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A novel dendrochronological approach reveals drivers of carbon sequestration in tree species of riparian forests across spatiotemporal scales

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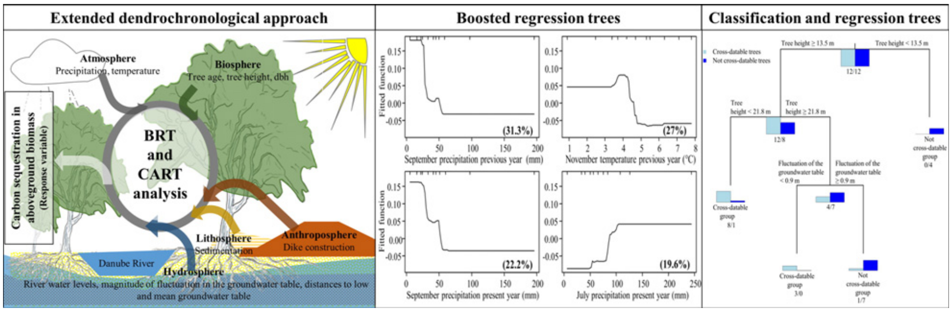
HIGHLIGHTS

- Understanding drivers of carbon (C) dynamics is vital for climate change adaptation.
- We assessed C sequestration in major tree species of temperate riparian forests.
- We developed an extended dendrochronological approach to reveal drivers.
- C sequestration is driven by temporal, site-specific and tree-trait related drivers.
- Results may support locally adapted forest management plans.

GRAPHICAL ABSTRACT



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ABSTRACT

Aboveground carbon (C) sequestration in trees is important in global C dynamics, but reliable techniques for its modeling in highly productive and heterogeneous ecosystems are limited. We applied an extended dendrochronological approach to disentangle the functioning of drivers from the atmosphere (temperature, precipitation), the lithosphere (sedimentation rate), the hydrosphere (groundwater table, river water level fluctuation), the biosphere (tree characteristics), and the anthroposphere (dike construction). Carbon sequestration in aboveground biomass of riparian *Quercus robur* L. and *Fraxinus excelsior* L. was modeled (1) over time using boosted regression tree analysis (BRT) on cross-datable trees characterized by equal annual growth ring patterns and (2) across space using a subsequent classification and regression tree analysis (CART) on cross-datable and not cross-datable trees. While C sequestration of cross-datable *Q. robur* responded to precipitation and temperature, cross-datable *F. excelsior* also responded to a low Danube river water level. However, CART revealed that C sequestration over time is governed by tree height and parameters that vary over space (magnitude of fluctuation in the groundwater table, vertical distance to mean river water level, and longitudinal distance to upstream end of the study area). Thus, a uniform response to climatic drivers of aboveground C sequestration in *Q. robur* was only detectable in trees of an intermediate height class and in taller trees (>21.8 m) on sites where the groundwater table fluctuated little (≤0.9 m). The detection of climatic drivers and the river water level in *F. excelsior* depended on sites at lower altitudes above the mean river water level (≤2.7 m) and along a less dynamic downstream section of the study area. Our approach indicates unexploited opportunities of understanding the interplay of different environmental

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drivers in aboveground C sequestration. Results may support species-specific and locally adapted forest management plans to increase carbon dioxide sequestration from the atmosphere in trees.

1. Introduction

Organic carbon (C) sequestration in aboveground biomass of forests is an important ecosystem function that can compensate for human-induced carbon dioxide emissions into the atmosphere (IPCC, 2007). Forests and wetlands store most of the terrestrial ecosystems' carbon. With a cover of 31% of the total Earth's land area (FAO, 2010), forests globally store approximately 861 Pg C (soil C pool to 1 m depth included) and are estimated to sequester 2.4 Pg C annually (Pan et al., 2011). Wetlands store about 20–30% of the global non-marine C (Bridgham et al., 2006; Mitsch et al., 2013), although they cover only 4–6% of the terrestrial Earth's surface (Mitra et al., 2005). Riparian forests at the interface between aquatic and terrestrial ecosystems exhibit an even greater potential for C sequestration and storage capacity than terrestrial forests (Naiman and Décamps, 1997) as a consequence of their reduced water deficit, optimal nutrient supply, e.g., phosphorus availability (Wright et al., 2001), input of C-enriched sediments (Cabezas and Comín, 2010; Rieger et al., 2014), and stabilization of allochthonous and autochthonous C due to the burial of topsoil material (Graf-Rosenfellner et al., 2016) and frequently wetter soil conditions (Sutfin et al., 2016).

The mechanisms of carbon storage in riparian forests depend on the spatial context (Cierjacks et al., 2011; Wohl et al., 2012). Furthermore, forest management is important for carbon storage (Beckman and Wohl, 2014; Ruffing et al., 2016) and for fostering the potential of existing forests to sequester carbon dioxide from the atmosphere. Much of the discussion in the forest sector concerning adequate forest management to mitigate climate change is related to the question of whether to harvest trees or not (IPCC, 2007). However, the limited knowledge on the conditions trees require for increasing C sequestration in aboveground biomass counteracts reliable forest management decisions (Bellassen and Luyssaert, 2014). This is aggravated by the fact that forest communities are often composed of different tree species with diverging environmental demands. Hence, a better understanding of the environmental drivers that influence individual tree growth and related C sequestration in aboveground biomass in different species may be of pivotal importance as it can provide the basis for locally adapted forest management plans to mitigate global climate change.

Annual C sequestration in aboveground biomass through net primary productivity is the main process of building up aboveground C stocks and may provide important insights into the C storage of ecosystems (Megonigal et al., 1997). It can be assessed either prospectively by measuring trunk diameter growth in trees over time (e.g., Rieger et al., 2015) or retrospectively by analyzing patterns in tree-ring growth (dendrochronology). Dendrochronological studies have been carried out in rather homogeneous forest ecosystems with low productivity, e.g., in forested tundra or taiga (Berner et al., 2013; Knorre et al., 2006; Stegen et al., 2011). In contrast, dendrochronological approaches considering highly productive and heterogeneous riparian forests are scarce, presumably due to the complexity of these ecosystems. Moreover, most tree-ring-based studies rely on the response of tree-ring width to climatic parameters that vary over time such as for climate reconstructions or climate response (Hughes, 2002). Although Pichancourt et al. (2014) recently emphasized the relevance of both climate and landscape position on aboveground C sequestration in forests, other environmental measures such as soil and hydrological conditions or competition between species are more commonly addressed as random noise in dendroecological studies rather than as predictors of C sequestration. Previous studies suggest that C sequestration and pools in floodplains can be affected by a range of environmental variables including landscape controls (i.e., geologic setting and biomes), local controls (i.e., valley and channel geometry as well as biotic influences), and human influences such as flow regulation (for a review, see Sutfin et al., 2016). Consequently, the environmental setting that controls C dynamics is highly variable over space and time: (1) Carbon dynamics depend on the lateral, vertical, and longitudinal position of floodplain forests within the hydrosystem (Cierjacks et al., 2010; Rieger et al., 2015, 2014, 2013). (2) Carbon dynamics are subjected to hydrogeomorphological processes that vary over time such as periodic flooding, which, regarding its strength, frequency, and duration, can lead to altered tree productivity and tree mortality, thus changing the forest stand structure and altering C sequestration patterns (Gloor et al., 2009; Predick et al., 2009). (3) Water engineering measures such as dike construction, groundwater pumping, or stream straightening (Anderson et al., 2008; Predick et al., 2009; Scott et al., 1999) often add to the natural complexity of floodplains. Finally, (4) tree species-specific responses to environmental conditions may also affect productivity and C sequestration in riparian systems as has been emphasized in terrestrial forests by Babst et al. (2013, 2012a). Overall, C sequestration in riparian forests reflects a complex pattern of responses to all these environmental drivers that vary in time (e.g., climate and river water level) and space (e.g., distance to the river, distance to the groundwater table, competition between trees) and that are individual tree- and species-specific.

The complex conditions within riparian forests force some tree individuals of a population to grow at the fringe of the species' individual ecological amplitude which make them more sensitive to environmental changes—while others in their vicinity may remain less affected. These differences in the response of individual trees and species in riparian forests at the small scale often mirror environmental gradients at a larger scale. Thus, we selected a highly productive and dynamic floodplain forest as a model ecosystem to test a new dendrochronological approach that aims to integrate environmental variables, which influence annual C sequestration in aboveground biomass of forest trees across time and space.

The traditional focus of dendrochronology relates to climate reconstructions and climate response. Dendroclimatological studies use those trees which show a climatic signal in their tree-ring growth patterns to reconstruct past climatic conditions, basing on the uniformitarian principle, e.g., that trees reacted to climate in the past as they react in the present (Fritts, 2001). For example, studied forest populations are often located at the margin of their climatic ecological amplitude (see Schweingruber, 1988) and are rather homogeneous in terms of tree age, forest structure, and social status. The studies also share a common classic sampling design, with a focus on at least 20 dominant, large and presumably old trees of the same species, without signs of damage and disease (Schweingruber et al., 1990). However, this study design does not account for other important parameters that influence C sequestration such as tree height or even diameter (Babst et al., 2012b; Cherubini et al., 1998) and is prone to errors as the "big-tree selection bias" (Brienen et al., 2012). The homogenization of site- and tree-specific characteristics allows for the isolation of a clear climate signal in cross-datable trees, assigning each tree ring of different tree individuals to a specific calendar year based on similar patterns in ring widths; at the same time, the results are essentially restricted to what can be deduced from these limited measures.

