

Drivers of carbon sequestration by biomass compartment of riparian forests

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Abstract. Riparian forests are expected to play a crucial role in the global carbon (C) cycle but the complex mechanisms of C sequestration in forests remain poorly understood. This study used a comprehensive approach to analyze C sequestration that included the main C compartments in forests, i.e., litterfall, fine roots, and aboveground woody biomass. We aimed at modeling each of them in response to an array of environmental drivers to untangle the functioning of C sequestration by compartment. The study was conducted in a Central European riparian forest that is part of the Donau-Auen National Park in Austria. Carbon sequestration by compartment was correlated with environmental parameters (climate, stream flow, hydrological, spatial, and forest stand parameters) using generalized linear mixed models (GLMM), and the correlations were prioritized by hierarchical partitioning. Our results suggest divergent responses of C sequestration in different ecosystem compartments under dry and wet soil conditions. In particular, dry conditions led to significantly higher C sequestration in aboveground woody biomass (larger distance to the low groundwater table), whereas wetter conditions fostered C sequestration in fine-root (smaller magnitude of fluctuation in the groundwater table) and leaf biomass (smaller distance to the low groundwater table). Fine roots and litterfall responded to short-term variations in climate (mean annual temperature) and flooding parameters (duration of the low to mean Danube River water level in the previous dormant season), highlighting the pivotal role of the dynamic fine-root and leaf biomass compartments for C uptake in forest ecosystems. Consequently, litterfall and fine roots should be considered to improve the sensitivity of C sequestration model responses to climate scenarios.

Key words: climate; Danube River; fine roots; flooding; *Fraxinus excelsior*; generalized linear mixed model; hydrology; litterfall; *Populus alba*; *Quercus robur*; *Salix alba*; stem production.

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INTRODUCTION

Carbon dioxide release from deforestation is the second largest source of human-induced global greenhouse gas emissions, accounting for about 17% (IPCC 2007). The potential loss of organic carbon (C) from deforestation can be estimated by the determination of C stocks in

forests (e.g., Pan et al. 2011, Baccini et al. 2012, Houghton et al. 2012). Many studies on C stocks have focused on large forest biomes at the continental scale. Pan et al. (2011) reported, for example, that approximately 471, 272, and 119 Pg C of the world's forests C stock are stored in tropical, boreal, and temperate forest ecosystems, with the contribution of the aboveground bio-

mass in comparison to soil C stock increasing in importance from boreal to tropical forests.

Identifying factors that drive C sequestration in forests is crucial for a mechanistic understanding of this ecosystem process that is increasingly understood as a critical ecosystem service in the face of the changing climate. Actual C stocks in forests are known to depend on an array of parameters such as forest age (Pregitzer and Euskirchen 2004), length of growing season, mean temperature, and precipitation or radiation balance (Reich and Bolstad 2001), along with forest fires, harvesting, herbivory, and climate change (Gloor et al. 2009, Pan et al. 2011, Sievänen et al. 2014). However, many approaches often fail to provide insights into the mechanisms of C sequestration which function at the local ecosystem scale and ultimately determine forest C stocks.

Analyzing C sequestration in different biomass compartments is a promising approach to understand the formation of C stocks. In contrast to C storage, which reflects the net outcome of carbon changes from different ecosystem compartments (Fahey et al. 2010), annual C sequestration immediately responds to changing climate and site-specific environmental parameters. This is particularly true for fine roots, which are the most dynamic compartment and represent a significant part of net primary production (NPP; Megonigal and Day 1992, Gordon and Jackson 2000). A similarly dynamic behavior may also be assumed for leaves, e.g., in terms of leaf-out times of temperate forests (Polgar and Primack 2011) along with variable periods of photosynthesis.

Riparian forests at the transition zone between aquatic and terrestrial forest ecosystems offer the unique opportunity to reveal mechanisms of biomass C sequestration along varying environmental gradients and for different key tree species. As a consequence of periodic flooding and associated geomorphological processes, natural riparian forests are characterized by a complex and shifting mosaic of forest patches that reflect the highly dynamic aspects of environmental gradients (Naiman and Décamps 1997). The myriad resulting microsites—and their variance across time and space (Gurnell 2014)—modify species biomass productivity, diversity and density within these ecosystems

(Mitsch and Gosselink 1993).

Owing to continuous water and nutrient supply, temperate moist (riparian) forests are among the most productive forest ecosystems (Naiman and Décamps 1997, Kiley and Schneider 2005, Keith et al. 2009). Overbank and below-ground flooding in many cases increases above-ground NPP (Burke et al. 1999, Dufour and Piégay 2008), litter production (Conner and Day 1992), and fine-root stocks and productivity (Williams and Cooper 2005, Rieger et al. 2013). At the same time, frequent and long-term flooding along with water saturation in the soil may also lead to reduced aboveground NPP (Megonigal et al. 1997, Rieger et al. 2013) and fine root amount and production (Day et al. 1988, Day and Megonigal 1993, Baker et al. 2001, Kiley and Schneider 2005). The resulting C sequestration patterns may be further modified by sedimentation rates (Cavalcanti and Lockaby 2005), the flooding tolerance of tree species (Burke and Chambers 2003, Predick et al. 2009), tree species richness (Giese et al. 2000), forest stand parameters (Giese et al. 2003, Meier et al. 2006, Cierjacks et al. 2011) and by the seasonality of flooding (see Day et al. 1988 for aboveground production; Day et al. 1988 and Burke and Chambers 2003 for fine-root production).

