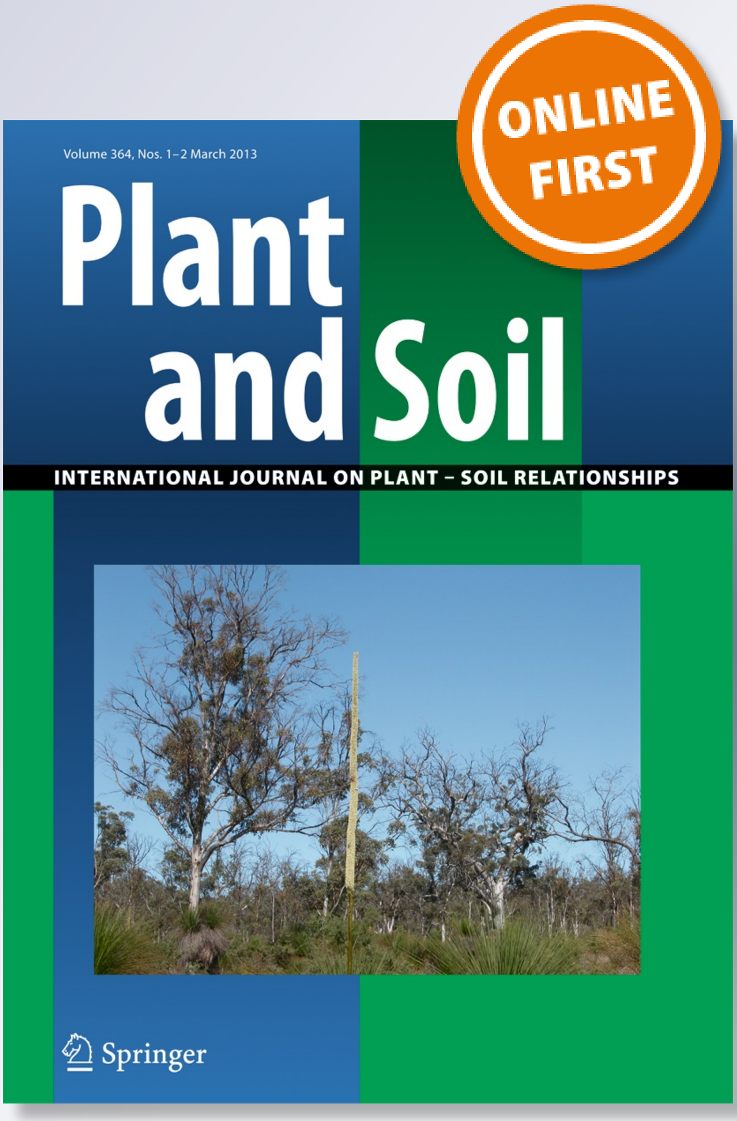
Fine root and aboveground carbon stocks in riparian forests: the roles of diking and environmental gradients

Isaak Rieger, Friederike Lang, Birgit Kleinschmit, Ingo Kowarik & Arne Cierjacks

Plant and Soil
An International Journal on Plant-Soil Relationships

ISSN 0032-079X

Plant Soil
DOI 10.1007/s11104-013-1638-8



Springer

Plant Soil
DOI 10.1007/s11104-013-1638-8

REGULAR ARTICLE

Fine root and aboveground carbon stocks in riparian forests: the roles of diking and environmental gradients

**Isaak Rieger · Friederike Lang ·
Birgit Kleinschmit · Ingo Kowarik ·
Arne Cierjacks**

Received: 13 September 2012 / Accepted: 5 February 2013

Abstract
Aims We analysed current carbon (C) stocks in fine root and aboveground biomass of riparian forests and influential environmental parameters on either side of a dike in the Donau-Auen National Park, Austria.
Methods On both sides of the dike, carbon (C) stock of fine roots (CFR) under four dominant tree species and of aboveground biomass (CAB) were assessed by topsoil cores (0–30 cm) and angle count sampling method respectively ($n=48$). C stocks were modeled, performing boosted regression trees (BRT).
Results Overall CFR was 2.8 t ha^{-1}, with significantly higher C stocks in diked (DRF) compared to flooded riparian forests (FRF). In contrast to CFR, mean CAB was 123 t ha^{-1} and lower in DRF compared to FRF. However, dike construction was consistently ruled out as a predictor variable in BRT. CFR was influenced by the distance to the Danube River and the dominant tree species. CAB was mainly influenced by the magnitude of fluctuations in the groundwater table and the distances to the river and the low groundwater table.
Conclusions Despite pronounced differences in FRF and DRF, we conclude that there is only weak support that dikes directly influence C allocation in floodplain forests within the time scale considered (110 years).

Responsible Editor: Alain Pierret.

Electronic supplementary material The online version of this article (doi:10.1007/s11104-013-1638-8) contains supplementary material, which is available to authorized users.