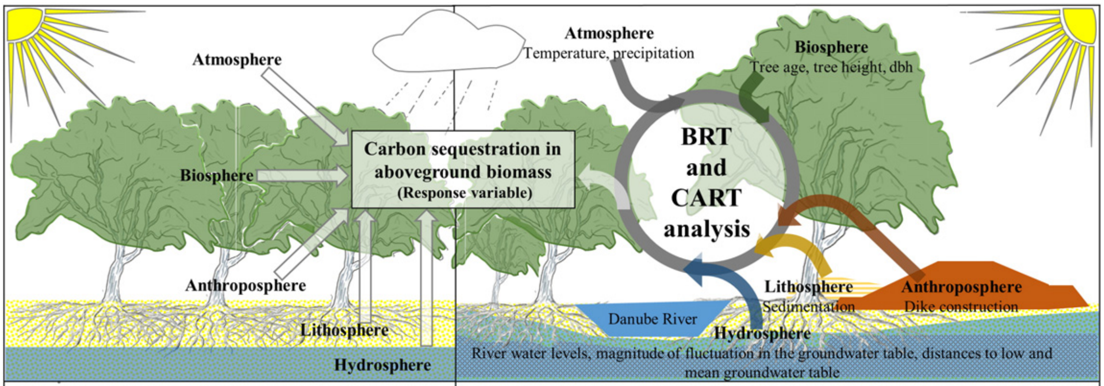
Yet the question of why some tree individuals are cross-datable, while others show a divergent tree-ring response over the same period of time has not been studied to date. These different responses may offer an opportunity to obtain further information on tree- or species-specific traits as well as on local spatial drivers of C sequestration in aboveground biomass. For these reasons, there remain further opportunities to use dendrochronology for modeling C sequestration in aboveground biomass of highly productive, heterogeneous forest ecosystems. To fully exploit such opportunities and to allow for a stepwise detection of environmental drivers of C sequestration in aboveground biomass that vary across time and space, the classic sampling design was adapted (Fig. 1). In this study, C sequestration refers to annual aboveground biomass growth of pedunculate oak (*Quercus robur* L.) and common ash (*Fraxinus excelsior* L.) based on the retrospective measurement of annual tree ring widths. We explicitly involved dominant, co-dominant, and suppressed floodplain trees as well as the rarely considered sub-group of trees presenting unequal C sequestration pattern in their rings among each other (not cross-datable group) compared to the cross-dated group. Accordingly, we set up a tree-specific and spatially randomized study design, performed a multiple boosted regression tree analysis (BRT) of cross-datable trees, and carried out a classification and regression tree (CART) analysis. The BRT allows drivers that vary over time to be detected in the cross-dated group; the CART detects local site- and species-specific drivers of C sequestration that separate cross-datable groups of trees from those that are not cross-datable. In particular, we aimed at better understanding the functioning (1) of changing climatic and flooding parameters in a riparian forest that vary over time and (2) of other factors limiting C sequestration in aboveground biomass that are related to varying local environmental factors and the respective major tree species. We hypothesize that in temperate riparian forests (1) C sequestration in aboveground biomass of *F. excelsior* and *Q. robur* is affected by variables that vary over time such as climatic and river water level parameters, and that (2) C sequestration in aboveground biomass of both species influenced by variables in time is modulated by limiting local spatial parameters and tree specific factors.

2. Methods and materials

2.1. Study area

The study area is part of the Donau-Auen National Park in Austria (Fig. 2), located between Vienna and Bratislava along the Danube River. The National Park was established in 1996 and is certified in accordance with the IUCN as a Riverine Wetlands National Park, category II; it protects one of the largest remaining riparian forests (approximately 6000 ha) in Central Europe. The western limit of the study area was the village Schönau at river kilometer 1910 (48°8′N, 16°36′E), and the eastern limit was located near the village Stopfenreuth at river kilometer 1889 (48°1′N, 16°88′E). Along this section, the Danube River is still free flowing and inundates large areas during high water levels (>5.5 m), although a part of the area has been protected from surface flooding since the construction of the Marchfeld dike in 1905.

Flooding events and hydrogeomorphological processes have created a complex mosaic of micro sites and thus a high variety of habitats for different plant species. Currently, the Donau-Auen National Park hosts >800 different vascular plants (Donau-Auen National Park, 2016) including 26 different woody plant species, i.e., *Acer campestre, Acer negundo, Acer pseudoplatanus, Ailanthus altissima, Alnus incana, Carpinus betulus, Clematis vitalba, Cornus sanguinea, Coryllus avellana, Crataegus monogyna, Fraxinus excelsior, Juglans regia, Malus sylvestris, Populus alba, Populus × canadensis, Populus nigra, Prunus padus, Quercus robur, Robinia pseudoacacia, Salix alba, Sambucus nigra, Tilia cordata, T. platyphyllos, Ulmus glabra, Ulmus laevis, and Ulmus minor* (forest stand diversity data according to studied dendrochronological plots based on the angle count sampling method). The riparian cottonwood forest is a vegetation type which is generally found close to the main and side river channels, both on sand and gravel aggradations and on sites with high groundwater levels and clayey sediment layers. These mixed forest stands are mainly composed of *Populus alba, Populus nigra*, and *Salix alba* (Drescher and Fraissl, 2006). *Quercus robur* and *Fraxinus excelsior* represent the main tree species of a second riparian forest vegetation type characterized by less morphodynamic conditions in terms of strength and frequency of sedimentation, erosion, and inundation (Drescher and Fraissl, 2006). Forestry activities have been banned since the establishment of the National Park (Austria's Federal Law; Art. 15a, B-VG). Extensive poplar plantations (*Populus × canadensis*) are still interspersed within both types of natural forests and prevail south of the Danube River. In other areas, *Populus alba* was planted after clear-cutting, resulting in pure stands of this species (Drescher and Fraissl, 2006). Recent studies on aboveground C stocks in the same study area with 123 (Rieger et al., 2013) and 202 t C ha^{-1} in average (Cierjacks et al., 2011) indicate a high productivity of the Danubian riparian forest since C stocks clearly exceed those of temperate upland forests in Germany with 110, 105, 93, and 67 t C ha^{-1} in *Fagus*, *Quercus*, *Picea*, and *Pinus* forests,



Common dendrochronological approach	**Extended dendrochronological approach**
➢ Site conditions: • Homogeneous site conditions (e.g., one-age-cohort forest)	➢ Site conditions: • Heterogeneous site conditions (i.e., riparian forest)
➢ Study design: • Non-randomized study design • Dominant and healthy trees • Cross-datable trees only	➢ Study design: • Randomized study design • Trees of all sociological classes (dominant, co-dominant, suppressed etc.) • Cross- and not-cross-datable trees
➢ Drivers: • Drivers of anthroposphere **or** atmosphere **or** lithosphere **or** hydrosphere **or** biosphere and its influence on carbon sequestration in trees	➢ Drivers: • Drivers of anthroposphere **and** atmosphere **and** lithosphere **and** hydrosphere **and** biosphere
➢ Statistics: • Mainly correlation analysis	➢ Statistics: • Boosted regression trees (BRTs) to reveal temporal drivers (e.g., climate, flooding) and classification and regression trees (CARTs) to reveal local site-specific drivers (e.g., groundwater table parameters, spatial parameters, tree traits…)

Fig. 1. Common and proposed extended dendrochronological approach: A comparison regarding site conditions, study design, environmental drivers, and statistical analyses.

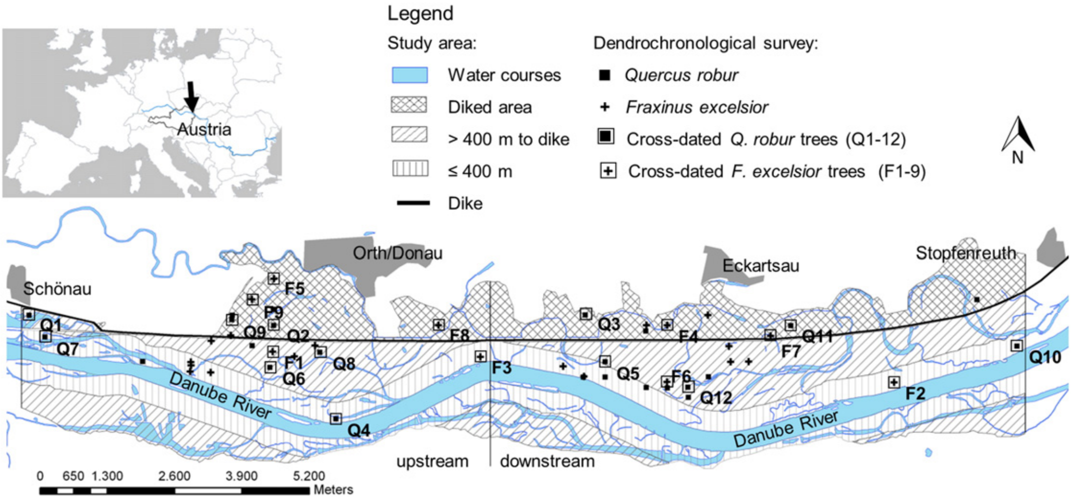


Fig. 2. Study area and dendrochronological survey of sampled *Quercus robur* and *Fraxinus excelsior* within the Donau-Auen National Park in Austria.

respectively (Wördehoff et al. 2012). Compared to other biomes in the world, aboveground C stocks of the Danubian riparian forest were only exceeded by tropical forests (216 t C ha^{-1}), whereas C stocks of temperate forests, boreal forests, tundra, croplands, tropical savannas, temperate grasslands, desert/semideserts, and wetlands were 100, 116, 12, 4, 52, 12, 4, and 76 t C ha^{-1} (Gorte, 2009). Even in comparison with aboveground C stocks of riparian forests in the world, carbon stock in our study area rather belongs to the above average part of the range documented by Sutfin et al. (2016). The increased C stocks in our study area can be attributed to a high C sequestration rate in aboveground biomass which was estimated to 4 t C ha^{-1} y^{-1} (Rieger, 2014b) and is thus about twofold higher than C sequestration in aboveground biomass of Germany's terrestrial forests with about 1.8 t C ha^{-1} y^{-1} (Wutzler et al., 2011; Dunger et al., 2009). Soil types vary from rambla to eutric calcaric fluvisols and haplic calcaric gleysols (Cierjacks et al., 2010; Sali-Bazze, 1981). The meteorological station at Schwechat (48°7′N, 16°34′E, 184 m asl) reports 9.8 °C as the mean annual temperature and 533 mm as the mean annual precipitation for the period between 1948 and 2008 (Zentralanstalt für Meteorologie and Geodynamik, 2002).