The trade-offs in C compartments have been the focus of other studies comparing, e.g., above- and belowground biomass stocks (Day and Megonigal 1993, Giese et al. 2003, Rieger et al. 2013), woody and litter biomass production (Megonigal et al. 1997, Burke et al. 1999), or root and shoot growth (Day et al. 1988, Megonigal and Day 1992). Increased winter and spring flooding, for example, may result in higher aboveground production but in decreased belowground production (Day et al. 1988). These results have been supported by some studies (Megonigal and Day 1992, Day and Megonigal 1993), but—for the same study area—different results for aboveground NPP in relation to soil moisture have also been reported (Day et al. 1988, Megonigal et al. 1997). In addition, C sequestration in moist forests equally depends on the interaction of site-related environmental gradients as well as climatic and flooding variables. In this context Dufour and Piégay (2008) could not find any influence of climate and stream flow time series on tree-ring growth,

whereas e.g., Kiley and Schneider (2005) attributed differences in annual root biomass to varying precipitation. Moreover, the influence of the above-mentioned environmental parameters presumably varies by tree species (Lambers and Poorter 1992).

To our knowledge, no study has yet addressed the manifold drivers of biomass C sequestration in different ecosystem compartments in riparian forests. As a consequence of studying a maximum of two C sequestration compartments and their responses to either site-, climate- or flooding-related variables by comparison of different study sites, the functioning of environmental drivers of C sequestration in moist forests still remains uncertain. In addition, most of the mentioned studies on C sequestration were carried out in forest swamps. González et al. (2010a) performed one of the few studies in riparian forests, and modeled one biomass compartment (litterfall production) in response to forest structure, soil, and spatial parameters. The study raised the question of whether the environmental factors that influence litterfall production have the same effects on the NPP of other compartments.

Following González et al. (2010a), we modeled C sequestration by biomass compartment and key tree species in response to climatic and site-related environmental variables in the riparian forest of the Donau-Auen National Park in Austria. With this comprehensive approach, we hope to untangle the complex mechanism of C sequestration in biomass.

Fine roots and leaves directly interact with their environment (Eisenstat and Caldwell 1988, Baker et al. 2001, Liu et al. 2004) to ensure the supply of nutrients for photosynthesis, whereas aboveground woody biomass fulfills a reserve function (Pallardy and Kozłowski 2008). Fine roots and litterfall are also sensitive indicators of environmental changes (Vogt et al. 1993, 1996) and are likely to be more responsive parts of NPP than aboveground biomass. We therefore hypothesized that (1) climatic and stream flow parameters are more relevant for predicting C sequestration in the fine-root and litterfall compartments than in the aboveground woody biomass compartment, which may be expected to buffer short-term environmental changes, and (2) fine roots and litterfall respond similarly to

environmental changes.

In particular, our study aims at (1) quantifying C sequestration in litterfall, fine-root and aboveground woody biomass of key tree species in a temperate riparian forest ecosystem and (2) modeling C sequestration in the different biomass compartments in response to environmental gradients (climate, stream flow, spatial, hydrological, and tree parameters) using generalized linear mixed models (GLMM).

METHODS

Study area and study design

Our study was performed in the Donau-Auen National Park in Austria, in the floodplains east of Vienna. Since 1997, the national park has been recognized as Category II of the IUCN (International Union for Conservation of Nature and Natural Resources). It preserves one of the largest remaining near-natural riparian forests in Central Europe. About 65% (6045 hectares) of the national park is covered by riparian forest (Donau-Auen National Park 2014a); the remainder comprises mostly meadows and water courses. Climatic conditions for the period 1948–2008 were characterized by a mean annual temperature of 9.8°C and mean annual precipitation of 533 mm (climate station: Schwechat 48°7' N, 16°34' E, 184 m above sea level; Zentralanstalt für Meteorologie und Geodynamik 2002).

In the studied river section, the main channel of the Danube River is approximately 350 m in width and drains an area of 104,000 km². The banks are predominantly fixed by riprap. In addition, a part of the area is diked. However, the Danube River still inundates large areas during high river water levels. The magnitude of fluctuation of the Danube River water level is up to 7 m and water discharge is mainly mediated by snowmelt in the Alps and by heavy rainfalls in the upstream watershed causing overbank flooding mainly in summer (Donau-Auen National Park 2014b). The slope of the river is 0.043% with low and mean annual discharges of 900 and 1,950 m³ s⁻¹, respectively. The mean annual flood discharge is 5,270 m³ s⁻¹ (Tockner et al. 1998).

The riparian forest is composed of different vegetation units with specific tree-species com-

position (Drescher and Fraissl 2006, Cierjacks et al. 2010). Cottonwoods dominated by *Populus alba*, *P. nigra*, and *Salix alba* prevail at sites characterized by a high frequency of overbank flooding and high flow velocities close to the main channel and side channels as well as at sites with a high groundwater table as in historic river beds. At less dynamic sites with a lower inundation frequency, *Ulmus laevis* initiates the formation of hardwood forests, which contain overstory tree species such as *Quercus robur* and *Fraxinus excelsior* (Drescher and Fraissl 2006). Forest structure and species composition are comparable on both sides of the dike (pers. observation). Forestry activities have been banned since the establishment of the National Park in 1996 (Austria's Federal Law; Art. 15a, B-VG), but areas of natural forest still alternate with older plantings of *Populus × canadensis* or monoculture sites where *P. alba* has regrown after clear cutting (Drescher and Fraissl 2006). Soil types are also very heterogeneous varying from rambla to eutric calcaric fluvisols and haplic calcaric gleysols (Cierjacks et al. 2010).

The study area comprised the riparian forest to the north of the Danube River. The villages Schönau in the west (48°8' N, 16°36' E, river kilometer 1910) and Stopfenreuth downstream to the east marked the beginning and end, respectively, of the study area (Fig. 1). To cover the entire spatial variability of the hydrosystem (Piégay and Schumm 2009) and a broad range of environmental gradients, the study area was divided into three lateral and two longitudinal zones. In two lateral zones (≤ 400 m and > 400 m to the Danube River), overbank flooding is still present, whereas in the area north of the dike, surface flooding is inhibited. Two longitudinal zones divide the lateral zones into an upstream and a downstream part of the study area. Within each of the resulting six zones, we randomly selected two—sociologically dominant—sample trees ≥ 25 cm diameter at breast height (DBH) out of the four main tree species using the national park's forest inventory database (100 × 400 m grid). The tree species *Q. robur* and *F. excelsior* were chosen as representatives of hardwood forest; *P. alba* and *S. alba* are typical species of cottonwood forests. Overall, 48 sample trees were included in this study (6 zones × 2 individuals × 4 tree species = 48 sample trees).