I. Rieger (✉) · I. Kowarik · A. Cierjacks
Department of Ecology, Ecosystem Science/Plant Ecology,
Technische Universität Berlin,
Rothenburgstraße 12,
12165 Berlin, Germany
e-mail: isaak.rieger@tu-berlin.de

F. Lang
Chair of Soil Ecology, Institute of Forest Sciences,
University of Freiburg,
Bertoldstraße 17,
79085 Freiburg i.Br., Germany

B. Kleinschmit
Department of Geoinformation in Environmental Planning Lab,
Technische Universität Berlin,
Straße des 17. Juni 145,
10623 Berlin, Germany

Keywords Aboveground biomass · Belowground biomass · Carbon distribution · Carbon sequestration · Dike · Ecosystem services · Floodplain forest

Abbreviations

BRT	Boosted regression trees
C	Carbon
CFR	C stock of fine root biomass
CAB	C stock of aboveground biomass
DBH	Diameter at breast height
DRF	Diked riparian forest
FRF	Flooded riparian forest
NPP	Net primary production
SE	Standard error
TRF	Total riparian forest

Introduction

Floodplains are among the most diverse and complex ecosystems and provide crucial ecosystem services, many of them related to the organic carbon (C) cycle (Naiman and Décamps 1997; Samaritani et al. 2011). In particular, riparian forests are known to store high amounts of organic C in vegetation and soil compared to other terrestrial forests due to high net photosynthesis rates and deep soils with C-enriched horizons (Giese et al. 2000, 2003; Fierke and Kauffman 2005; Hazlett et al. 2005; Cierjacks et al. 2010). Most studies on riparian C stocks have focussed on rather stable C stocks such as aboveground woody biomass and soil organic matter (Cabezas and Comín 2010; Cierjacks et al. 2010, 2011). In contrast, few data are available on the belowground biomass stocks of fine roots, particularly in riparian forests (Baker et al. 2001), likely owing to the time-consuming laboratory work required and methodological concerns (Burke and Raynal 1994; Baker et al. 2001).

Fine roots are known to play a vital role in ecosystem functioning as they link all compartments of the forested system through the provision of water and nutrients (Raich and Nadelhoffer 1989; Jackson et al. 1997; Baker et al. 2001). Additionally, fine roots contribute to important ecosystem functions such as C allocation (Jackson et al. 1997). Fine root biomass stocks such as those of temperate mixed deciduous forests range from 0.6 to 8.7 t ha^{-1} (Meinen et al. 2009). Despite the fact that the biomass stored in fine roots at the global scale barely exceeds 2 % of the total terrestrial ecosystem C stocks (Vogt et al. 1996), fine root growth is expected to account for 33 % of the annual net primary production (NPP; Jackson et al. 1997). Grier et al. (1981) even stated that up to 73 % of the annual NPP in a mature *Abies amabilis* forest ecosystem can be related to fine root growth.

The vast majority of floodplain ecosystems have been subjected to heavy alterations such as destruction of natural forests and construction of dikes and levee systems (Baird et al. 2005; Fierke and Kauffman 2005; Erwin 2009; Piégay and Schumm 2009). In Germany, only one third of the original floodplains are still connected to the flooding regime and not even 1 % (5,700 ha) is still covered by semi-natural floodplain forests (BMU 2009). Such interventions have severely affected the sedimentation and vegetation dynamics of riparian ecosystems (Merritt and Cooper 2000; Elderd 2003; Williams and Cooper 2005; Hohensinner et al. 2011), which has also brought about changes in C cycling (e.g. Haubenberger and Weidinger 1990; Samaritani et al. 2011). Since forests play an important role in C sequestration, there is a strong interest in describing and predicting C stocks in relation to human activities (IPCC 2001). However, the impact of river engineering measures on the C stocks of floodplain forests has to our knowledge not yet been studied systematically in terms of different ecosystem compartments. In particular, the highly dynamic CFR may be a very sensitive indicator of possible long-term changes in more stable CAB and soil carbon pools.

Thus far, only a few studies on forested wetlands have addressed the ratios between CAB and CFR due to the absence of data on fine roots in riparian forests. Although generalised results emphasise fine roots' sensitivity to microsite conditions (Day et al. 1996; Vogt et al. 1998; Baker et al. 2001), findings on the relation of below- and aboveground biomass allocation are controversial. For example, the CFR in bald cypress forests decreased in response to flooding, as the aboveground biomass remained constant or increased (Megonigal and Day 1992; Day and Megonigal 1993). In contrast, Nadelhoffer and Raich (1992) stated that below- and aboveground production are positively correlated and respond to the same environmental factors.

In floodplain ecosystems, the C distribution depends on vegetation characteristics (Giese et al. 2003), soil type and hydrological conditions (Friedman et al. 1996; Bendix and Hupp 2000; Jacobson et al. 2003; McTammany et al. 2003), which in turn are related to the main spatial gradients of the hydrosystem (Piégay and Schumm 2009): the longitudinal gradient (upstream/downstream distance), the lateral gradient (main channel/side channel distance) and the vertical gradient (depth of the groundwater table). Consequently, a comprehensive analysis of C stocks should include belowground and aboveground biomass and consider possible impacts of spatial gradients along with vegetation and soil conditions.

