® with 3 cm vertical accuracy. The shortest distance from the centroid of each plot to the main river channel at the summer level (DIST, m) was calculated using ArcGis 9.2.

Topsoil collection and processing

Soil samples were taken at the end of the vegetation growing season in September and October 2006, coinciding with low water levels prior to autumn floods and before the main peak of litterfall that typically occurs in November in the study area (González, 2012a). This sampling period was chosen to minimize the influence of the litter fall over the soil organic matter analyses, thus focusing on the consolidated organic matter soil pool. At each plot, three topsoil (0–10 cm) samples were collected using an undisturbed soil sampler (5 cm diameter steel tube, P.1.31 Eijkelkamp®) after carefully removing the living vegetation and litter layers. At the larger plots (>500 m^2, 6 plots), more samples were collected to obtain a composite of three samples that better represented the heterogeneity of the soil in the plot. Samples were air dried before being passed through a 2 mm sieve to remove rock and larger organic matter fragments. Total organic C (TOC, %) was measured with a LECO SC 144 DR® elemental analyzer. The fine fraction (i.e., FINE silt + clay, % of particles <63 µm) was calculated gravimetrically by sieving sub-samples
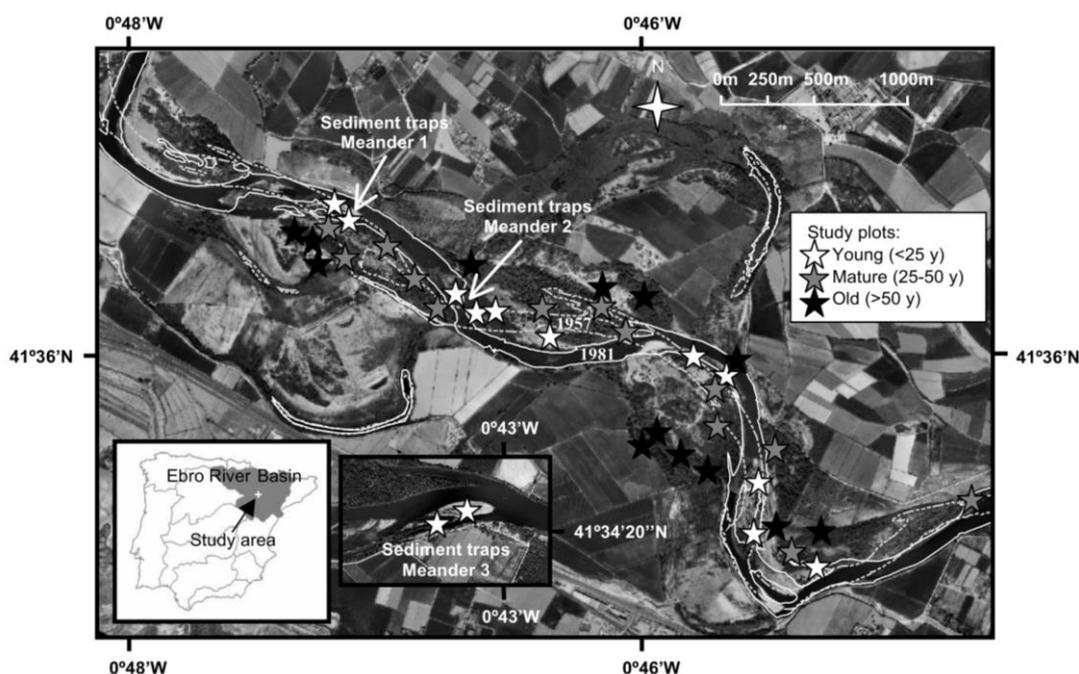

Fig. 1 Location of the study sites in a 8 km segment of the Ebro River. The aerial picture was taken in 2007. Lines correspond to the main channel tracks in 1957 and 1981

of the < 2 mm material into a 63 μm screen previously treated with a 10% hydrogen peroxide solution to eliminate the organic matter and with a polyphosphate solution to facilitate particle dispersion. In young plots, a framework of gravels, cobbles and/or boulders was usually present in the surface layer and the soil sampler could not be used. Then, the soil analyses were performed using the finer sediments filling the pore spaces between the framework grains.