Site-related environmental parameters were measured once between January and June 2010.

Carbon sequestration in litterfall

Beneath the canopy of each sample tree, one litter trap (0.5 × 1 m) was randomly placed at an elevation of one meter above the ground. Due to the fact that we considered all relevant tree species of the study area, we assume litterfall values to be representative for the studied riparian forest. Litterfall traps were installed in April 2010 and remained in the forest until March 2013. Annual litter samples (2010, 2011, and 2012) were collected in the last week of November. Each trap was post-controlled in February of the following year to collect late litterfall, which was most notable in *S. alba* sample trees. Leaves, woody material, and generative tissues of *Q. robur* and *F. excelsior* were analyzed separately. Samples were dried at 65°C in a ventilated oven to a constant mass. Biomass was weighed and doubled to calculate the annual litterfall production per m². Biomass was then multiplied by 0.475 to derive the C amount in the leaves, woody material, and generative tissues (Magnussen and Reed 2004, González 2012).

Carbon sequestration in fine roots

Annual fine-root productivity was estimated using ingrowth cores. We placed two ingrowth cores 50 cm apart in November 2010. Both cores were buried 2 m from the sample tree to avoid the effects of local sedimentation caused by the trunk. Ingrowth cores were cylindrical (3.5 cm in diameter and 30 cm in length) and made of fiberglass fabric of 1.2 mm mesh size and a fishing line (0.15 mm, Berkley Fireline, Columbia, South Carolina, USA) sewn with a sewing machine (Singer 354, Singer, New York, New York, USA). The position of each core was recorded and labeled with a plastic card at the end of a ca. 20 cm long nylon thread to facilitate retrieval after sediment deposition. To ensure relative comparability between different sites, all cores were filled with the same root-free silty to sandy sediment that is typically deposited by the Danube River during surface flooding. Sediment was directly taken from the shore of the Danube River. The first core per sample tree was harvested after one year, the second after two

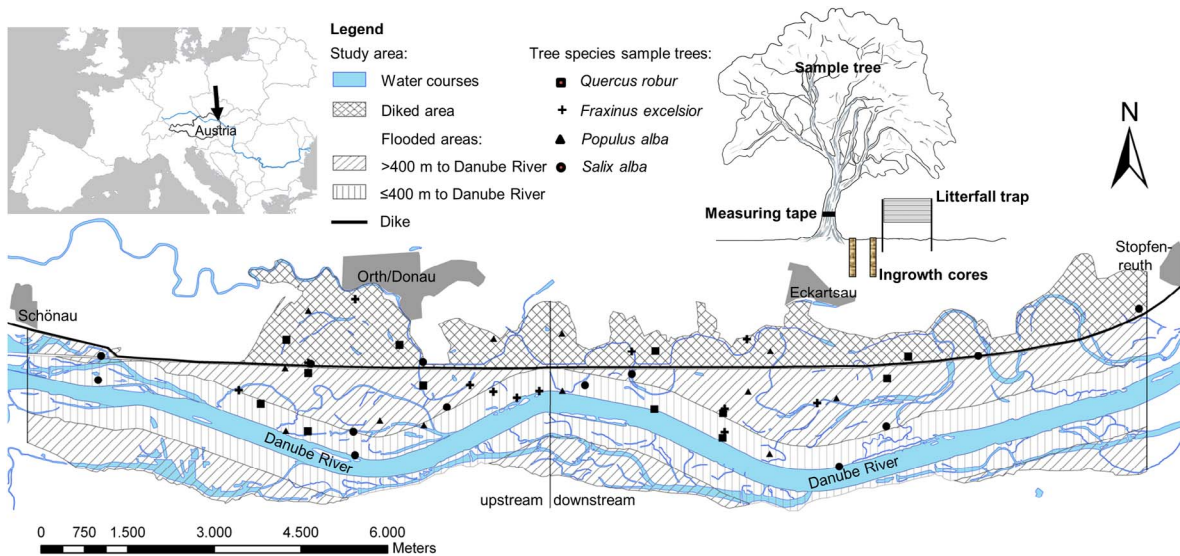


Fig. 1. Study area within the Donau-Auen National Park in Austria and study design.

years. In total, we were able to harvest 46 intact ingrowth cores in November 2011 and 45 cores in November 2012. Fine roots of each ingrowth core were washed, using a series of sieves of different mesh sizes (2.5 mm on the top, 0.5 and 0.2 mm in the middle, and 0.063 mm at the bottom), and then stored at 4°C in a refrigerator. They were then separated by size and phenology classes (usually within 24 hours). For classification, fine roots were homogeneously distributed in a petri dish which was lined with millimeter paper. Six of twenty marked square centimeters were randomly chosen as a sub sample to classify fine roots according to their diameter size (<0.49, 0.5–1.49, 1.5–2.99, and 3–5 mm) and into living and dead fine roots using a stereo microscope (Leica Wild M3C, Leica, Wetzlar, Germany). Living fine roots and necromass were separated according to Persson (1980a, b) and McClaugherty et al. (1982). Fine root samples were dried to constant weight and weighed. Carbon amount was calculated by multiplying biomass values by 0.5. Fine-root growth rates for 2012 were calculated as the difference between biomass measured in 2012 and in 2011.