Therefore, this study aims (1) to assess the hydrological regime in floodplain soil (including depth of the low and mean groundwater table and magnitude of the fluctuation between low and mean groundwater table, both in relation to the distance to the Danube River) for total riparian forest (TRF), FRF, and DRF; (2) to quantify CFR and CAB in TRF, FRF and DRF and to evaluate possible differences between FRF and DRF; and (3) to model CFR and CAB in response to dike presence, other abiotic environmental (spatial, hydrological) parameters and forest stand variables.

Methods

Study area

With a length of 2,857 km and a total watershed area of 817,000 km^2, the Danube River is the second longest river in Europe. Mean annual discharge into the Black Sea is about 6,500 m^{3}s^{-1} (BMU 2003). Our study area is part of the Donau-Auen National Park in Austria, located between Vienna and the border of Slovakia (Fig. 1). The National Park preserves one of the last remaining riparian forests of Central Europe over a length of approximately 38 km and a maximum width of 4 km. About 65 % (6,045 ha) of the National Park is covered by floodplain forest. In this section of the Danube, river water level varies within a range of up to 7 m and inundates large areas during high water levels caused by seasonal meltwater and periods of rain. Larger inundations of the floodplain take place approximately every 5 years (Baumgartner, pers. comm.). To enable constant shipping travel, riverside embankments of the Danube have been fixed, mainly with riprap. Moreover, at the end of the 19th century (1882–1905), the Marchfield dike was constructed to protect a part of the territory from surface flooding.

The study was carried out between the villages of Schönau in the west (48°8′ N, 16°36′ E, river kilometer 1910) and near Hainburg in the east (48°1′ N, 16°88′ E, river kilometer 1889) in the northern part of the Danube floodplain, which includes both flooded and diked floodplain forests. Soils of the study area are fluvisols (calcaric, eutric) and gleysols (haplic, calcaric) (Sali-Bazze 1981; Cierjacks et al. 2010). Climate conditions are characterised by an annual mean temperature of 9.8 °C and a moderate average annual precipitation of about 533 mm (1948–2008) (climate station: Schwechat 16°34′N, 48°7′E, 184 m above sea level; Zentralanstalt für Meteorologie und Geodynamik 2002). The Donau-Auen National Park lies within a sub-watershed of the Danube that covers about 104,000 km^2. The main channel is characterised by width of 350 m, a mean annual discharge of 1,950 m^3 s^{-1} (low water: 900 m^3 s^{-1}; annual flooding event: 5,270 m^3 s^{-1}), and a slope of 0.045 %. Surface water velocity ranges from 1.9 to 2.2 m s^{-1} (Tockner et al. 1998).

Sampling design

To cover broad ranges of environmental (spatial, hydrological, forest stand) gradients, the study area was stratified into three lateral zones: (1) undiked areas less than 400 m from the Danube River; (2) undiked areas more than 400 m from the main channel of the Danube River and (3) areas diked by the Marchfeld dike. These lateral zones were further divided into the western upstream part and the eastern downstream part of the study area. Within each of these six zones, two sample trees per species were randomly selected. To exclude any impact of possible shifts in species composition due to terrestrialization (Hohensinner et al. 2011) from dike construction, we focussed on the four dominant tree species, *Quercus robur*, *Fraxinus excelsior*, *Populus alba*, *Salix alba*, on both side of the dike

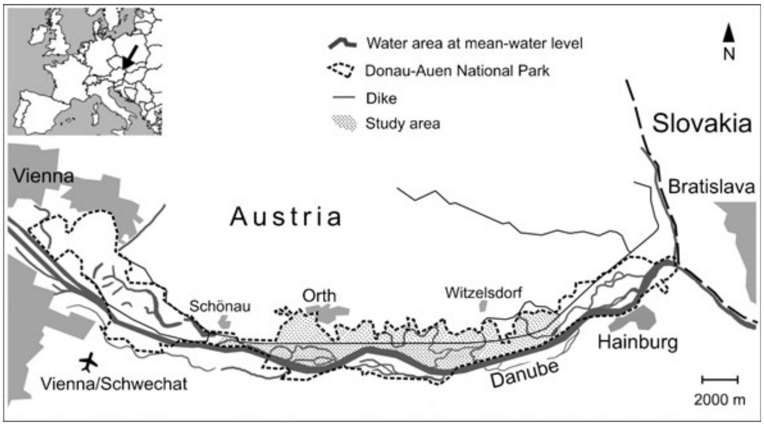


Fig. 1 Location of the study area within the Donau-Auen National Park in Austria

using the National Park's forest inventory database, which is based on a 100×400 m raster. This approach led to 48 sample trees (16 located within the diked floodplain forest) which formed the basis for the analysis of CFR and CAB and environmental parameters.