The Donau-Auen National Park is located within a subwatershed that covers an area of 104,000 km^2. The river channel averages 350 m in width with a slope of 0.043%. Mean surface water flow velocities range from 1.9 to 2.2 m s^{-1}. Within the study area, the Danube River has a mean annual discharge of 1950 m^3 s^{-1} which increases to 5270 m^3 s^{-1} during once-yearly flooding events (Tockner et al., 1998).

2.2. Dendrochronological study design

For several reasons, classic dendrochronological sampling is not applicable to dynamic and heterogeneous ecosystems such as riparian forests: (1) The complex mosaic of site conditions within riparian forests clearly limits the existence of homogeneous sites with a sufficient number of tree individuals of the same species. (2) Compared to tree species in mountainous regions, temperate floodplain forest species are usually at their optimum in terms of nutrient and water supply (Ellenberg et al., 2010). This makes it difficult to isolate a uniform growth response to these factors, and therefore may complicate cross-dating. (3) Riparian trees react individually to environmental parameters that vary annually, such as temperature, precipitation, and flooding, but also to parameters that are stable and related to the site's position within the hydrosystem or to river engineering measures such as dike construction.

In order to avoid the “big-tree selection bias” (Brienen et al., 2012) and to account for the fact that the largest trees have likely changed their competitive status over their lifetimes, which can lead to overestimates of growth rates (Brienen et al., 2012; Cherubini et al., 1998, 1999), we applied a randomized dendrochronological sampling design and included all diameter classes of the population as proposed by Nehrbass-Ahles et al. (2014). Because our approach aims to detect not only climatic drivers but also spatial gradients and tree traits such as tree height or the diameter at breast height (DBH) as predictors of C sequestration in aboveground biomass, we avoided standardization techniques. These techniques are commonly used for climate reconstructions, such as detrending, which removes the age-related or non-climatic trends from tree-ring data (Briffa et al., 1996).

As study species, we selected *Q. robur*, and *F. excelsior*. These are among the most abundant woody species colonizing less morphodynamic sites in the National Park. The timber stock of these species represent about 3 and 14% of the total timber stock in the Donau-Auen National Park (Posch, 1999) with *Q. robur* ranked at the sixth position and *F. excelsior* at the third position among all tree species in the Donau-Auen National Park. The timber stock of the studied tree species was surpassed only by tree species of the cottonwood forest type (*Populus alba*, *Populus* × *canadensis*, *Populus nigra*, *Salix* spec.) which were not amenable to the analyses due to predominantly rotten cores.

To cover a broad range of *Q. robur* and *F. excelsior* sites in terms of flooding duration and frequency, groundwater depth, and distance to the Danube River and the nearest side channel, the whole study area was divided into three lateral zones. One lateral zone covered a 400 m strip parallel to the northern Danube River shore, the second zone covered the area from the 400 m border to the Marchfeld dike, and the third zone included the area of the diked floodplain forest where overbank flooding is excluded (Fig. 2). The lateral zones were further divided into two longitudinal zones (upstream: east of the village Orth/Donau; downstream, south and west from Orth/Donau; Fig. 2). Within each of the six resulting zones, we randomly selected four sample trees of both *Q. robur* and *F. excelsior* from the National Park's forest inventory database based on a 100 × 400 m grid (6 zones × 4 trees × 2 species = 48 cores, plus one additional *F. excelsior* tree). To consider both young and old individuals, two of the four sample trees had a DBH of 12–20 cm, and two had a DBH >20 cm. Cores were taken in February 2010 at breast height and from the trunk side that faces away from the prevailing wind and water flow direction to avoid reaction wood. An increment borer (Suunto®) 0.5 cm in diameter was used. We took a second core of the same tree in November 2010 to facilitate cross-dating.

Cores were air-dried and fixed on a profiled batten. In January and February 2012, cores were transferred to the laboratories and prepared for tree-ring measurement using a core microtome (Gärtner and Nievergelt, 2010) to ensure a smooth, dust-free surface. Tree-ring widths were measured to the nearest 0.01 mm on a measuring table

LINTAB™. Record-keeping, graphical analysis, and statistical cross-dating of tree-ring series (based on the correlation value Gleichläufigkeit >60% and the significance level of the correlation $P < 0.05$) were performed with the software package TSAP-Win™ Professional 4.68 (Frank Rinn, Heidelberg, Germany). To facilitate the modeling of responses to climatic and flooding parameters, mean raw ring chronology of cross-dated tree-ring series was determined for the time period between 1940 and 2008.

Based on the tree-ring widths and the DBH at the time of coring, historic DBHs for each calendar year were computed backwards to the first tree-ring formed at DBH. The DBH values were used to assess the biomass for each calendar year based on allometric equations (Table 1) for *F. excelsior* and *Q. robur* (Zianis et al., 2005). Following Giese et al. (2003), biomass values were multiplied by 0.5 to derive the tree's C stocks for each year, and, in the final step, these values were transformed into annual carbon sequestration rates in aboveground biomass as the difference between two consecutive years.

2.3. Variation in time: Climate and river water levels

Climate (precipitation, temperature) and river water levels were included as the two parameters that varied significantly over time. Long-term monthly temperature and precipitation data (1940–2008) were derived from the climate station Vienna–Hohe Warte (48°25′N, 16° 36′E, 209 m asl; provided by Zentralanstalt für Meteorologie und Geodynamik, 2002).

Both processes, changing river water levels and groundwater tables, influence soil saturation. However, the predominant process in the study area is groundwater exfiltration in the Danube River. Only particularly high river water levels, which occur for a short time, are able to induce a brief infiltration of river water (up to two days, Derx et al., 2010) and thus an increase of the groundwater table and soil saturation. In contrast, groundwater-related hydrological variables at a specific location in the hydrosystem are assumed to be rather constant over time. Data on river water level were obtained from the water level monitoring station Fischamend (48°07′N, 16°38′E; provided by via donau-Österreichische Wasserstraßen-Gesellschaft mbH, 2012). These data covered the longest time period and are less affected by impoundments than water level data from other monitoring stations. River levels were measured daily at 7 am for the period 1940–2008.

Except for two years (1943, 1944), river water level records are complete. Our raw-ring chronology covered a shortened time period (1940–2008) to reduce the effects of river incision from channelization, water hydropower stations, artificial levees or groundwater pumping stations in the upstream watershed (Hohensinner et al., 2005, 2011) on the water level data. Based on processed data of river water levels, we studied the influence of different water levels as days per year above or below a given river water level (altitude asl) at the monitoring station Fischamend in the year 2010 (for an overview of the river water level parameters and abbreviations, see Table 2).

2.4. Variation in space: Hydrology, stand structure, tree traits

The position of each sample tree was determined as exactly as possible (<10 cm) within the hydrosystem of the floodplain before foliation in the year 2010 using a handheld GPS (Trimble GeoXH™ 2005 series). The position was expressed in terms of the lateral gradient (distances to the Danube River and the next side channel) and the longitudinal gradient (distance to the upstream beginning of the study area in Schönau: 48°8′N, 16°36′E) with the help of digital maps from the Donau-Auen National Park (ArcInfo in ArcGIS 9.2; for more details, see Rieger et al., 2014, 2013). In addition, we recorded whether the location of each sample tree is diked or not. Doing so, we were able to evaluate the influence of surface flooding on C sequestration in aboveground biomass. The position relative to the vertical gradient of the hydrosystem was analyzed using the distances to the low/mean groundwater levels, the magnitude of fluctuation between low and mean groundwater level, and in terms of the height above the mean river water level. Location data were ultimately determined by combining (1) position data (Gauß-Krüger coordinates of each sample tree), (2) a digital elevation model, (3) altitudes asl of mean river water level (both provided by via donau–Österreichische Wasserstraßen-Gesellschaft mbH) and (4) a groundwater model (provided by Vienna University of Technology; see Rieger et al., 2013, 2014 for details on assessing hydrological gradients). Furthermore, we determined the rate of sedimentation by relating tree age to the depth of the trunk base burial (for more details please see Rieger et al., 2014a).