Determination of ALLOC and AUTOC

The particle-size composition of sediments partially determines the amount of organic C that is deposited locally during floods. The sediment deposited during one flood event was collected using 92 sediment traps made of artificial grass mats (25 x 25 cm) set up in 3 meanders of the study area (*Fig. 1*). Details on the experimental setup can be found in Cabezas et al. (2010). Artificial grass mats have been commonly used to study contemporary sedimentation rates in river floodplains, especially when it was necessary to recover the sediment deposited during one individual flood event as in the present study (see Steiger et al. 2003 for a review). The flood occurred in January 2006 and lasted for 8 days. It had a flood peak at the gauging station of Zaragoza of 754 m^3 s^{-1} and a recurrence interval for the 1927-2003 period of 0.23 yrs. A few days after the flood, mats re-emerged with only 7% of them having been flushed away by the river. Mats were collected, brought to the laboratory and oven-dried at 60 ºC. The deposited sediment was then carefully removed by hand using a metallic brush and their proportion of fine particles and TOC determined as described above for the topsoil samples. A polynomial function was adjusted to model the relationship between the fine fraction and TOC measured in the sediment gathered from the mats. The function served to calculate the theoretical proportion of TOC that was deposited during floods at each topsoil sample in the 39 study plots (i.e., ALLOC), using the fine fraction as independent variable. In other words, it was considered that the ALLOC within a given topsoil sample could be predicted as a function of its grain size (Pinay et al., 1992; Bechtold and Naiman, 2006; Cabezas and Comín, 2010). It follows that the difference between observed and predicted TOC values (TOC residuals) would be an indicator of the organic C produced and accumulated *in situ* at each topsoil sample (i.e., AUTOC). Our objective was not to calculate *absolute* organic C accumulation rates, which would have also required to measure local sedimentation rates, which was not done here. Instead, the aim was to obtain a quantitative estimate of the accumulated organic C that had been produced *in situ* (TOC residual = AUTOC), compared to the accumulated organic C deposited by floods (predicted TOC = ALLOC). Negative values in the TOC residuals of some plots were an unavoidable artifact of our experimental approach and were explained by the fact that the floods that were actually responsible for the ALLOC deposition in those plots contained a lower organic content than the flood used to build the predictive function. However, negative TOC residuals were interpreted as indicators of a lower probability of

having AUTOC accumulation (or as a higher certitude in the absence of AUTOC accumulation) and were included in the analyses explained below.

Evaluating the relative importance of AUTOC vs. ALLOC along the biogeomorphic gradient

In a first step, predicted and observed TOC values were plotted together grouped by plot age and, within each age category, their medians compared by means of nonparametric Wilcoxon matched-pairs signed-ranks tests. Therefore, it was examined whether erosion-sedimentation processes controlled only the TOC topsoil levels (i.e., that if predicted and observed TOC values were not significantly different, no AUTOC was accumulated) or whether an accumulation of AUTOC effectively occurred (i.e., that observed TOC values were significantly higher than the predicted TOC values) along the floodplain forest chronosequence. The significance levels were set up at 0.05.

Statistical modeling of AUTOC accumulation

Once evaluated the relative importance of AUTOC *vs*. ALLOC along the biogeomorphic gradient, the influence of abiotic and biotic factors on the variability of the TOC residuals was assessed using linear mixed effect models (LME, Pinheiro and Bates, 2000) and hierarchical partitioning. LME are a type of multiple regression that do not assume that all observations are independent from each other, and so can be used to analyze data from clustered experimental designs where observed subjects are nested within larger units. Different LME models were run using all the variables representing the vegetation succession and hydrological connectivity (*Table 1*) as fixed factors, plot as random effect, and TOC residuals as the dependent variable, with n = 117 (39 forest plots x 3 topsoil replicates). A backward selection of predictors was performed to retain only the most significant (P < 0.05) explaining the response of TOC residual, testing each step with a likelihood ratio-test (Crawley, 2002). Pearson's product–moment correlation between the observed and predicted values and the Akaike Information Criterion were used to assess the goodness-of-fit of the final models. Once identified the main predictors, the sum of independent and shared variance in the TOC residuals explained by each significant predictor (i.e., the relative contribution) in each model was assessed through hierarchical partitioning (Chevan and Sutherland, 1991). The LME models and hierarchical partitioning were run using functions available in the package "nlme" (Pinheiro et al., 2007) and "hier.part" (Walsh and McNally, 2007) of the R 2.14.0 software (R Development Core Team 2011). Different transformations were applied to the explanatory variables to correct for the effect of asymmetry, given that most of them were not normally distributed (Kolmogorov-Smirnov test). The exploratory analyses showed that TOC residuals had a strong positive and heteroscedastic relationship with "observed TOC" (i.e., higher TOC residuals and higher variance were observed at higher TOC values). To remove that con-