Carbon sequestration of aboveground woody biomass

At each sample tree, a permanent measuring tape (Permanent D) was fixed at breast height to

determine the annual growth in DBH. From February 2010 to February 2013, DBH was recorded every two months. Based on DBH and height of the sample tree, we used allometric equations (Table 1; Zianis et al. 2005) to calculate the total aboveground biomass in 2010, 2011, and 2012. Increment of aboveground biomass was calculated as the difference in biomass stocks between two consecutive years. Aboveground biomass equations were not available for *S. alba*, so stem volume equations were used for this species and were transformed to biomass using the factor 0.5321 according to Lehtonen et al. (2004). Carbon stocks were derived from biomass values as described for litterfall. One *Q. robur* sample tree was excluded because the measuring tape was stolen.

Due to the heterogeneity of the studied riparian forest surrounding the sample tree, e.g., forest stock, basal area, age of different tree species, coverage etc., we decided to present tree-based values for C sequestration in aboveground woody biomass instead of extrapolated hectare values with great uncertainties.

Spatial and hydrological parameters

The spatial position of each sample tree was recorded before foliation in 2010 to a precision of approximately 10 cm with the help of a differential GPS (Trimble GeoXH 2005 series handheld,

Table 1. Allometric equations by tree species used for biomass calculations in the study area (Abbreviations: AB = aboveground biomass, ABW = aboveground woody biomass, SV = stem volume, D = diameter at breast height, H = height, App. = Appendix).

Species	Equation	Units					Equations used from Zianis et al. (2005)
		AB	ABW	SV	D	H	
<i>Quercus robur</i>	$\ln(\text{AB}) = (-0.883) + (2.14 \times \ln(\text{D}))$	kg			cm		App. A, #600
<i>Fraxinus excelsior</i>	$\ln(\text{ABW}) = -2.4598 + 2.4882 \times \ln(\text{D})$		kg		cm		App. A, #134
<i>Populus alba</i>	$\text{AB} = 0.0519 \times \text{D}^{2.545}$	kg			cm		App. A, #514
<i>Salix alba</i>	$\text{SV} = -1.8683 + 0.2146 \times \text{D}^2 + 0.0128 \times \text{D}^2 \times \text{H}^2 + 0.0138 \times \text{H}^2 \times \text{D} - 0.0631 \times \text{H}$			dm ³	cm	m	App. C, #218†

† Equation for *Salix caprea* was used.

Trimble, Sunnyvale, California, USA). For each sample tree, we determined the following spatial parameters: the lateral distances to the Danube River and to the nearest side channel, the vertical distance to the mean Danube River water level, and the longitudinal distance, which is the distance to the upstream beginning of the study area to the west near the village Schönau (Fig. 1).

Our hydrological parameters were based on a groundwater model provided by the Technical University of Vienna. We calculated the distance to the groundwater table at its lowest level and the magnitude of fluctuation of the groundwater table between its low and mean levels (see Rieger et al. 2013, 2014 for more details).

Climatic and stream flow parameters

As no meteorological data for 2012 were available for the nearest climate station (Schwechat), mean monthly and annual climatic parameters (temperature, precipitation) for 2009–2012 were derived from the meteorological station of Vienna–Hohe Warte, located at about 23 km westwards from the upstream beginning of the study area (48°25' N, 16°36' E, 209 m asl; Zentralanstalt für Meteorologie und Geodynamik 2013).

Daily river water levels for the period 2009–2012 were provided by via donau–Österreichische Wasserstraßen-Gesellschaft mbH for the water-gage monitoring station Wildungsmauer (Danube River kilometer 1894.72; 48°06'57" N, 16°48'25" E). Flooding parameters were calculated for each year, with the same value for all sample trees, as total days per growing season (April–September) and dormant season (October–March) in which the Danube fell below, ranged between, or exceeded long-term average

water levels defined by via donau–Österreichische Wasserstraßen-Gesellschaft mbH (2012; Table 2). We used the number of days with Danube River water levels below RNW (water level duration exceeding ca. 343 days/year), between RNW and MW (averaged water level), between MW and HSW (water level duration exceeding ca. 3.6 days/year), or above HSW (abbreviations according to Table 2). Our study includes two periods with overbank flooding in June 2010 and January 2011.

Statistics

The whole data set of continuous variables was analyzed in terms of homogeneity (Fligner test), normality (Shapiro-Wilk test), outliers or missing values (Zuur et al. 2010). Generalized linear mixed models (GLMM) were chosen to determine which environmental gradients were influential in determining C sequestration in litterfall, fine roots and aboveground woody biomass since our data set is based on repeated measurements over three consecutive years on the same sample trees, which causes temporal autocorrelation (Crawley 2007, Zuur et al. 2009). Spatial, hydrological and climatic variables were defined as fixed effects, whereas sample tree and time were defined as random effects. Owing to negative values in the Poisson family, which are not allowed in the calculation, we transformed three negative values of the data set to zero to meet the requirements of modeling C sequestration in aboveground woody biomass and fine roots, respectively. Verification of the final model's variable selection was done using both stepwise forward and backward selection of predictor variables. To facilitate model selection based on minimum AIC values, we used the lmer

Table 2. Danube River water levels used to describe the flooding intensity of the Danube River (River water levels according to the reference via donau-Österreichische Wasserstraßen-Gesellschaft mbH [2012]).

Status	Definition	River water level Wildungsmauer (altitude, m asl)
RNW	water level that is exceeded 94% of the year (ca. 343 days)	141.1
MW	mean water level	142.41
HSW	water level that is exceeded 1% of the year (ca. 3.6 days); corresponds approximately to the bankful discharge, highest navigable water level	145.12

function of the lme4 package. The calculated models include spatial (e.g., vertical, lateral and longitudinal gradients) and hydrological (e.g., magnitude of fluctuation in the groundwater table, distance to low groundwater table) variables, tree species and annual climatic and flooding parameters. The relative contributions of all significant variables in the final models to the explained variance were calculated using the hier.part function of the gtools package.

All calculations were performed with R version 1.19.4.7 using the packages AED, gtools, hier.part, mass, lme4, and nlme (R Development Core Team 2011).