The forest stand structure in the neighborhood of the sample tree was measured using the angle count sampling method (Kramer et al., 1988; Rieger et al., 2013). With the sample tree in the middle, we determined DBH, height, sociological status, and vitality of all trees and shrubs included in the sample circles. According to Roloff (2001), each tree was grouped into one of the following vitality classes: exploratory phase (tree without signs of damage, none or very little dead wood), degeneration phase (tree weakened, little deadwood), stagnation phase (clearly damaged tree, increased deadwood). The DBH was calculated based on the circumference determined by a measuring tape. Height was assessed trigonometrically using a BLUME-LEISS BL 6 altimeter. The social status of each tree was classified as predominant, dominant, slightly dominant, dominated, or suppressed (tree classes by Burschel and Huss, 2003).

2.5. Statistical analyses

Following Zuur et al. (2010), data were explored descriptively before modeling. The initial set of continuous and independent predictor variables comprised monthly temperature and precipitation means for each growth year and the previous year and eight flooding parameters divided into growing and dormant seasons. All variables were tested for normality (Shapiro-Wilk test) and homogeneity of variance (Fligner test). Because of intern model restrictions and for a sound interpretation of the relative influence of each predictor variable remaining in the final boosted regression tree model (BRT), we reduced the initial number of predictor variables by detecting collinearity (VIF values) between them. We then eliminated the predictor variable which correlated least with C sequestration in aboveground biomass. This procedure led to the exclusion of 17 temperature and 9 precipitation variables out of 48 monthly means from the whole data set due to collinearity. The finally considered predictor variables separated by model type are shown in Table 3.

In floodplain forests, C sequestration of aboveground biomass is expected to depend both on parameters variable over time such as climate and flooding and on site-specific conditions that are highly variable in space. To determine the most relevant time-dependent variables

Table 1
Allometric equations for *Fraxinus excelsior* and *Quercus robur* used for biomass calculations in the study area (Abbreviations: AB = aboveground biomass, ABW = aboveground woody biomass, DBH = diameter at breast height, Z = Zianis et al. (2005), App. = Appendix).

Species	Equation	Units of			Reference
		AB	ABW	DBH	
Fraxinus excelsior	$\ln(ABW) = -2.4598 + 2.4882 \times \ln(DBH)$		[kg]	[cm]	Z, App. A, #134
Quercus robur	$\ln(AB) = (-0.883) + 2.14 \times \ln(DBH)$	[kg]		[cm]	Z, App. A, #600

Table 2
River water levels used to describe the flooding intensity of the Danube River at the monitoring station Fischamend, Austria (KWD 2010 refers to the reference via donau-Österreichische Wasserstraßen-Gesellschaft mbH, 2012).

Status	Definition	River water level, Fischamend [altitude m asl]	Reference
RNW	River water level that is exceeded 94% of the year (ca. 343 days)	146.08	KWD 2010
MW	Mean river water level	147.55	KWD 2010
HSW	River water level that is exceeded 1% of the year (ca. 3.6 days); corresponds approximately to the bankfull discharge, highest navigable water level	150.51	KWD 2010
HW30	30-year river water level event; corresponds to area-wide surface flooding	153.25	KWD 2010

(temperature, precipitation, and flooding parameters), we used the mean chronology of C sequestration in aboveground biomass of the cross-dated carbon growth rate series and applied a BRT analysis. In contrast to classic dendrochronological approaches that often rely on correlation analysis, BRT is based on decision tree analysis and shows improved predictive power due to the technique of boosting (Elith et al., 2008; Schapire, 2003). Furthermore, BRT is a multiple analysis that is rather robust in terms of outliers; distribution of the response variable, e.g., Gaussian, Poisson, binomial; missing values or different data types in the predictor variables, e.g., numeric, categorical data. The results can be easily interpreted as each predictor is ranked against the others, and the partial dependence of C sequestration in aboveground biomass regarding the individual predictor variables remaining in the final model is plotted (Elith et al., 2008). Since tree age did show a significant influence on C sequestration in a pre-analysis overlaying the relative influence of all other climatic and flooding variables, we excluded tree age as a predictor variable from BRT analysis but not from CART analysis. In summary, BRT analysis offers the advantage of both estimating the predictive power of the model and to facilitate model interpretation with collinearity among predictor variables explicitly addressed as opposed to repeated correlation analysis of each climatic variable.

In a second step, we related spatial, site-related drivers (position along spatial gradients, sedimentation rate, dike construction, hydrology, forest stand parameters, and sample tree traits such as DBH, tree height, tree age, social status, and vitality) to the two classes of sample trees (cross-dated vs. not cross-datable) using classification and regression trees (CART; Breiman, 1993). This method provides the best prediction success compared to logistic multiple regression, generalized linear models, or principal component regression (Muñoz and Felicísimo, 2004). Furthermore, CART handles categorical response variables (cross-datable and not cross-datable trees) as well as predictor variables characterized by the absence of normality and rather nonlinear relationships to the response (De'ath and Fabricius, 2000). Classification and regression trees yield decision trees by repeated binary splits at

Table 3
Response and predictor variables used for modeling C sequestration in aboveground biomass of *Quercus robur* and *Fraxinus excelsior* (BRT = Boosted regression tree model, CART = Classification and regression tree model, ABM = Aboveground biomass, Abbreviations and meaning of flooding parameters according to Table 2).

Models	Response variables	Predictor variables
BRT	Mean annual C sequestration in ABM of cross-datable individuals of: — *Quercus robur* (n = 12) — *Fraxinus excelsior* (n = 9)	Climatic parameters — Mean monthly temperatures of the present year (Feb., Oct., Nov., Dec.) — Mean monthly temperatures of the previous year (Aug., Nov., Dec.) — Monthly precipitation of the present year (Feb., Mar., May., Jul., Sep., Oct., Nov.) — Monthly precipitation of the previous year (Feb., Mar., Apr., May, Jul., Sep., Oct., Nov.) Flooding parameters — RNW growing season (Apr.–Oct.) — RNW dormant season (Nov.–Mar.) — HSW growing season (Apr.–Oct.) — HSW dormant season (Nov.–Mar.) — HW30 growing season (Apr.–Oct.) — HW30 dormant season (Nov.–Mar.)
CART	Cross-datable vs. not cross-datable individuals of: — *Quercus robur* (n = 24) — *Fraxinus excelsior* (n = 25)	Spatial parameters — Distance to Danube River — Distance to next side channel — Longitudinal distance Hydrological parameters — Distances to low/mean groundwater level — Magnitude of fluctuation between low and mean groundwater level — Height above mean river water level Rate of sedimentation Tree parameters — Diameter at breast height — Tree age — Tree height — Social status — Vitality

explicit threshold values of the respective predictor to increase homogeneity within and heterogeneity between groups (cross-dated vs. not cross-dated trees). These thresholds generate a general prediction rule for cross-datable trees, which can be interpreted as spatial, site-specific limiting drivers homogenizing the ecological response of C sequestration in the cross-dated tree pool in a way that members of the pool respond similarly to annually changing climatic and river water level parameters. To avoid overfitting, proper tree size was estimated by using the cross-validation error estimate. The number of cross-validations (CV) was set to 40 and 30 for *Q. robur* and *F. excelsior*, respectively. All calculations were performed with R version 2.10.0 using the packages AED, brt, car, gbm, gtools, mass, mvpart, and vegan (R Development Core Team, 2011).

3. Results

3.1. Mean ring width and carbon sequestration chronologies

Tree-ring series were successfully cross-dated for 12 cores of *Q. robur* and nine cores of *F. excelsior* (Fig. 2, Table 4). For the cross-dated cores, we built chronologies of both ring width (Fig. 3a) and derived C sequestration in aboveground biomass (Fig. 3b). In the first 30 years of the considered period of time, averaged tree ring width of cross-dated cores were higher for *F. excelsior* than for *Q. robur*. In the early 1970s, tree ring widths of *F. excelsior* first strongly decreased and then remained similar as *Q. robur* tree ring widths in the years from 1994 to 2008 (Fig. 3a). Carbon sequestration pattern in aboveground biomass was reversed with first higher annual rates for *Q. robur* compared to *F. excelsior* until 1970. In subsequent years, both tree species showed similar C sequestration rates in aboveground biomass (Fig. 3b).

Annual C sequestration chronology of aboveground biomass was then used for further BRT modeling. Twelve cores (50%) of *Q. robur* and 16 cores (64%) of *F. excelsior* were not cross-datable as statistical correlation values (Pearson's) were not significant. The generated chronologies of *Q. robur* and *F. excelsior* contained tree-ring series from sites with pronounced ecological differences such as flooded and diked riparian forests. In addition, the spatial distance among the cross-dated sample trees was remarkably high. Maximum, minimum, and average distances between trees were 19.1, 0.5, and 6.9 km for *Q. robur* and 12.5, 0.6, and 5.6 km for *F. excelsior* (Fig. 2).

3.2. Response of carbon sequestration to climate and river water levels

The calculated BRT model of *Q. robur* explained 28% of the overall variance in the response of annual C sequestration in aboveground biomass. Contrary to our expectations, none of the river water levels remained in the ranking of the model's significant predictor variables (Fig. 4). The most important drivers of C sequestration in aboveground biomass were climate variables with precipitation showing a more pronounced correlation (accumulated relative influence: 73%) than temperature (relative impact: 27%; Fig. 4). In particular, *Q. robur* responded to the monthly precipitation in July and September during the present year, and even more clearly to the September precipitation of the previous season. The influence of temperature was limited to the previous dormant season.