founding effect, "observed TOC" was included in the models as covariable. All variables were standardized before running the models.

RESULTS

Forest succession and hydrogeomorphic gradient

The classification of plots into three age-groups along a forest succession and hydrological connectivity gradient fitted with their forest structure and with their local hydrological connectivity descriptors, with significant differences between young, mature and old plots in all variables reported (*Table 1*). Young plots were dominated by pioneer tree species *Populus nigra*, *Tamarix* spp. and *Salix alba* (sum of their IV = 0.99) and were in a very active recruitment phase, as shown by their significantly higher stem density and lower basal area compared to mature and old plots. This reflected the prevalence of small stems in the forest structure. Compared to the older plots, young plots also displayed the highest hydrological connectivity, with a significantly higher water table, flood duration and frequency as direct consequences of their lower topographical position and shorter distance to the main channel. Mature plots represented an intermediate successional stage along the chronosequence. Pioneer species were still dominating

(sum of their IV = 0.81) but formed less dense patches than in young plots (stem density decreased eight-fold while basal area slightly increased). In addition, late-seral stage species, namely *Ulmus minor* and *Fraxinus angustifolia*, were now more frequent. The higher elevation plots in the floodplain were located at a greater distance from the main channel and were three-fold less flooded (in terms of duration) than young plots. Within the mature plots, the lowest water tables recorded were 1 m deeper on average than in the young plots, but flood events were still frequent. In the old plots pioneer species did not dominate (sum of their IV = 0.44), although not only as a result of their replacement by late-seral species (IV = 0.25) but also caused by the appearance of a new successional pathway dominated by *Populus alba* (present in 7 out of the 13 old plots surveyed). Old plots were the hydrologically most disconnected sites along the chronosequence, being rarely flooded and with lowest water tables recorded reaching a mean depth of ~3.5 m below the floodplain surface.

Topsoil

Overall, the soil descriptors also followed the biogeomorphic gradient (*Table 1*). Sandy soils predominated in young sites. However, mature and old topsoil forests

Table 1 Summary of the forest structure and hydrological connectivity descriptors for 39 forest patches divided into three age categories: young, mature and old. Values are means ± 1 SE. Letters indicate homogeneous groups after independent t tests implemented in SPSS v 13.0 (P < 0.05)

	Young	Mature	Old
N	13	13	13
Age (years)	<25	25-50	>50
Plot size (m^2)	130^b ± 33	386^a ± 21	545^a ± 86
Forest structure			
Basal area (BA, m^2 ha^{-1})	34^b ± 8	48^{ab} ± 7	67^a ± 11
Stem density (SD, stems ha^{-1})	26395^a ± 8365	3270^b ± 749	5771^b ± 1178
IV (unitless)			
Populus nigra (IVPn)	0.48^a ± 0.10	0.35^{ab} ± 0.07	0.18^b ± 0.07
Populus alba (IVPa)	0.00^b ± 0.00	0.00^b ± 0.00	0.30^a ± 0.10
Tamarix spp. (IVTx)	0.42^a ± 0.10	0.29^a ± 0.08	0.24^a ± 0.08
Salix alba (IVSa)	0.09^a ± 0.03	0.17^a ± 0.08	0.02^a ± 0.01
Fraxinus angustifolia (IVFx)	0.01^b ± 0.00	0.11^a ± 0.03	0.03^b ± 0.01
Ulmus minor (IVUm)	0.00^c ± 0.00	0.07^b ± 0.02	0.21^a ± 0.05
Other species (IVOt)	0.00^b ± 0.00	0.01^{ab} ± 0.00	0.01^a ± 0.00
Hydrological connectivity			
Maximum depth to water table (WT, m)	1.28^c ± 0.15	2.25^b ± 0.19	3.49^a ± 0.21
Flood duration (FD, % of time)	24^a ± 4	9^b ± 3	2^c ± 1
Flood frequency (FF, events y^{-1})	5^a ± 1	4^b ± 0	2^c ± 0
Topography			
Elevation a.s.l. (ELEV, m)	178^b ± 1	180^a ± 0	181^a ± 0
Distance to river channel (DIST, m)	42^c ± 10	117^b ± 22	221^a ± 37
Topsoil (first 10 cm)			
Total organic carbon (TOC, %)	1.22^c ± 0.16	2.28^b ± 0.11	2.73^a ± 0.18
Fine fraction (FINE, %)	47^b ± 7	88^a ± 3	86^a ± 5