RESULTS

Carbon sequestration in biomass compartments

Mean annual C sequestration in aboveground biomass was 20.6 kg C yr⁻¹ per studied tree, whereas litterfall and fine roots summed up to 0.5 kg C m⁻² yr⁻¹. Carbon sequestration in litterfall was 63% greater than in fine roots (Table 3).

The majority of litterfall consisted of leaf biomass (74%). In fine roots about 95% could be attributed to living fine-root biomass, and most was found in the size classes <0.5 mm (48%) and 0.5–1.49 mm (30%; Table 4).

Correlation analysis did not reveal significant interactions among biomass compartments (Pear-

son's product moment correlation $p > 0.05$)—regardless whether the mean values for C sequestration in litterfall, fine roots, and aboveground woody biomass were considered for the whole time period or separated by calendar year.

Environmental drivers of carbon sequestration

When the water level of the Danube River remained below average for longer periods in the previous dormant season, C sequestration in litterfall decreased. This was the most meaningful driver of C sequestration in litterfall and improved significantly the model that based on spatial, hydrological or tree species as drivers only (AIC = 1093.9, $p < 0.001$). Overall, this stream flow parameter explained 92% of the variance in the dependent variable (Fig. 2; for model documentation see Appendix B).

Among all spatial and hydrological drivers only the distance to the low groundwater table and tree species remained in the final model of C sequestration in litterfall (Fig. 2). Carbon sequestration in litterfall increased with smaller distances to the low groundwater table, i.e., trees produced more litter when the groundwater remained closer to the surface. When the interaction between low groundwater level and tree species was analyzed, it was revealed that C sequestration of litterfall differed according to the individual response of each species to the low groundwater table. In this context, C sequestered

Table 3. Mean annual C sequestration per study tree (means ± SE) in a riparian forest from 2010 to 2012 (ABW = aboveground woody biomass, litterfall) and from 2011 to 2012 (fine roots, sum) by compartment and separated into leaves, twigs, and seeds (litterfall) as well as living biomass and necromass (fine roots).

Litterfall compartment	Litterfall (kg C m ⁻² yr ⁻¹)	Fine root phenology classes	Fine root (kg C m ⁻² yr ⁻¹)	ABW (kg C yr ⁻¹)
Leaves	0.23 ± 0.008	Living biomass	0.18 ± 0.031	...
Twigs	0.08 ± 0.011	Necromass	0.004 ± 0.003	...
Seeds	0.008 ± 0.003			
Total	0.31 ± 0.01		0.19 ± 0.03	20.57 ± 1.67

Table 4. Annual C sequestration in fine roots of a riparian forest by size class and phenology (means ± SE) in 2011 and 2012.

Size (mm) and phenology class	C sequestration (kg C m ⁻² yr ⁻¹)	
	2011	2012
<0.50		
Living biomass	0.039 ± 0.006	0.144 ± 0.031
Necromass	0.004 ± 0.001	-0.002 ± 0.001
0.50–1.49		
Living biomass	0.023 ± 0.005	0.091 ± 0.022
Necromass	0.003 ± 0.001	0.000 ± 0.002
1.50–2.99		
Living biomass	0.01 ± 0.005	0.025 ± 0.011
Necromass	0.002 ± 0.001	-0.001 ± 0.001
3.00–5.00		
Living biomass	0.005 ± 0.004	0.030 ± 0.019
Necromass	0.000 ± 0.000	0.000 ± 0.000
Total		
Living biomass	0.077 ± 0.011	0.283 ± 0.051
Necromass	0.009 ± 0.002	-0.002 ± 0.003
Living biomass and necromass	0.085 ± 0.011	0.281 ± 0.051

in litterfall under *P. alba* was significantly lower than under *F. excelsior*, *Q. robur*, and *S. alba* (Fig. 2; for model documentation see Appendix B).

Sequestration of C in fine roots correlated mainly with the mean annual temperature. Furthermore, C sequestration in fine roots increased with (1) greater distances to the upstream boundary of the study area (longitudinal gradient) and (2) lower magnitudes of fluctuation in the groundwater table (hydrological gradient).

At 68%, the mean annual temperature explained the major part of variance, whereas the longitudinal and hydrological gradients accounted together for only 32% (Fig. 3; for model documentation see Appendix D). Considering the annual temperature as a climatic parameter increased model predictability significantly (AIC = 712.0, ANOVA, *p* < 0.001).

The C sequestration of aboveground woody biomass was significantly influenced by the distance to the low groundwater table (59%) and by tree species (37%; Fig. 4). Greater distances to the low groundwater level generally increased C sequestration in aboveground woody biomass in all tree species. Furthermore, C sequestration of aboveground woody biomass was significantly higher for *P. alba* compared to *S. alba*, whereas *F. excelsior* and *Q. robur* occupied an intermediate position (Fig. 4). Among the climatic parameters neither temperature nor precipitation improved the final model significantly. However, the duration of the Danube River water level between the mean and the ten-year flooding event in the current growing season significantly improved the spatial model as demonstrated by a lowered AIC (ANOVA, *p* < 0.05), which indicates that long-lasting flooding events significantly reduce C sequestration of the aboveground woody biomass (for model documentation see Appendix I).