Spatial analyses and hydrology

To analyse the spatial position of the sample trees, position data were recorded using a Trimble® GeoXH™ 2005 series handheld in February and March 2010 before foliation. GPS data were post-processed by a differential correction with Rinex data (base station: Leopoldsau) to increase position accuracy. To determine the distance to the upstream beginning of the study area and the distances to the Danube River or the nearest channel for all sample trees, we used the "NEAR" tool (ArcInfo) in ArcGIS 9.2.

The distances to mean/low groundwater level of each study plot were calculated by combining a groundwater model of the survey area provided by the Vienna University of Technology and a digital elevation model provided by via donau – Österreichische Wasserstraßen-Gesellschaft mbH. We performed the "Extract Values to Points" tool (ArcInfo) in ArcGIS 9.2 to derive altitudes of mean/low groundwater table. Altitudes asl of the mean and low groundwater level were subtracted from the altitude asl of each sample tree base to assess the distances to mean and low groundwater level. The magnitude of fluctuation between mean and low groundwater table was calculated as the difference in altitudes asl of mean and low groundwater level.

Fine root C stock

Following Vogt et al. (1998), we used soil coring to assess CFR. Fine root biomass usually accumulates within the upper 30 cm of soil with an estimated 59–91 % of the overall fine root biomass found there (Burke and Raynal 1994; Baker et al. 2001; Kiley and Schneider 2005; Meinen et al. 2009). The low content of coarse stony fragments or aggregates (>2 mm in diameter) of the analysed soil with a more or less even distribution of fine roots allowed for a representative root sample extracted from soil cores of 30 cm in length and 1.8 cm in diameter (76 cm^3). To exclude possible effects of the stem on the local sedimentation regime and fine root stock, we systematically took one soil core at a distance of 1.5 m to the east of each sample tree using a steel auger. All soil cores (n=48) were extracted between November 15 and 26, 2010, and transferred to plastic bags. Until laboratory analysis, samples were stored at 4 °C. Soil cores were washed using a series of sieves with 2.5, 0.5, 0.2 and 0.063 mm mesh size. The collected roots were uniformly distributed on a petri dish tagged with millimetre paper for exact area measurement. Six of 20 permanently marked squares of 1 cm^2 were randomly selected to obtain a subsample of fine roots. This entire subsample was classified according to its phenology ["living biomass" or "necromass"; according to the methods described by Persson (1980a, b) and McClaugherty et al. (1982)] using a stereo microscope (Leica Wild M3C). The diameter threshold for fine root classification varies considerably in the literature (Nadelhoffer and Raich 1992; Kiley and Schneider 2005; Cavalcanti and Lockaby 2005). Here, we followed Nadelhoffer and Raich (1992) and considered all nonwoody roots ≤5.0 mm as fine roots and classified them into four size categories (<0.50, 0.50–1.49, 1.50–2.99, 3.00–5.00 mm). These data served for the estimation of the percentage of each phenology and size class in the entire soil core. For biomass measurement, the root fractions were transferred to paper bags, oven-dried for 48 h at 65 °C and weighed. Root C stock per soil core was calculated by multiplying biomass stocks by 0.5 (Jackson et al. 1997; Giese et al. 2003). Results were then extrapolated to derive tons C per hectare.

Aboveground biomass C stock

To enable comparisons between CFR and CAB, we analysed the forest stand adjacent to each sample tree. We applied the angle-count sampling method developed by Bitterlich in 1948 to access surrounding forest stand parameters of each sample tree (Kramer and Akça 2002) and subsequent CAB. Measurements were performed with a Dendrometer II by Kramer. With the sample tree as the centre, we counted each tree and shrub included in the variable radius of the sample area. The radius of the sample area depends on the diameter at breast height (DBH) and the distance of each tree and shrub to the centre. If the DBH exceeded a given opening angle (we used the count factor k=5.5), we recorded the species of trees and shrubs and the number of each present as well as the height (using a BLUME-LEISS BL 6 altimeter and subsequent trigonometrical calculation), the DBH of all trees and shrubs, and the percent cover of trees, shrubs, and herbs. These data were used to derive mean DBH and hectare values of forest stand variables (for basal area and stem number). Then data were transformed to biomass using allometric equations (additional data are given in Online Resource ESM 1) for aboveground (woody) biomass compiled by Zianis et al. (2005). When only stem volume equations were available, we multiplied stem volume by 0.5321 to derive stem biomass according to Lehtonen et al. (2004).

Lying woody debris >10 cm in diameter was measured within a radius of 8 m around the central sample tree. Based on the work of Chave et al. (2006), volume was transformed to mass using the factor 0.6 to derive tons per cubic meters. Biomass values of standing stock and lying deadwood were multiplied by 0.5 to estimate C stocks (Giese et al. 2003). Results were then extrapolated to hectare values.

Statistical analysis

All continuous variables were tested for outliers, normality (Shapiro-Wilk test), homogeneity of variance (Fligner test) and collinearity (VIF values) (Fox 2008; Zuur et al. 2010). In case of violation of normality and homogeneity, differences in the response variables were tested using the Kruskal-Wallis test. Otherwise, we used the Welch *t*-test. Correlations among spatial and hydrological variables were tested for significance using Pearson's product–moment correlation.