were basically composed of fine sediment. TOC progressively increased along the chronosequence starting at young sites near the river channel.

Determination of ALLOC and AUTOC

The fine-texture of the sediment deposited on the mats by the studied flood event was positively correlated with the associated TOC deposited following a quadratic relationship (*Fig. 2*). The polynomial function predicted well the proportion of organic C contained in the topsoil samples of the young and mature forests (no significant differences were found between predicted and observed TOC median values after Wilcoxon tests, *Fig. 3*).
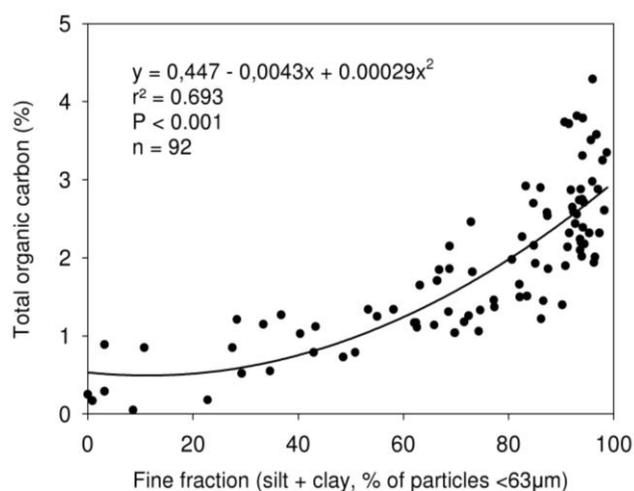

Fig. 2 Scatter plot of sediment texture (silt plus clay, %) and Total Organic Carbon (TOC, %) in the sediments deposited during a flood on 1 January 2006 in the study area

That means that all the organic C had an allochthonous origin and no AUTOC was being accumulated in the plots < 50 year-old. On the contrary, the function under-estimated the proportion of organic C that was found in the topsoil of the old age-forest category (> 50 year-old). That is, the observed TOC median was significantly higher than the predicted TOC median (*Fig. 3*). This fact was interpreted as a proof of a significant accumulation of AUTOC. However, even in this situation, the contribution of the autochthonous fraction to the organic C stock was more than six-fold lower than that of the

allochthonous origin (median TOC residual in old plots, AUTOC = 0.41%; median predicted TOC in old plots, ALLOC = 2.64%).
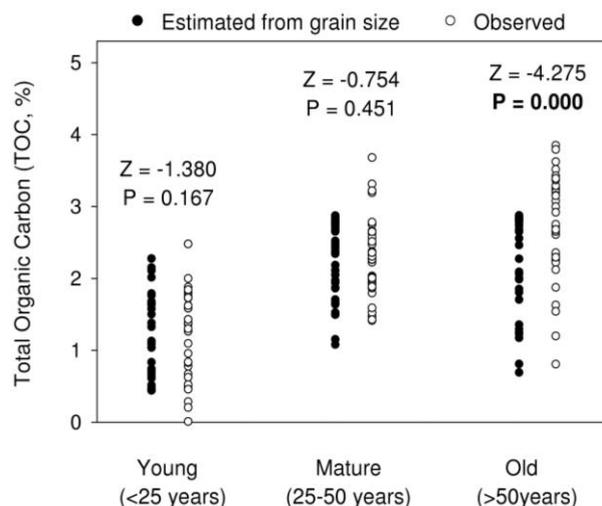