Formula: lmer (Carbon sequestration litterfall ~ Duration of the low to mean Danube River water level in the previous dormant season + Distance to low groundwater table * Tree species + (1|Site/Year), family=poisson)

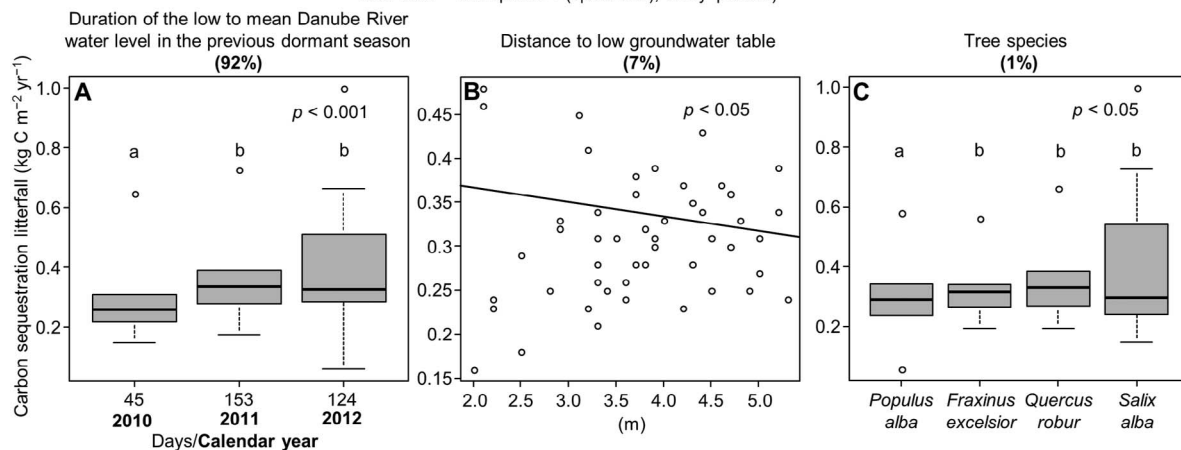


Fig. 2. Generalized linear mixed model for predicting C sequestration in litterfall of riparian forests based on (A) the Danube river water level, (B) hydrology, and (C) tree species (for model documentation see Appendix B); values in parentheses refer to the relative influence of each predictor variable to the explained variance.

Formula: lmer (Carbon sequestration in fine roots ~ Mean annual temperature + Distance to the upstream boundary of the study area + Magnitude of fluctuation in the groundwater table + 1|Site/Year, family=poisson)

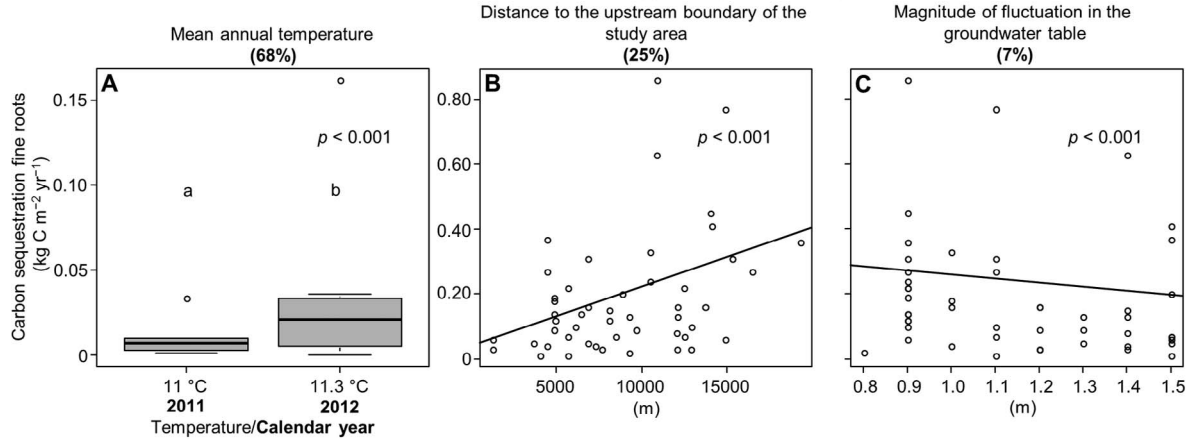


Fig. 3. Generalized linear mixed model for predicting C sequestration in fine roots of riparian forests based on (A) the mean annual temperature, (B) spatial, and (C) hydrological variables (for model documentation see Appendix D); values in parentheses refer to the relative influence of each predictor variable to the explained variance.

The relative contributions of significant variables to the explained variance in C sequestration show that the highly dynamic compartments of litterfall and fine roots mainly responded to variable climatic and flooding parameters (92 and 68%; Figs. 2 and 3). In contrast, aboveground biomass mainly responded

to more stable environmental gradients such as the vertical distance to the low groundwater table and tree species (59 and 37%; Fig. 4). Modeling total C sequestration (combining litterfall, fine roots, and aboveground woody biomass) was not satisfactory (for model documentation see Appendix J).

Formula: lmer (Carbon sequestration aboveground woody biomass ~ Distance to low groundwater table + Tree species + Duration of the Danube River water level between mean and 10-year water level in the current growing season + 1|Site/Year, family=poisson)

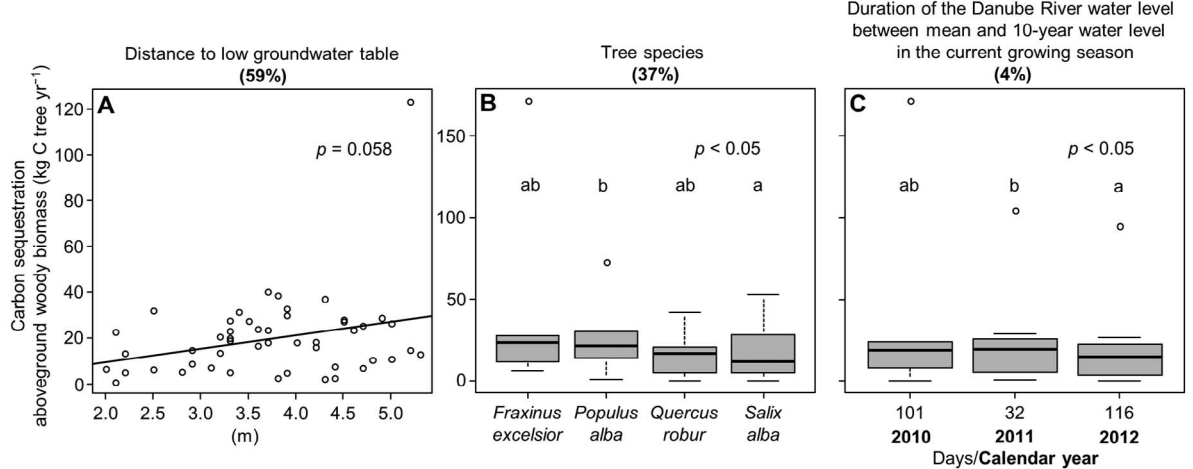


Fig. 4. Generalized linear mixed model for predicting C sequestration in aboveground woody biomass of riparian forests based on (A) the distance to the low groundwater table, (B) tree species, and (C) the Danube River water level (for model documentation see Appendix I); values in parentheses refer to the relative influence of each predictor variable to the explained variance.