To model the impact of environmental parameters on CFR and CAB, we applied a boosted regression trees (BRT) analysis. This technique combines the advantages of regression trees (De'ath and Fabricius 2000) and boosting to improve model accuracy (Schapire 2002). BRT are ideally suited to handle typically complex ecological data (unbalanced, missing values, many zeros), and their output can more easily be interpreted due to modelling fitted functions (Elith et al. 2008). Furthermore, BRT analysis allows interactions among predictor variables to be detected. The set of environmental parameters used for the analysis of CFR and CAB included (1) spatial parameters, i.e. distances to the Danube River, the nearest side channel, the upstream beginning of study area, and the relation to the dike (waterside vs. landside); (2) hydrological parameters, i.e. distances to mean/low groundwater level, magnitude of the fluctuations in the groundwater table; and (3) forest stand parameters, i.e. dominant tree species, number of tree species, stem number per hectare, basal area and coverage of herb, shrub and tree layers. In a first analysis, soil parameters (soil type, bulk density, number and thickness of C-enriched soil horizons, content of sand, rate of sedimentation) were included, but because they did not show an influence on the studied C stocks, these data are not shown here. All calculations were performed with R version 2.10.0 using the packages "AED", "brt", "car", "gbm", "gtools", "mass" and "vegan" (R Development Core Team 2012).

Results

Hydrological parameters

Mean fluctuation between mean/low groundwater table and distances to mean and low groundwater table in TRF were 1.2±0.0, 2.6±0.1 and 3.7±0.1 m respectively. The magnitude of the fluctuation in the groundwater table (Fig. 2a) and the distance to the low groundwater table (Fig. 2b) decreased significantly with greater distances to the Danube River. However, the distance to the river and the mean groundwater level were not significantly related. Study sites located waterside of the dike were characterised by significantly larger fluctuations of the groundwater table (Kruskal-Wallis test, $P<0.001$) and distances to the low (Welch two-sample *t*-test, $P<0.001$) and mean groundwater table (Welch two-sample *t*-test, $P=0.021$) compared to sites landside of the dike. Mean fluctuations in the groundwater table and distances to low and mean groundwater table in FRF were 1.3±0.0, 4.0±0.15 and 2.7±0.15 m. Mean values for above mentioned hydrological parameters in DRF were lower (0.9±0.0, 3.1±0.15, 2.2±0.16 m).

Carbon stock of fine root and aboveground biomass

Total CFR in the upper 30 cm of soil in the sampled floodplain forests was about 2.8 t ha^{-1} with 1.57 t ha^{-1} from living biomass and 1.25 t ha^{-1} from necromass (Table 1). Fine roots <1.5 mm in diameter accounted for about 82 % of the total CFR with proportions shared nearly equally between living biomass and necromass (Table 1). The total CAB was 123±7 t ha^{-1}.

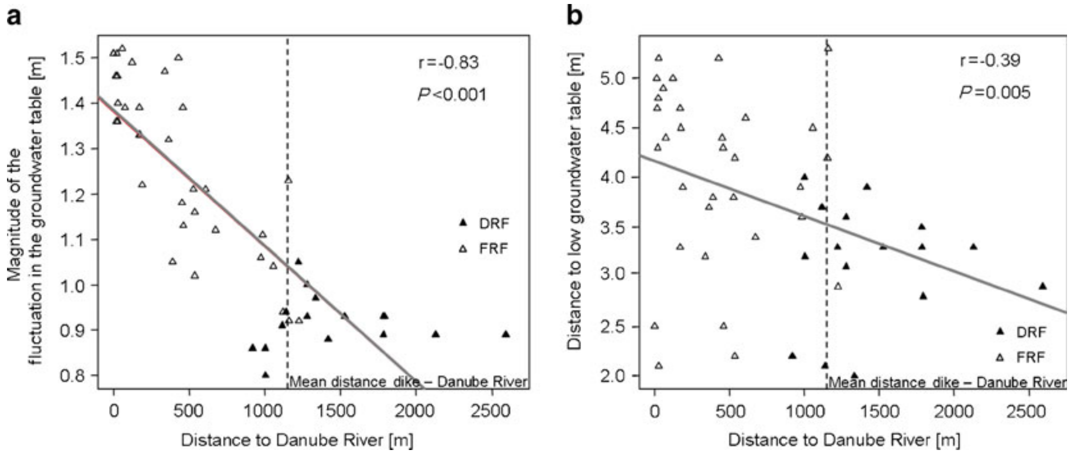


Fig. 2 Hydrological parameters. **a** Magnitude of the fluctuation in the groundwater table and **b** Distance to low groundwater table in relation to the distance to the Danube River *DRF* diked riparian forest, *FRF* flooded riparian forest

Therefore, total CAB contributed 44 times more C to the C stock than CFR.