A closer look at the response plots (Fig. 4) shows that above average values of C sequestration in aboveground biomass for *Q. robur* were linked to monthly precipitation rates below 50 mm in September of the present and the past growing season and to monthly precipitation rates above ca. 90 mm in July of the present growing season. In addition, C sequestration in aboveground biomass of *Q. robur* was influenced by November temperatures with above average C sequestration when the monthly temperature was below 4 °C. Surface and belowground flooding parameters were ruled out as predictor variables in this model.

The BRT model of *F. excelsior* explained overall 32% of the variation of C sequestration in aboveground biomass. Flooding ranked first of all the significant predictor variables and explained 22% of the total variance in C sequestration of *F. excelsior*, whereas accumulated precipitation and temperature variables accounted for 46 and 32%, respectively (Fig. 5). In terms of river water levels, a longer period of low river water level during the dormant season showed a positive correlation. In addition, September precipitation (20%) and August temperature of the previous year (17%) along with February temperature (15%), March precipitation (13%), and September precipitation of the present year (13%) were positively correlated with annual C sequestration in aboveground biomass of *F. excelsior*.

Table 4
Overview of all cross-dated sample trees used to generate the chronologies of *Quercus robur* (Q1–12) and *Fraxinus excelsior* (F1–9) (abbreviations: GLK, Gleichläufigkeit (year-to-year agreement between the interval trends of tree-ring series as a percentage of cases of agreement); GSL, statistical significance of the GLK: ***99.9%, **99%, *95%; DRF, diked riparian forest; FRF, flooded riparian forest; AVG1–10, cumulative averaged chronology based on the tree ring series of the Tree ID Sample and/or the averaged chronology).

Tree ID sample	Reference	Average	GLK (%)	GSL	Innermost-outermost ring (calendar year)	Location
Q1_711334	Q2_758332	AVG1	78	***	1976–2009	DRF
Q3_818334	AVG1	AVG2	76	***	1910–2009	DRF
Q4_770314	AVG2	AVG3	63	*	1957–2009	FRF
Q5_822325	AVG3	AVG4	81	**	1992–2009	FRF
Q6_757323	AVG4	AVG5	75	**	1985–2010	FRF
Q7_7143301	AVG5	AVG6	66	*	1971–2010	FRF
Q8_767327	AVG6	AVG7	84	***	1990–2010	FRF
Q9_750333	AVG7	AVG8	85	***	1981–2009	DRF
Q10_902328	AVG8	AVG9	64	**	1903–2010	FRF
Q11_858332	AVG9	AVG10	61	**	1850–2011	DRF
Q12_838320	AVG10		71	*	1991–2009	FRF
F1_758327	AVG1		83	***	1943–2009	FRF
F2_878321	AVG1		62	*	1952–2009	FRF
F3_798326	AVG1		74	***	1940–2009	FRF
F4_834332	AVG1		85	***	1947–2009	DRF
F5_758341	AVG1		70	***	1949–2009	DRF
F6_834321	AVG1		73	***	1967–2009	FRF
F7_854330	AVG1	AVG2	90	***	1955–2009	DRF
F8_790332	AVG2	AVG3	80	***	1983–2009	DRF
F9_754337	AVG3		74	**	1983–2009	DRF

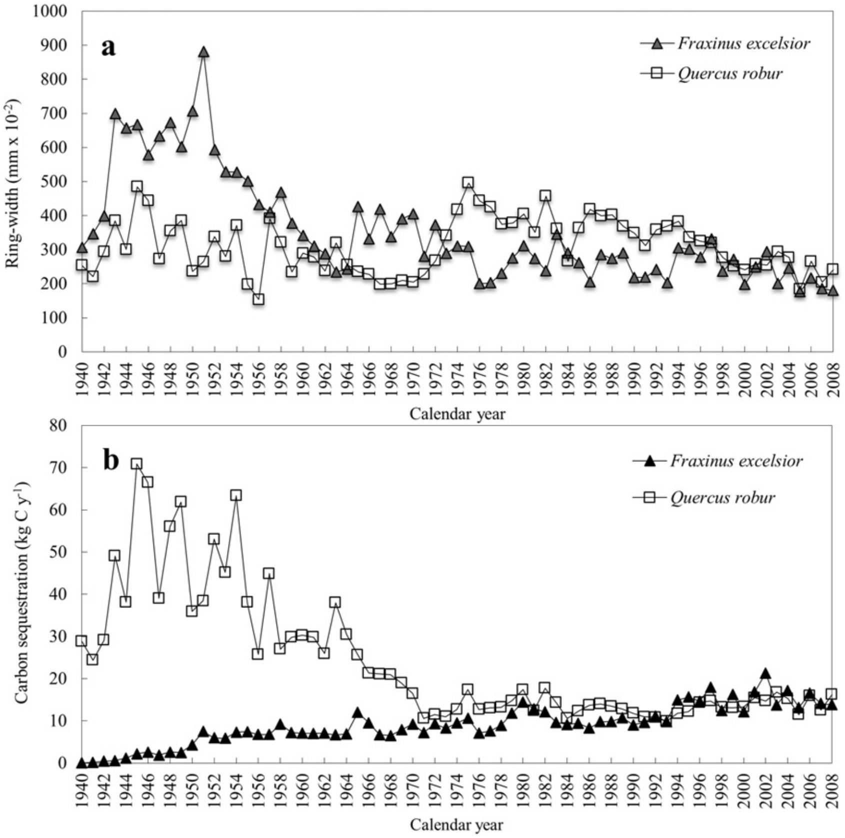


Fig. 3. (a) Mean ring-width and (b) carbon sequestration in aboveground biomass chronologies of *Quercus robur* (tree-ring series n = 12) and *Fraxinus excelsior* (tree-ring series n = 9) in the Danube floodplain forest.

The fitted functions indicate that C sequestration of aboveground biomass was below average in years when the river water level during the dormant season was low for fewer than 8 days, i.e., more C was sequestered under drier conditions (Fig. 5). In contrast, C sequestration of aboveground biomass of *F. excelsior* exhibited above average values when September precipitation was above 40 mm, August temperatures

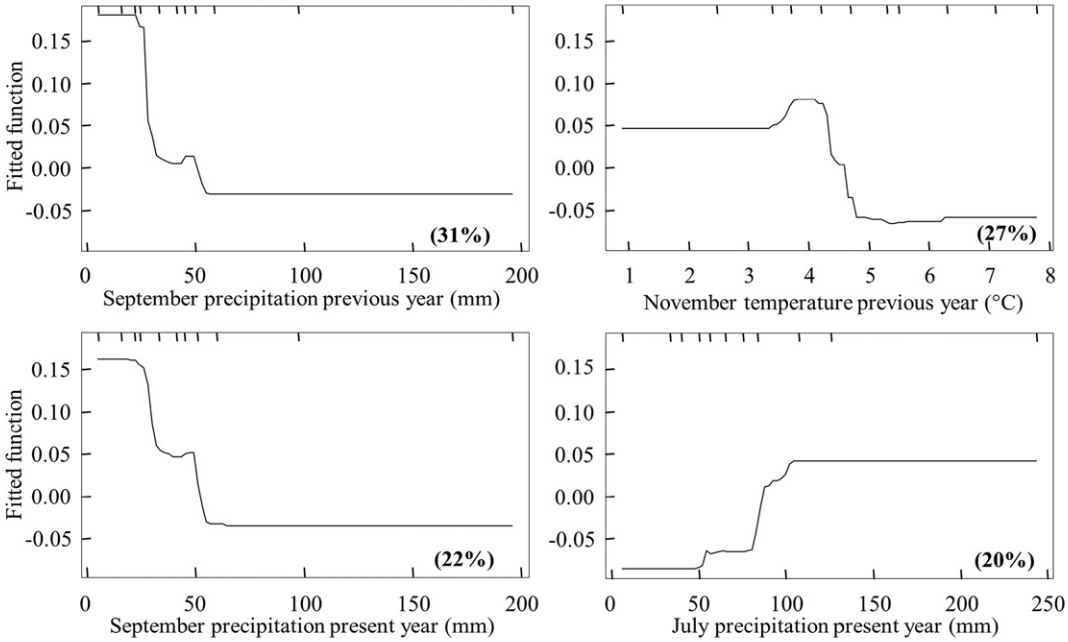


Fig. 4. Relative influence (%) and partial responses (fitted function) of the most influential variables in the BRT model for carbon sequestration in aboveground biomass of *Quercus robur* (model documentation: explained variance: 28%, CV correlation: 0.33, CV correlation (se): 0.11; see Table A.1 for further information).