DISCUSSION

This study provides detailed insights into the functioning of C sequestration in different compartments (litter, fine-root and aboveground woody biomass) of riparian forest ecosystems. Our results highlight the role of annually changing climatic and flooding parameters as the main drivers of C sequestration in fine roots and litterfall, which makes them more sensitive indicators for environmental changes than aboveground woody biomass. Furthermore, litterfall and fine root production proved to respond similarly to wetter soil conditions. A positive correlation (Pearson's product-moment correlation = 0.47, $p < 0.001$; data not shown) between the groundwater-related predictor variables for litterfall (distance to the low groundwater table) and fine roots (magnitude of fluctuation in the groundwater table) supports this assumption. Our study also revealed pronounced differences among biomass compartments and the tree species involved. However, we could not find a direct correlation between the studied compartments in terms of C allocation, which implies a high plasticity within and among species.

Mean C sequestration in litterfall increased with a smaller distance to the low groundwater table, which indicates that wetter soil conditions in our study area are favorable for litterfall production. Enhanced litterfall production, e.g., owing to increased size or number of leaves, can be a possible response of plants to optimized soil water conditions and would reflect increased photosynthesis rates and carbon dioxide uptake from the atmosphere (Lüttge et al. 1999). Similarly, Poorter et al. (2009) reported a positive correlation between leaf mass per unit area (LMA) and soil water saturation. Correspondingly, Brando et al. (2008) found that litterfall decreased by 23% compared to control after three years of simulated drought. In contrast, González (2012) reported a general increase in litterfall production at greater distances to the groundwater table and in locations closer to the Middle Ebro River in Spain. However, these varying results are not necessarily contradictory as the distances to the mean groundwater table between our study and the Ebro River study were quite different (250 vs. 70 cm, data derived from

González et al. 2010b), suggesting that our study sites are at the drier end of the spectrum, and the Ebro study sites were more toward the wetter end of the ecosystem's ecological amplitude, where wetter soil conditions could have been present. Litterfall productivity increases as the ecosystem moves towards the optimal hydrological regime. In the case of the Danube River these are rather wet soil conditions, while drier soil conditions are more favorable in the Middle Ebro River system. The observations by González (2012) support this assumption because the author also attributed decreasing litterfall, in particular of *S. alba* and *P. alba*, to sudden and long-lasting low-water periods at drier sites.

Similarly to Meier et al. (2006) and González (2012) who attributed differences in litterfall productivity to species composition, our results showed a significant influence of the tree species on C sequestration in litterfall. Including the distance to the low groundwater table as an interaction term in our model showed that litterfall production of *P. alba* was significantly lower compared to *S. alba*, *F. excelsior*, and *Q. robur*, indicating that *P. alba* was less tolerant to lower groundwater tables. Riparian cottonwoods are known to respond very pronouncedly to drought stress by reducing stomata aperture and photosynthesis, which leads to lower growth rates and canopy dieback (Rood et al. 2003, Pallardy and Kozłowski 2008). *Populus alba* is a fast-growing, water-consuming tree species which exhibits higher transpiration rates and less efficient water use compared to genera such as *Fraxinus* (Manzanera and Martínez-Chacón 2007). The significantly lower values of litterfall in *P. alba* compared to *S. alba* seem contradictory to findings of González et al. (2010c, 2012). Still, the authors explain this fact by a clearly higher canopy dieback in *S. alba* in their study area. Accordingly, lower values of total and twig (Kruskal-Wallis test $p < 0.05$; data not shown) biomass in litterfall along with a higher mean tree age (data derived from Rieger et al. 2014) in *P. alba* compared to *S. alba* in the Danube River floodplain forest point to a similar effect of canopy dieback on litterfall—albeit here related to *P. alba*. Furthermore, *S. alba* sites tend to be slightly wetter than *P. alba* sites (3.3 vs. 3.7 m distance to the low groundwater table) which may explain the decreasing C sequestration in

leaves as the depth to the groundwater table increases (see also Horton et al. 2001). Increased depths to the groundwater table may be particularly severe during sunny days at the beginning of the growing season when bud expansion and growth of leaves cause maximum water demand. Wetter soil conditions furthermore increase soluble phosphatases and therefore enhance nutrient availability and uptake (Scheffer et al. 2010), which may increase litterfall production (Gonzalez et al. 2010a).

The response of present plant growth to conditions in the previous season is well documented. The number of leaf primordia and the leaf area of trees can be lowered by hot and dry weather in the previous year (Kozłowski 1971). The results of our study support the assumption that—in addition to climate—flooding parameters during the dormant season cause changes in leaf C sequestration. Carbon sequestration in litterfall responded positively to longer periods of intermediate Danube River water levels in the previous dormant season (Fig. 2), which may indicate conditions that enhance overwintering of leaf primordia in buds. Our analysis shows significantly higher values for litterfall in the years 2011 and 2012 compared to 2010, which reflects well the number of days of intermediate water levels during the previous dormant season of 45 days (2010), 153 days (2011) and 124 days (2012). The river level is related to other climatic parameters in the upstream region. Above average temperatures during the dormant season in the Alps and Alpine foothills can, for example, induce earlier snow melt or rainfall and thereby increase the Danube River to an intermediate level, possibly leading to higher bud survival and subsequent leaf development.