Mean total CFR in FRF was significantly lower than in DRF (2.28 vs. 3.97 t ha^{-1}) (Fig. 3a). Differences in total CFR were related to necromass C stock, with FRF showing lower necromass C stock (0.90 t ha^{-1}) than DRF (1.97 t ha^{-1}), whereas differences in living biomass were not significant between FRF and DRF. However, living CFR in FRF tended to exceed necromass C stock (1.38 vs. 0.90 t ha^{-1}). There was no pronounced difference between living biomass C stock and necromass C stock in DRF.

In contrast, CAB (Fig. 3b) responded inversely to the presence of the dike (although not significantly; Welch two-sample *t*-test, P=0.08) with higher values in FRF (132 t ha^{-1}) compared to DRF (106 t ha^{-1}).

Table 1 Carbon stock of fine root biomass of floodplain forests in the Donau-Auen National Park (SE = standard error)

Size class [mm]	Phenology class	Mean (SE) [t C ha^{-1}]
<0.50	Living biomass	0.55 (0.09)
	Necromass	0.62 (0.10)
0.50–1.49	Living biomass	0.62 (0.14)
	Necromass	0.53 (0.10)
1.50–2.99	Living biomass	0.12 (0.09)
	Necromass	0.00 (0.00)
3.00–5.00	Living biomass	0.28 (0.14)
	Necromass	0.10 (0.07)
Total	Living biomass	1.57 (0.24)
	Necromass	1.25 (0.19)
Total	Living biomass and necromass	2.82 (0.29)

Role of abiotic environmental parameters and forest stand variables

The BRT model for the total CFR explained 23 % of the variation in the dependent variable. Our analysis detected the lateral distance to the Danube River (relative influence 58.8 %) and tree species (relative influence 41.2 %) as the two most influential variables explaining the variation in C stocks of fine root biomass. The pattern of the fitted functions shows that above average CFR levels were found at distances of >1000 m from the Danube River and in forest stands dominated by *F. excelsior* and *S. alba*. Interactions among predictor variables were not detected. The presence of the dike was not influential for fine root prediction (Fig. 4).

Similarly, living CFR was equally influenced by the distance to the Danube River (35 %) and by tree species (27 %). Moreover, the BRT model revealed that 38 % of the total explained variance was related to the distance to the nearest side channel. The fitted function of all model parameters predicted above average living CFR for sites within 50 m of the nearest side channel and at distances of >1,000 m to the Danube River. These sites were dominated by *F. excelsior* and *S. alba* (additional data are given in Online Resource ESM 2).

The BRT model of dead CFR in floodplain forests (additional data are given in Online Resource ESM 2)

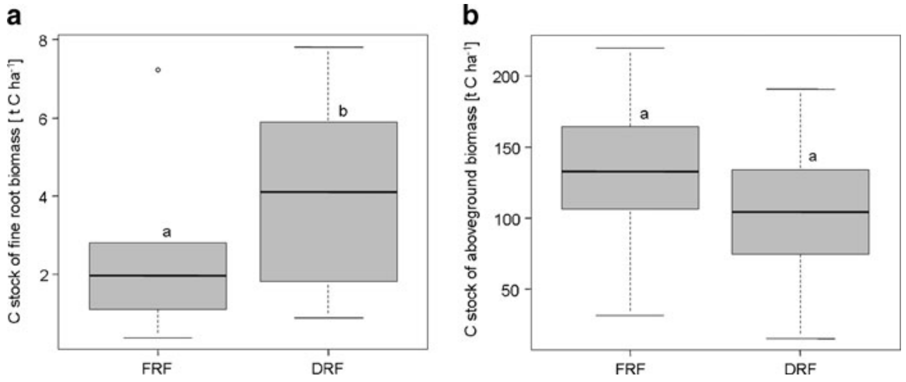


Fig. 3 Total carbon stock of **a** fine root and **b** aboveground biomass in FRF and DRF (for carbon stock of fine root biomass, Kruskal-Wallis test: chi-squared=6.7658, df=1, P=0.009; for carbon stock of aboveground biomass, Welch two-sample t-test, t=1.7884, df=29.868, P=0.084). Different *lowercase letters* (a, b) indicate significant differences. *FRF* flooded riparian forest, *DRF* diked riparian forest

also identified the distance to the Danube River (44 %) and tree species (18 %) as most influential. Interestingly, *S. alba* showed the lowest necromass C stock, whereas the pattern of the other tree species resembled the findings on total and living CFR. In addition, upstream distance contributed 38 % to the explained variance of the model. High contents of dead CFR were located at distances >1,000 m from the Danube River and >7,500 m from the upstream beginning of the study area. Again, neither living nor dead CFR responded to the presence of the dike in these models.