Fig 3 Observed and predicted TOC values from Equation in *Fig. 2* along a biogeomorphic gradient. Wilcoxon matched-pairs signed-ranks tests were used to compare the median value of the observed and predicted TOC values of each age-forest category, with their Z-values and probability associated represented in the figure

Modeling the accumulation of AUTOC

The capacity of the 14 parameters representing the forest structure and hydrological connectivity gradients (*Table 1*) as predictors of AUTOC was first tested individually using Spearman correlation tests and controlling for the effect of "observed TOC" on "TOC residuals" (TOC residuals = -0.275 + 0.206 * observed TOC; $F_{1,109}$=18.94; r^2 = 0.14; P < 0.001). Only three variables had a significant correlation with the TOC residuals, namely SD (ρ = 0.30), IVFx (ρ = -0.44) and IVSa (ρ = -0.24) at a P < 0.05. However, a LME model could be significantly fitted to the whole dataset and is summarized in *Table 2*. The model explained 24% of the variability in AUTOC with a combination of three forest structure variables and one hydrological connectivity

Table 2 Result of the best LME model run between autochthonous organic C accumulated in the first 10 cm of soil (response variable) and different forest structure and hydrological connectivity surrogates (*Table 1*, fixed factors) and plot as random effect. Note that the degrees of freedom are only 109 because six outliers were removed from the initial 117 soil samples (39 plots x 3 soil replicates) due to their abnormally high or low TOC values

	Model fit	Pearson's correlation	Explanatory terms	Type of predictor	Relationship sign	*p*-value	Relative contribution
AUTOC (% of OC with an autochthonous origin)	AIC = 269.6525	R^2=0.24 t=5.9271 d.f.=109 *p*<0.001	logIVFx	Forest structure	-	0.0002	39%
			logSD	Forest structure	+	0.0006	27%
			WT	Hydrological connectivity	+	0.0001	24%
			logIVPn	Forest structure	+	0.0036	10%

variable. In particular, it predicted higher AUTOC accumulation with lower relative dominance of *Fraxinus angustifolia*, higher stem densities, higher importance of *Populus nigra* (the three relationships following a logarithmic ratio) and deeper water table levels (i.e., less subsurface hydrological connection). The joint contribution to the model of the forest structure variables was 76%, versus 24% explained by the hydrogeomorphic regime surrogate. Six topsoil samples of the 117 that originated from randomly distributed plots of young and old forest patches were considered to be outliers and therefore removed from the statistical analyses. The analytical results obtained for the samples showed abnormally low or high TOC values detected during the exploration of the residuals of preliminary models and assumed to be incorrectly collected in the field.

DISCUSSION

Organic C that accumulates in the floodplain soil had a predominant allochthonous origin

The results of our study suggest that most of the organic C that accumulated in the forested floodplain soils had an allochthonous origin; presumably from flood-driven sedimentation processes. This occurred even at the more disconnected sites that were only flooded twice a year and where the forest had established for several decades. In particular, ALLOC accumulation was more than six times more important than AUTOC in forests older than 50 years. At the more connected and younger sites, it was impossible to identify any accumulation of organic C in the soil produced by *in situ* vegetation, reflecting that its importance was marginal relative to that deposited by floods. This was a surprising result as far as vertical litterfall in the Ebro (563 g dry matter m^{-2} yr^{-1}) is an important input of organic matter in the floodplain that is within the range of litterfall values reported in other Mediterranean riparian settings and floodplain forests of the warm temperate zone (Gonzalez et al., 2010b). Although the river has dramatically lost its geomorphic dynamics since the 1980's (Cabezas et al., 2009a), sedimentation still plays a much more important role in organic C accumulation than the autochthonous organic matter produced *in situ* by vegetation. Our results provide evidence to support that ALLOC tends to dominate along the floodplain despite flow regulation and embankment, as long as it remains connected with quasi-annual floods (return period of 2.33 yrs. *sensu* Osterkamp and Hedman, 1982). However, this conclusion does not imply that the loss of geomorphic dynamics caused by human impacts on the river system has not had an effect on ALLOC accumulation. In fact, Cabezas et al. (2009b) showed within the same river reach of the Middle Ebro River, that ALLOC floodplain accumulation rates within a floodplain forest patch dating from at least 1957 and in two oxbow lakes with an origin <1946 were higher before completion of dam constructions built for flood risk reduction and river train-