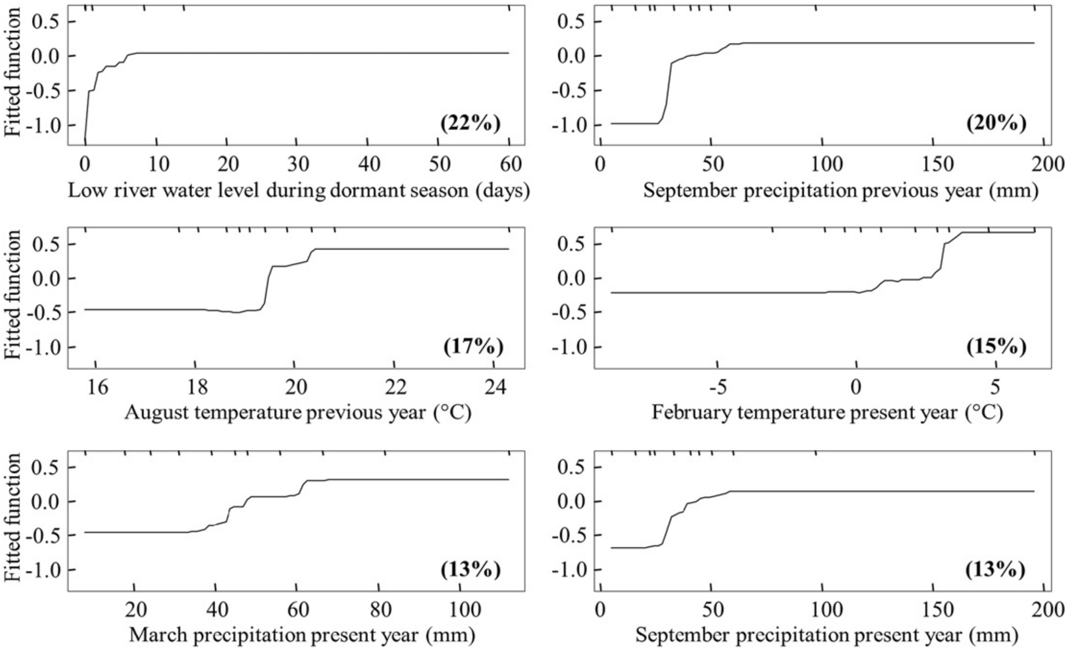


Fig. 5. Relative influence (%) and partial responses (fitted function) for the most influential variables in the BRT model for annual carbon sequestration in aboveground biomass of *Fraxinus excelsior* (model documentation: explained variance: 32%, CV correlation: 0.40, CV correlation (se): 0.12; see Table A.1 for further information).

of the previous year were above 19 °C, February temperatures were above 4 °C, March precipitation was above 50 mm, and September precipitation of the present year was above 50 mm.

3.3. The influence of spatial environmental drivers

CART analysis of cross-dated and not cross-dated trees revealed site-specific parameters that homogenize C sequestration in aboveground biomass and hence lead to a cross-datable subset of spatially independent sample trees. The nodes of the regression trees can be interpreted as environmental thresholds of local site-specific drivers that reduce the variability in C sequestration of the cross-dated tree pool such that the trees in each group respond similarly to changing parameters in time. Consequently, our approach allows for growth-limiting factors that are not variable in time, but that reflect static conditions at a given location to be detected and quantified in dendrochronological data sets.

As indicated by the classification tree (Fig. 6), tree height and the magnitude of fluctuation in the groundwater table are the most decisive tree- and site-specific explanatory variables to differentiate between the cross-datable and not cross-datable *Q. robur* individuals. The highest branching level of the regression tree indicates that all trees <13.5 m in height could not be cross-dated due to heterogeneous rates of C sequestration in aboveground biomass. In contrast, most *Q. robur* individuals 13.5–21.8 m in height belonged to the cross-dated group. In addition, trees ≥21.8 m in height could be cross-dated if the magnitude of fluctuation in the groundwater table was <0.9 m. At drier sites with a more pronounced groundwater fluctuation (≥0.9 m), the majority of sampled *Q. robur* could not be cross-dated (n = 7; Fig. 6). These trees showed clearly different sequences of annual tree ring widths and thus annual C sequestration pattern in aboveground biomass compared to the cross-datable *Q. robur* pool. The misclassification rate of the whole classification tree was very low: 8% (2 of 24 individuals) compared to 50% in the null model. In addition, the prediction of the two cross-dated clusters was quite successful. Thus, 67% of the cross-dated *Q. robur* were between 13.5 and 21.8 m in height (8 of 12 individuals) and 25% of the individuals were ≥21.8 m tall (4 of 12 individuals) and growing on sites where the groundwater table fluctuated by <0.9 m (Fig. 6).

The classification tree for *F. excelsior* highlighted the relevance of the vertical and longitudinal gradients for C sequestration in aboveground biomass of this species. In particular, tree individuals located at an altitude of ≥2.7 m above the mean river water level could not be cross-dated. In contrast, the cross-dated trees were found in sites <2.7 m above the mean river level or ≥4269 m from the upstream study boundary. Trees closer to the upstream boundary were again not cross-datable (Fig. 7). As shown for *Q. robur*, the misclassification rate of the *F. excelsior* model was low (8%; 2 of 25 individuals), and the prediction level for the cross-dated group was 100%.

4. Discussion

This study presents a novel methodology based on random dendrochronological sampling for modeling C sequestration in aboveground biomass as a highly relevant ecosystem function of temperate forests. We illustrate that dendrochronological approaches may also be applicable in heterogeneous ecosystems such as temperate riparian forests where trees grow at their ecological optimum in terms of water and nutrient supply. The BRT models relying on cross-dated tree individuals revealed that C sequestration in aboveground biomass of riparian tree species responded in different ways to river water level, temperature, and precipitation which act over time. However, in a random tree sample, these river water level- and climate-induced limitations on C sequestration in aboveground biomass are exclusively detectable at sites where the ecological amplitude and C sequestration pattern in aboveground biomass of the trees are homogenized and limited by spatial, site-specific drivers. The CART analysis is a technique for reliable determination and estimation of such conditions.

We hence revealed drivers of C sequestration in aboveground biomass of the two major tree species whose vegetation type covers about 30% of the floodplain forest in the Donau-Auen National Park (see Cierjacks et al., 2010; data derived from hardwood forest). Because Cierjacks et al. (2010) did not consider diked floodplain forest (where less dynamic hydrogeomorphological processes prevail), it can be assumed that the percent coverage of the *Q. robur* and *F. excelsior* vegetation type is even higher.

However, albeit including cross-dated and not cross-dated trees, we in total considered only 24 cores of *Q. robur* and *F. excelsior*. Consequently, the sample size of cores in this study is much lower compared to classical dendrochronological studies analyzing more cores, e.g. for the

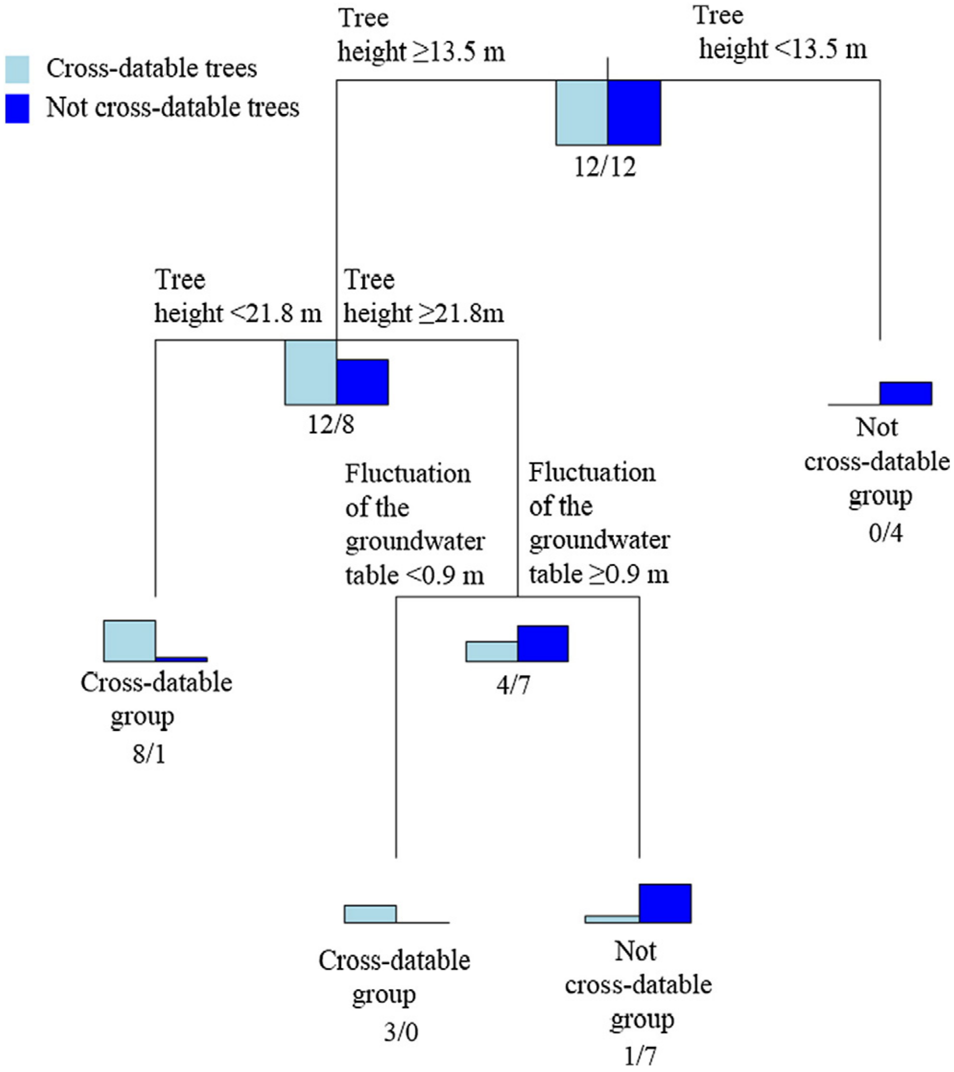


Fig. 6. Classification tree of the cross-dated and not cross-dated individuals of *Quercus robur* in relation to site-specific parameters (model documentation: error: 0.167, CV error: 0.417, SE: 0.166; misclassification rates: null = 0.5, model = 0.0833, CV = 0.208).

reason of climate reconstruction. The expressed population signals for cross-dated *Q. robur* and *F. excelsior* were 0.85 and 0.63, respectively (data not shown) and thus for *F. excelsior* below the commonly accepted minimum threshold of 0.85 to estimate whether the built chronology represents the entire theoretical population (Wigley et al., 1984). Our extended dendrochronological approach shows that a lower sample size may be sufficient. The low misclassification rate in the CART analysis provides evidence that, even with this low sample size, influential environmental parameters beyond climate and river water levels were detectable. The proposed minimum value of the population signal is based on the classical dendrochronological study design of dominant trees in rather homogenous forests which may explain the lower value for *F. excelsior* at our sites. This indicates that the tree growth response of cross-dated *F. excelsior* subsample in this study was not only governed by climate and river water level but also by local, site-specific drivers. The CART analysis gives insights into the individual spatial drivers (very dry sites at the upstream beginning of the study; see Fig. 7) that influence C sequestration in aboveground biomass of *F. excelsior.* Even though, many of our results are confirmed by previous studies in the study area (see Sections 4.1 and 4.2), our proposed extended approach is new. We thus encourage further studies to involve more tree individuals and tree species.