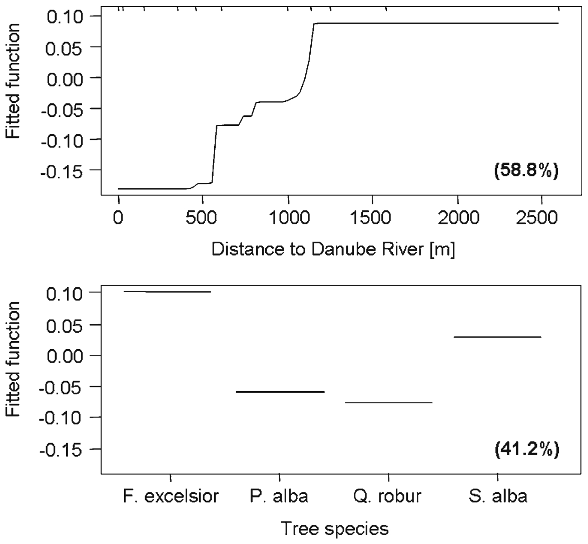


Fig. 4 Relative influence (*bold value in brackets*) and partial responses (*fitted functions*) for the two most influential variables (distance to Danube River, tree species) in the boosted regression tree model for carbon stock of fine root biomass (model documentation: explained variance: 23 %; CV correlation: 0.503; CV correlation (SE): 0.12; additional data are given in Online Resource ESM 2)

Modelled CAB (Fig. 5) depended on hydrological and spatial parameters. Predictive power of this model was low (10 %) compared to belowground models. The hydrological parameter fluctuation in the groundwater level and the two spatial parameters (i) distance to the Danube River and (ii) distance to the low groundwater table accounted for 41, 37 and 22 % of the total explained variance respectively. The CAB increased with the greater fluctuations between low and mean groundwater table (with above average values at distances greater than 1 m). In contrast to CFR, CAB decreased with the distance to the Danube River. Above average values of CAB were found within 500 m of the river, whereas beyond 1,000 m from the Danube River, CAB was unaffected. Relatively high groundwater tables within 2 and 3.5 m of the surface were associated with below average CAB.

Discussion

Carbon stock and drivers of fine root biomass

Our study provides novel data on CFR and CAB, considering dike presence and spatial and hydrological parameters at the riparian ecosystem level in central Europe by using a multi-species approach. As in other forest ecosystems, fine roots accounted for a rather low percentage of overall carbon stock. Despite different methodological approaches, our data on fine root C

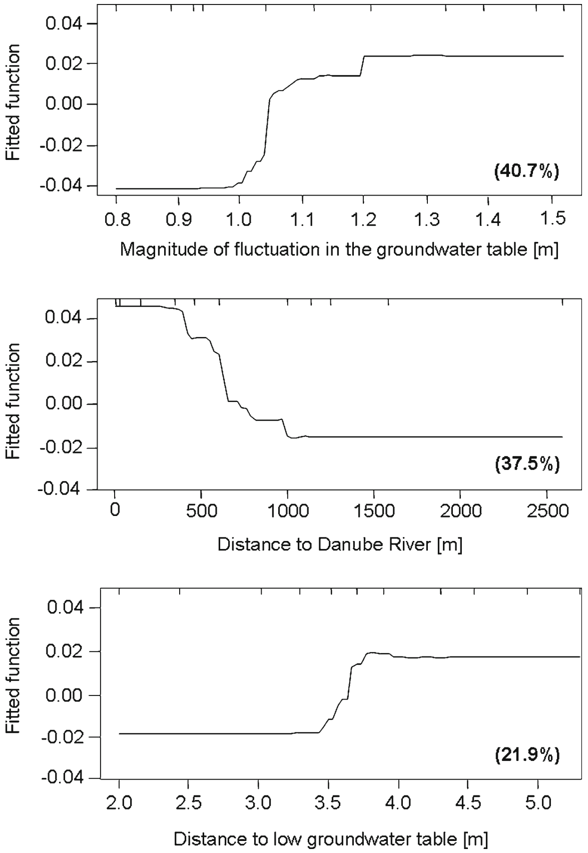


Fig. 5 Relative influence (*bold value in brackets*) and partial responses (*fitted function*) for the three most influential variables (fluctuation in the groundwater table, distance to the Danube River, distance to the low groundwater table) in the boosted regression tree model for carbon stock of aboveground biomass (model documentation: explained variance: 10 %; CV correlation: 0.28; CV correlation (SE): 0.13; additional data are given in Online Resource ESM 2)

stocks are in line with other studies on fine root biomass of terrestrial and riparian forests. Burke and Chambers (2003) compared different forest types of bottomland forests of which we report here the values for permanently moist and periodically flooded conditions, which are expected to be comparable to our study system. Total CFR as calculated from biomass values for the upper 45 cm of soil ranged from 1.2 to 2.8 t ha^{-1} and fine root necromass from 0.7 to 1.2 t ha^{-1} (Burke and Chambers 2003). Although these values are similar to our results (Table 1), exact comparisons of total CFR remain more challenging than for CAB. In particular, the assumption that most fine roots are located within 30 cm of the surface does not necessarily apply to floodplain ecosystems as high sediment deposition may increase the distance to the groundwater table, which is known to stimulate plants to expand their fine root system into greater soil depths (Day et al. 1996; Williams and Cooper 2005). Therefore, we may have underestimated CFR, particularly in FRF.