ing works (<1963). Dams and river training works did not prevent overbank flooding and thus it could have been expected that ALLOC accumulation within the studied forest patch and the two oxbow lakes did not decrease. River training works implied the cutting off of meanders, partially disconnecting the forest patch and the oxbow lakes from the main channel and thus being less frequently flooded.

Relative role of the abiotic and biotic factors in controlling AUTOC accumulation

According to our results, we suggest that organic C accumulation was controlled mainly by allogenic forces, namely the hydrological regime that ultimately controlled the sedimentation processes. The role of vegetation in organic C accumulation would be more important as a consequence of its physical modulation of hydrogeomorphic fluxes rather than of its own primary productivity, even at the more disconnected and older sites, where late-seral successional stages of vegetation dominated. The presence of non-pioneer trees such as *Fraxinus angustifolia* and *Ulmus minor* at the older sites seems to indicate that vegetation develops autogenically. However, our results suggested that, even then, the soil evolved mainly allogenically. Whether the vegetation and soil succession drivers are uncoupled or the non-pioneer species are much more controlled by the hydrological regime than expected remains an open question that deserves further study. Unlike pioneer riparian tree species, the ecology of non-pioneer floodplain tree species has surprisingly received very little attention up to date.

The capacity of the hydrological regime as driver of organic C accumulation goes beyond its influence on sedimentation processes since surface and sub-surface hydrological connectivity partially controls the accumulation of AUTOC as well. Our LME model showed that a higher accumulation of AUTOC occurs with deeper water tables. Deeper water tables were correlated with lower flood frequency and duration, probably resulting in lower sedimentation and in turn in a decrease of the importance of ALLOC *vs.* AUTOC along the biogeomorphic gradient from the channel to the outer floodplain. However, a further explanation of this relationship may also be the control exerted by the hydrologic regime both on the production of organic C and on its decomposition. Numerous studies have shown that primary production of floodplain forests and forested wetlands is largely controlled by the hydrologic regime (Megonigal, et al. 1997, Burke et al., 1999, Clawson et al., 2001 and many others). In our study area, González et al. (2010b; 2010c; 2012b) showed that the flooding regime explained up to 35% of the litter production variability, directly or indirectly by its effects on the N and P cycles. They also found a weak but positive relationship between deeper water levels and litter production. Therefore, the higher accumulation of AUTOC with deeper water levels in our LME model could be partly due to a higher litter production in those more oxygenated soils. The influence of hydrological connectivity on organic matter decomposition, and hence on the C cycle, has also

been proven before (e.g., Baker et al., 2001; Ozalp et al., 2007). Recurrent floods alternating aerobic conditions are supposed to favor organic matter decomposition (Brinson, 1981; Lockaby et al., 1996). It might be the case that deep water tables in our old plots (>50 yr) did not enhance those wetting and drying cycles and hence slowed down decomposition and favored organic C accumulation. No differences in the magnitude of water table fluctuations were observed between plots in the relatively small study area. Therefore, this variable did not contribute to the models and was not shown. However, water table fluctuations at sites with deep water tables are related to less flood submersion episodes than at sites with higher water tables (see WT and FF, *Table 1*). Although it was out of the scope of our study, decomposition must play a key role in the C net accumulation over the long-term in the floodplain soils. With shallower water tables, the young (<25 yrs.) and mature (25-50 yrs.) plots may also be experiencing higher decomposition rates, ultimately reducing C accumulation.

Although the subsurface hydrological connectivity by means of the water table depth below the floodplain surface explained part of the variability in the accumulation of AUTOC, it was the forest structure that most contributed (76%) to the adjusted LME model. The positive effect of stem density on C accumulation was also probably the result of the higher litter production that exhibit floodplain forest patches with higher stem density (Gonzalez et al., 2010b). The inclusion of the IV of *F. angustifolia* and *P. nigra* in the models might respond to a lower productivity and faster decomposability of the organic matter produced by the former and to a higher productivity and lower decomposability for the later (see respective negative and positive contributions in the LME model, *Table 2*), but more studies should be done to confirm this hypothesis.