4.1. Climatic drivers and river water level

We were able to successfully cross-date C sequestration in aboveground biomass of *Q. robur* and *F. excelsior* and analyze the response to annually changing parameters such as river water level and climate. The comparably low explained variance of aboveground C sequestration in *Q. robur* (28%) and *F. excelsior* (32%) points to influential environmental parameters on C sequestration in aboveground biomass that could not be considered in the BRT model. Even though periodical (below) surface flooding induced by changing river water levels is present in the study area, this seems to be less influential on C sequestration in aboveground biomass than climate. This is supported by a recent study over three years in the same study area which indicated that C sequestration in aboveground woody biomass was rather influenced by hydrology (59%) than by climate (0%) and river water level fluctuation (4%) (Rieger et al., 2015). Similar to a study performed by García-Suárez et al. (2009), the two tree species responded differently to environmental parameters with rainfall explaining a higher proportion of the explained variance than temperature. Carbon sequestration in aboveground biomass of *Q. robur* did not respond to the changing river water levels. This supports the results of a survey on this species conducted approximately 60 km downstream of our study area that

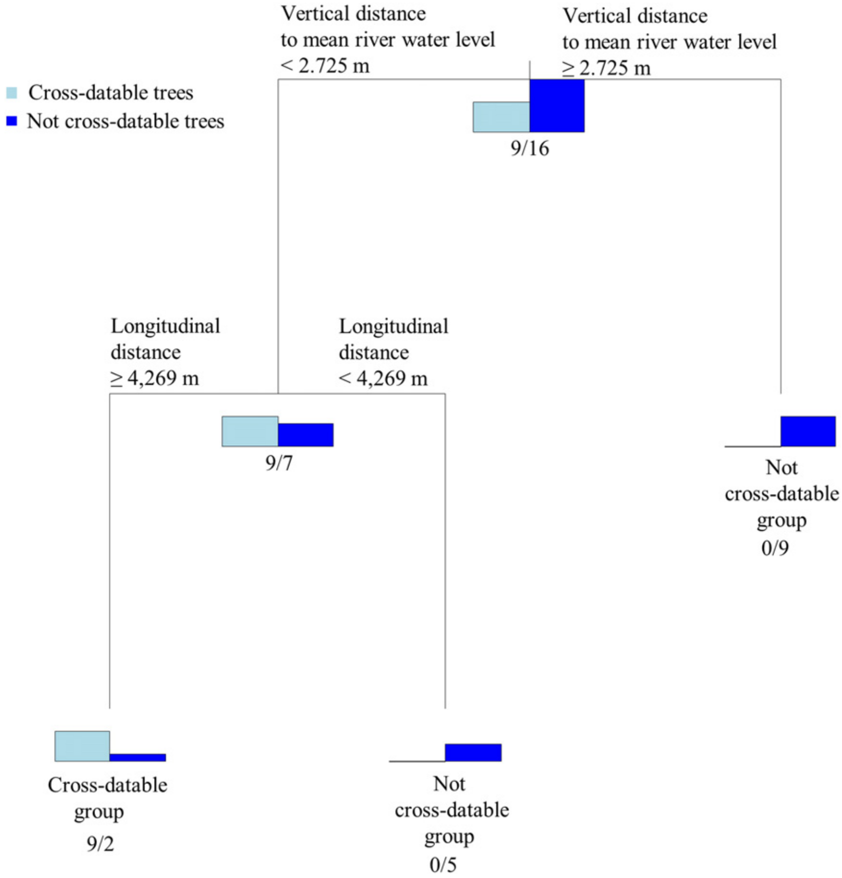


Fig. 7. Classification tree of the cross-dated and not cross-dated individuals of *Fraxinus excelsior* in relation to site-specific parameters (model documentation: error: 0.222, CV error: 0.556, SE: 0.222; misclassification rates: null = 0.36, model = 0.08, CV = 0.2).

found rainfall to be the only significant factor affecting diameter growth (Šmelko and Scheer, 2000).

We found a direct influence of a river water level, i.e., low river water level during the dormant season, only for C sequestration in aboveground biomass of *F. excelsior* (Fig. 5), although the effect was minor (22% of overall variation). For other tree species such as *Larix laricina* and *Acer rubrum* near the St. Lawrence River, a similar effect size of river water fluctuations (9 and 30%) on total growth variation compared to climatic parameters (temperature, 46 and 51%) has been found (Jean and Bouchard, 1996). In our study, a shorter period (<8 days) of low water levels (Fig. 5) during the dormant season resulted in low C sequestrations in the subsequent growing season. This result points to a negative impact of water-logged conditions on C sequestration in aboveground biomass. A comparison of the C sequestration in different biomass compartments has shown that under wetter soil conditions trees allocate a higher proportion of C in fine roots and leaves which may explain the negative impact of water-logged conditions on C sequestration in the stem (Rieger et al., 2015). Groundwater levels are closely linked to river water levels, with the predominant process being the infiltration of groundwater into the hyporheic zone, when river levels are high (Derx et al., 2010; Peyrard et al., 2008).

Fraxinus excelsior is less tolerant of permanent soil saturation and surface flooding than *Q. robur* (Kölling and Walentowski, 2002) owing to differences in the root systems of the two species, particularly the vertical distribution of fine roots. Compared to *Q. robur*, the total, living, and dead fine-root pool of *F. excelsior* is more concentrated in the topsoil (0–30 cm, see Rieger et al., 2013). Furthermore, significantly lower altitudes above the mean river level (*t*-test, $P = 0.02$) and reduced distance to the shallow groundwater table (*t*-test, $P = 0.009$) for cross-dated *F. excelsior* sites compared to *Q. robur* sites may force *F. excelsior* to develop shallow root systems to avoid water-saturated soil conditions. However, a shallow root system limits water and nutrient uptake from deeper soil horizons during dry periods. Along with that, fine roots near the soil surface are more sensitive to frost damage and must be regenerated in the subsequent growing season. This may reduce C sequestration in aboveground biomass of *F. excelsior* under water-logged conditions compared to *Q. robur*.

Carbon sequestration in aboveground biomass of *Q. robur* responded negatively to September precipitation but positively to July precipitation of the present year (>50 mm, Fig. 4). Friedrichs et al. (2008) reported similar positive correlations of *Q. robur* growth response to monthly precipitation in the growing season for June precipitation in temperate, terrestrial lowlands and low mountain ranges in Germany and also emphasized the importance of the June precipitation of the previous year. Moreover, Kern et al. (2013) showed a positive influence of June and July precipitation levels on tree-ring growth in the northeastern part of the Great Hungarian Plain. As in our study, the authors found a negative trend in ring width in response to September precipitation. In contrast, *F. excelsior* responded to precipitation by exhibiting above average C sequestration in aboveground biomass when precipitation in September of the present and previous years was >40 mm as well as when precipitation in March of the present year was >50 mm (Fig. 5).

The high relevance of the previous year's climate for tree growth is a common phenomenon that can be attributed to the fact that bud formation and leaf primordia or root growth in the current year are triggered by available moisture of the previous growing season (Fritts, 2001). In particular in trees with ring-porous wood such as *F. excelsior* and *Q. robur*, the initiation of earlywood formation is closely linked to the consumption of carbohydrates stored in past growing seasons (Barbaroux and Breda, 2002). In addition, soil water deficit during the current growing season stops stem growth while carbohydrate accumulation remains unaffected (Barbaroux and Breda, 2002), which may explain the positive effect of increased July precipitation on C sequestration in *Q. robur* (Fig. 4) and of March and September precipitation in *F. excelsior* (Fig. 5).

Interestingly, *Q. robur* showed a contrasting growth response to September precipitation with a clear negative relationship to C sequestration in aboveground biomass. This may result from the hydrological regime of the Danube River, which is mainly mediated by snow and glacier melt water with the highest water levels in June, July, and August. The combination of abundant summer rainfalls (June, July, and August comprise approximately 33% of the annual precipitation) and a wet September (>50 mm precipitation) may lead to water levels that exceed the (belowground) flooding tolerance of *Q. robur* and result in a loss of fine roots (Day and Megonigal, 1993; Megonigal and Day, 1992) along with reduced C sequestration in aboveground biomass. Consequently, the negative response of *Q. robur* to September precipitation points to similar growth limitations during water-logged conditions as revealed for *F. excelsior*.