Similarly to litterfall, C sequestration in fine roots was positively correlated to wetter soil conditions, i.e., the lower the magnitude of fluctuation between the low and mean groundwater table, the higher the C sequestration in fine roots. Carbon stocks of fine roots reflect net annual C sequestration rates in fine roots. Consequently, Carbon stocks of fine roots on the same study plots also increased at greater distances from the Danube River, where magnitudes of fluctuation in the groundwater table are significantly lower (Rieger et al. 2013). That the largest portion of living fine-root biomass is

found in the smallest size classes points to a good nutrient supply and aerated soil conditions—at least in the top 30 cm—which both reduce fine root mortality (Rieger et al. 2013) and accelerate fine root decomposition (Day and Megonigal 1993, Rotkin-Ellman et al. 2004). Moreover at sites with a low magnitude of fluctuation in the groundwater table, sedimentation rate is low (Rieger et al. 2014), which may additionally increase fine-root growth (Simm and Walling 1998, Cavalcanti and Lockaby 2005); these conditions are more frequently found at greater distances to the upstream boundary of the study area. The re-connection of formerly cut-off side arms with the main channel of the Danube River in the upstream region of the study area may have led to decreased fine root growth due to increased sedimentation rates.

Carbon sequestration in fine roots also responded significantly to annually changing parameters such as mean annual temperature. Increased mean annual temperatures, particularly at the beginning and the end of the growing season, can improve fine-root productivity in temperate zones (Pregitzer et al. 2000) as a result of better nutrient availability in warmer and wetter soils due to elevated mineralization rates (Zak et al. 1999, Davidson and Janssens 2006). In accordance, Leppälammil-Kujansuu et al. (2014) linked higher soil temperatures and nutrient-rich soil with increased below-ground litter production (dead fine roots <1 mm) for *Picea abies*. The authors report up to fourfold higher below-ground litter production for a treatment with soil warming, fertilization, and irrigation compared to one with irrigation only. Although C sequestration in aboveground litterfall and fine roots was not directly correlated in our study, the same response to wetter soil conditions parameters points to a similar C uptake strategy in both compartments. Under advantageous site conditions (wetter soil), photosynthesis is supported and linked to an increase in leaf production for greater C uptake. In parallel, enhanced fine-root production ensures the supply of additional water and nutrients.

In contrast to litterfall and fine roots, our results show that C sequestration in aboveground woody biomass tended to respond positively to greater distances to the groundwater table, i.e., drier soil conditions. This supports

findings on tree C stocks, which also increased with distance to the groundwater table and decreased with distance to the main channel (Rieger et al. 2013). Both results point to a decrease in stem growth under wet soil conditions with risk of anoxia and water saturation which presumably forces the trees to allocate more biomass in fine roots and less in radial growth. However, our data do not provide final evidence for a direct negative correlation of fine root and stem growth and further research is needed to illuminate this aspect. In addition, C sequestration in aboveground woody biomass of riparian forests was also determined by tree species and was higher in *P. alba* than in *Q. robur* and *F. excelsior*. This may be attributed to lower mean tree age in the pioneer species *P. alba* (derived from data of Rieger et al. 2013) which suggests that this species indicates an earlier succession state with higher C sequestration in aboveground biomass than climax species such as *Q. robur* and *F. excelsior*. Interestingly, *S. alba* had the lowest C sequestration in aboveground woody biomass despite its character as a fast-growing pioneer tree. We suppose that diameter growth in this species is generally lower than that of *P. alba* which may explain the significant differences between both pioneer species.

CONCLUSIONS

In accordance with our first hypothesis, the relative contribution of all explanatory variables clearly showed that C sequestration in litterfall and fine roots was mainly determined by annually changing environmental variables (i.e., duration of the mean water level in the Danube River during the previous dormant season and mean annual temperature). These tree biomass compartments can therefore be considered as the more responsive in terms of NPP compared to the aboveground woody part. However, a three-year study is probably too short to draw fundamental conclusions on this topic, and we strongly recommend long-term studies to verify the results. In contrast, C sequestration in aboveground woody biomass was predominantly determined by site-specific variables (i.e., distance to the low groundwater table) and tree species. Carbon sequestration in aboveground woody biomass can be assumed to function as a

nutrient and carbohydrate reservoir that is able to compensate for the impact of adverse short-term fluctuations in litterfall and fine root productivity. It is well known that sequestered C can fulfill a reserve function, when C is accumulated in wood and bark tissues (Pallardy and Kozlowski 2008). However, this pattern seems to be modified by environmental parameters that vary over time, such as temperature or flooding, and that are related to soil moisture (distance to and magnitude of fluctuations in the groundwater table). The latter imply that short-term C sequestration in litterfall or fine roots is strengthened if environmental conditions become wetter. Still, both compartments also show pronounced differences in terms of their response to particular environmental inputs.

Overbank flooding in our study area seemed to have a less pronounced influence on C sequestration in biomass in comparison to belowground flooding. Aboveground woody biomass C sequestration was the only parameter which was directly influenced by overbank flooding, but the contribution to the explained variance was very low, just 2%. In contrast, the groundwater regime played an important role in the majority of the models. These findings coincide with the results on C dynamics from the same study area for C stocks in biomass (Rieger et al. 2013) and soil (Rieger et al. 2014), where both C pools also responded most notably to groundwater. A rough estimate of hectare-related values of C sequestration in aboveground woody biomass (12.98 t C ha⁻¹ based on the stem number per hectare (Appendix K: Table K1) and C sequestration values (Table 3) shows that litterfall and fine roots account for approximately 23.9% (3.1 t C ha⁻¹) and 14.6% (1.9 t C ha⁻¹) of this amount. Owing to the suggested contribution of litterfall and fine roots, and the pronounced spatial and temporal variability in C sequestration, we strongly recommend including different ecosystem compartments in C sequestration models to improve the reliability of predictions of the C cycle at the ecosystem scale.

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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

Appendices A–K are available online: <http://dx.doi.org/10.1890/ES14-00330.1.sm>