Limitations of the study

An important limitation of our study may come from the fact that only the first 10 cm of the soil were collected. In certain locations it may have occurred that one single flood event deposited more than 10 cm of sediment, burying the organic C produced *in situ*. In that case, our methodology could have underestimated the AUTOC because it assumed that the topsoil is representative of a likely heterogeneous soil profile (Cooper et al., 1999; Cierjacks et al., 2011). However, this limitation would probably only affect the sites where accumulation is higher than erosion. For example, most of the young plots were covered by gravel, cobbles or sand depositions, and it is very unlikely that a much less denser material such as organic matter has been buried instead of been flushed away. Even at sites where net accretion occurred in our study area, it has been shown that it does at a rate much lower than 10 cm yr^{-1} (Cabezas et al., 2009b) and that the higher rates are localized on narrow margins adjacent to the main channel and on small areas that were the first to be submerged during overbank flooding (Cabezas et al., 2010).

Another source of error may have come from our predictive function ALLOC = f(fine-texture) that was built from one single flood event only and could have been biased towards the ALLOC or AUTOC fraction if its organic matter load was respectively higher or lower than the average of all floods. Different flood events may have different sediment-TOC relationships depending on the flood characteristics in respect to magnitude and flow depths and velocities, timing, frequency, as well as sediment availability and fluxes. Although this is a major limitation of our study, the marginal weight of AUTOC relative to ALLOC (more than six times lower) allows the assumption that with a more consistent predictive function even major deviances from our estimate values would not substantially change the conclusions drawn from our work. For example, the sampled flood in January 2006 did not inundate all 39 plots. Thus, if larger floods inundating all these plots had been sampled and included in the fine sediment fraction-TOC function for ALLOC, the sedimentation pattern would have represented the entire floodplain. Furthermore, this would partially account for the effect of the high spatial variability of sedimentation dynamics and quality (Cabezas et al., 2010). Unfortunately, it is hard to predict the timing of high magnitude, exceptional floods, which makes logistics regarding sample design, i.e. the setup of mats covering the whole natural hydrogeomorphic gradient in the floodplain, very difficult.

Our approach also assumed that the relationship between TOC and the fine sediment fraction was constant during the 50 years covered by the chronosequence. Given that flood control measures have been carried out for decades, sediment sources and availability controlling quantities and quality (e.g. texture, organic matter content) of overbank deposits might have changed over the years. We believe that this assumption, as well as the fact that our model was based on one single flood sampled only, may have influenced our ALLOC/AUTOC ratio quantitatively, but not qualitatively.

Because of the limitations of this exploratory study, the soil texture method applied to identify autochthonous vs. allochthonous C in floodplains (Cabezas and Comín, 2010) needs to be further validated in order to be used more widely within different biogeomorphological settings and according to varying flood characteristics. It would benefit from future comparisons with alternative methods of partitioning AUTOC and ALLOC, such as exploring C budgeting (C depositional fluxes, litterfall fluxes, litterfall decomposition and soil respiration) and C/N ratios, carrying out isotopic characterization or expressing soil C net accumulation rates on a mass basis (g C m^{-2} yr^{-1}) instead of a relative concentration (%).

CONCLUSIONS

This study showed that the accumulation of autochthonous organic C in the Ebro floodplain topsoil only occurred in floodplain forests older than 50 year-old, but even then, it was more than six-fold less abundant than that with an allochthonous origin. Flow regulation and embankment may have substantially reduced the hydrogeomorphic dynamism of the river, but sedimentation by overbank flooding still occurs and probably controls floodplain soil succession and organic C accumulation in

the floodplain. Despite the abovementioned limitations of the present study, a promising method to distinguish the relative contributions of autochthonous versus allochthonous C in floodplains was presented here. Thus, this study eventually contributes to the better insights of the role of floodplains in the overall carbon budget and in providing ecosystem services, such as water quality improvement or climate regulation.

Acknowledgements

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