In accordance with previous studies (Friedrichs et al., 2008; Kern et al., 2013), we found that temperature played a minor role for growth trends in *Q. robur* compared to precipitation (relative influence in our study: 27 vs. 73%). While Friedrichs et al. (2008) showed a positive growth correlation to temperature in February, Kern et al. (2013) observed negative growth correlations to temperatures in April and June in the Great Hungarian Plain. We detected a negative correlation of *Q. robur* C sequestration in aboveground biomass to temperature in November. These contrasting results are presumably due to differences in (local) climate between our study site and the location of the study by Kern et al. (2013) in northeast Hungary. Rather continental climate and terrestrial site conditions along with higher temperatures and water limitation in the growing season may force stomatal closure and therefore limit tree growth in June and April in northeast Hungary. The latter was not relevant for the growth of *Q. robur* in our study area. In addition, other basic factors may favor C sequestration in aboveground biomass of riparian forests. Along the Austrian Danube (Machland), Wendelberger-Zelinka (1952) reported humidity levels 20% higher and more fog in the floodplain compared to the areas outside the floodplain even in midsummer. These climate aspects buffer temperature extremes in the growing and dormant seasons. *Quercus robur*'s significant response to November temperatures of the previous year—with below average sequestration values when the temperature rose above ca. 4.5 °C—suggests that this species is highly sensitive to dormancy interruption as the premature activation of cambium cells may lead to increased mortality during subsequent low temperatures at night, the so-called winter sunscald (Kozlowski, 1971). In contrast to *Q. robur*, the relative response of C sequestration in aboveground biomass of *F. excelsior* to temperature was higher (32 vs. 27%) and was characterized by a positive correlation between C sequestration of *F. excelsior* and temperature. This perhaps highlights a pronounced sensitivity of *F. excelsior* to late frost (Aas, 2002), which is related to embolism and a subsequent loss of hydraulic conductance in trees with ring-porous wood (Sperry and Sullivan, 1992; Sperry et al., 1994) following repeated freezing and thawing cycles. As the need to renew vessels in spring (Hacke and Sauter, 1996) is low at February temperatures >4 °C, *F. excelsior* shows above average C sequestration in aboveground biomass under these conditions.

4.2. Site- and species-specific drivers

The selected parameters were related to the positions of the sample trees within the hydrosystem, to the groundwater regime, and to competition (derived from the social status and the tree height of neighboring trees) within the forest stand. For cross-dated *Q. robur* individuals, CART analysis detected a reduced fluctuation in the groundwater table (<0.9 m) to be a limiting factor for C sequestration in aboveground biomass. Carbon sequestration in cross-dated *F. excelsior* individuals was limited by lower altitudes above the mean river level (<2.8 m) and by a distance of ≥4269 m to the upstream boundary of the study area, which corresponds well to the transition between a very dynamic floodplain section near Schönau characterized by very sandy sediments, which ensure a fast aeration of the soil after flooding events, and a less morphodynamic river section characterized by rather silty and clayey sediments with higher water holding capacity. Furthermore, a slight net shift from infiltration of river water into the groundwater to an exfiltration of groundwater into the Danube River near the village Orth/Donau was observed by Blaschke and Schmalfuß (2009), which indicates higher groundwater tables at larger distance from the upstream boundary of the study area. In accordance, aboveground C stocks in the floodplain forests were also found to be lower where belowground flooding caused fluctuations in the groundwater table of <1 m or where the distance to the groundwater table was <3.5 m (Rieger et al., 2013), which supports our findings regarding limiting factors for C sequestration in aboveground biomass. Overall, these findings on hydrology and spatial gradients indicate that C sequestration in aboveground biomass of our study species is limited by high groundwater levels and related soil oxygen deficit.

In *Q. robur* however, a magnitude of fluctuation of the groundwater table of <0.9 m was exclusively limiting for trees with a height above 21.8 m. Constant soil water saturation along with rather long-lasting anoxic conditions is probably a particular constraint for taller trees owing to their deeper root systems. This is supported by a study on stagnosols in Germany, where *Q. robur* exhibited a pronounced tolerance to high water level fluctuations (Scharnweber et al., 2013) presumably because of a deep root system which, in turn, may be disadvantageous under reduced water level fluctuations and saturated soil conditions.

For *Q. robur* trees with heights of 13.5–21.8 m, an even more important influence on C sequestration in aboveground biomass was found. Trees in this height class are individuals that have not reached the forest canopy (mean canopy height = 25.2 m). At this development stage, the limiting factor is light availability (van Hees et al., 1996). The cross-dated *Q. robur* individuals hence show similar growth patterns reflecting common light deficiency, which forces them to exist at the margin of their ecological amplitude and points to competition as a more influential driver on C sequestration in aboveground biomass than climate or groundwater level.

Surprisingly, diking of parts of the floodplain did not affect aboveground biomass C sequestration in the model species. Cross-datable trees of *F. excelsior* and *Q. robur* (Fig. 2) were evenly distributed in flooded and diked riparian forests. Since cross-datable tree ring curves respond to the same limiting factors, we can clearly reject dike presence as a relevant parameter from the models on C sequestration in aboveground biomass. This is supported by the fact that none of the river water levels indicating surface flooding and thus being directly influenced by the dike remained in the BRT models. In contrast, belowground water levels, which remain unaffected by the dike, had a negative influence on aboveground biomass C sequestration in our study trees as shown directly for *F. excelsior* and indirectly for *Q. robur*. Consequently, our results back previous studies which showed that the influence of surface flooding on tree growth is often overestimated compared to soil saturation from belowground flooding (Day and Megonigal, 1993; Rieger et al., 2013). The failure of the dike to be a relevant factor in C dynamics of the studied floodplain forest also supports previous results from the same study area (Rieger et al., 2014, 2013). Yet the conclusion should be tested in other regions where the dike is closer to the river or has been present for a much longer time.

5. Conclusions

The high predictability of our models for *Q. robur* and *F. excelsior* compared to models on C stocks (Explained variance = 10%; see Rieger et al., 2013) suggests that our approach may be used in C sequestration analyses as it (1) includes a wide array of predictor variables, (2) may be carried out with relatively small sampling amount, and (3) is expected to work both in heterogeneous forests and in rather homogenous ecosystems such as temporal terrestrial or boreal forests. Owing to the fact that the cross-datable pool of *Q. robur* and *F. excelsior* included dominant, co-dominant, and suppressed trees, a selection bias on big trees cannot have influenced the modeled climate-C sequestration relationships. Our results provide evidence that C sequestration in heterogeneous riparian forests is closely linked to both static site-specific conditions and climate and flooding parameters that vary over time. In particular, the site-specific thresholds shown in the CART analysis suggest profound limitations of species-specific C sequestration related to high groundwater levels and tree height. We therefore conclude that the response of C sequestration in temperate riparian forests to climatic and flooding variables is fundamentally governed by the interplay of local site- and species-specific factors. Investigations on contemporary C sequestration in stems of the same study area based on an independent data set support this interpretation (see Rieger et al., 2015). By revealing growth-limiting drivers, our approach may allow for the detection of adequate sites to realize classical dendrochronological studies in temperate heterogeneous forests based on correlation analysis. That is especially true for forests where the interplay of drivers is still unknown and climatic drivers are not limiting tree ring growth. However, the applicability of our approach beyond the considered ecosystem and studied tree species needs evidence from further studies and testing.

Overall, the randomized dendrochronological design along with combined BRT and CART analyses revealed novel insights into the mechanisms of C sequestration in aboveground biomass of heterogeneous forest wetland ecosystems which are—albeit low overall area—highly relevant in the global C cycle and at the same time extremely threatened by human disturbances. In the face of increased likelihood of severe summer-time flooding caused by higher temperatures in Europe (Christensen and Christensen, 2003), modeling C sequestration in aboveground biomass based on tree-, site-, and climate-related parameters becomes even more relevant. Our approach provides a powerful tool for assessing C sequestration in aboveground biomass and its response to manifold environmental factors. It may therefore contribute to enhancing the applicability and the predictive power of dendrochronological approaches, in particular in very productive and dynamic forest ecosystems, and to assessing the role of these ecosystems in C sequestration of aboveground biomass at different temporal and spatial scales. That holds true in particular for the local scale where forest management plans (e.g., tree species selection) and river engineering measures need to be established and adapted in order to mitigate global climate change.

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Appendix A

Table A.1
Documentation of calculated BRT models for *Quercus robur* and *Fraxinus excelsior*.

Dependent variable	Carbon sequestration *Quercus robur*	Carbon sequestration *Fraxinus excelsior*
Distribution	Poisson	Gaussian
Bag fraction	0.6	0.6
Number of trees	10,000	10,000
Mean total deviance	8.374	21.252
Mean residual deviance	6.003	14.418
Explained deviance	28%	32%
Estimated CV deviance	7.746	18.426
Estimated CV deviance (se)	1.288	2.044
Training data correlation	0.645	0.738
CV correlation	0.333	0.4
CV correlation (se)	0.111	0.115

Map. KML file containing the Google map of the most important areas described in this article.

Appendix B. Supplementary data

Supplementary data associated with this article can be found in the online version, at http://dx.doi.org/10.1016/j.scitotenv.2016.07.174. These data include the Google map of the most important areas described in this article.

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