Overall CFR in DRF was almost twice as high as in FRF (Fig. 3a). In particular our findings on total CFR in DRF (4 t ha^{-1}) are comparable to derived C stocks from fine root biomass results reported by Meinen et al. (2009) for different beech stands in Central Europe. Yet, BRT analyses surprisingly ruled out dike presence as the main reason for these differences and identified instead the distance to the Danube River and dominant tree species as main predictors of total CFR.

Accordingly, the presence of the dike did not remain as an explanatory variable in any of the models we ran. In particular, the lateral gradient indicated by the distance to the Danube River proved to significantly influence CFR, with the dike separating river-near from river-far sites. The mean distances from the Danube River of 441 m and 1,458 m for flooded and diked plots respectively, supports this viewpoint. Consequently, plots of FRF represent below average C stocks, and plots of DRF beyond 1,150 m are classified in the above average section of the fitted function (see Fig. 4). However, the fitted function of distance to the Danube River and total CFR may reflect a minor direct impact of dike construction as the first substantial increase in the function at around 600 m distance to the Danube River coincides with the mean distance of all plots to the dike (622 m). This may point to a possible impact of the sedimentation regime on CFR.

It is commonly accepted that hydrology is the most important driver of ecosystem dynamics in floodplain forests (Brinson et al. 1981; Conner et al. 1981; Day et al. 1988). Still, surface flooding is only one part of the hydrological regime and often widely overestimated compared to the influence of the hydrodynamics belowground such as soil water saturation (Day and Megonigal 1993). Although dike construction obviously disconnects DRF from surface flooding, our study suggests that other hydrological factors, such as changes in the distance to the groundwater table along the lateral gradient from the river to the border of the floodplain, shape the CFR under dominant tree species.

Williams and Cooper (2005) similarly attributed the response pattern of fine roots to changing groundwater conditions. In accordance with our data, their study revealed a substantial loss of root density (40 %) and root biomass (25 %) in *Populus* species with a decreased floodplain groundwater table. In our study area, groundwater tables were lower in the surface flooded area compared to the DRF (*t*-test, $P \leq 0.021$). Although low and mean groundwater tables of DRF did not normally occur in the upper 30 cm topsoil, in general higher groundwater tables may be an indicator of longer water-saturated conditions in the topsoil before and after surface flooding events in FRF along with seepage water in DRF, which may have led to the observed differences.

Distance to the Danube River and tree species were consistently identified as main predictors of total, living and dead CFR. The predictive power of the underlying BRT models was relatively high (>20 %). Previous studies emphasised that spatial and vegetation structures are relevant drivers of aboveground and soil C stocks in floodplain ecosystems (Cierjacks et al. 2011). However, the prediction of soil and aboveground C stocks has remained difficult as in many cases differences in vegetation units characterised by different tree species were not reflected in differences in C stocks (Cierjacks et al. 2010). Our findings show that spatial and forest stand parameters are also powerful predictors of CFR.

Necromass was the part of CFR that most clearly corresponded to dike presence. In DRF, necromass was more than twice as high as in FRF. Dead fine roots usually remain in the soil if root decomposition is reduced due to anaerobic conditions (Day and Megonigal 1993; Rotkin-Ellman et al. 2004). Again, such conditions are more frequent at greater distances from the river where clay content is higher in the topsoil (data not shown) and groundwater tables are higher. Additionally, higher clay content in turn increases the matrix potential (Schachtschabel et al. 1998), which leads to water-saturated conditions in the topsoil even during drought periods in DRF. Consequently, we observed differences between flooded and diked areas, although the dike was not the main driver of this phenomenon.

At the same time, sediment deposition, which exclusively takes place in flooded riparian forests, is known to reduce fine root growth (Simm and Walling 1998; Cavalcanti and Lockaby 2005). In our study area, major flood events that inundate large areas of the FRF resulted in sedimentation rates of up to 0.9 cm year^{-1} (unpublished data). Cavalcanti and Lockaby (2005) showed that rates as low as 0.3 cm year^{-1} induce a pronounced decrease in fine root biomass. Consequently, dike construction may add to the hydrological impact on the CFR by preventing sediment deposition.

CFR differed among dominant tree species (Fig. 4). Locations dominated by *F. excelsior* and *S. alba* had above average total and living CFR. In contrast, the highest dead CFR was found in forest stands of *F. excelsior,* whereas *S. alba* stands showed the lowest dead CFR. Carbon stocks of fine root biomass for *P. alba* and *Q. robur* were more or less at an intermediate level between *F. excelsior* and *S. alba*. Meinen et al. (2009) also found the highest fine root biomass values for *F. excelsior* in comparable multi-species terrestrial forest stands. *Salix alba* and *F. excelsior* are typical species of softwood and hardwood forests respectively, with a root system which is able to adapt rapidly to specific site conditions. In comparison to *S. alba*, *F. excelsior* exhibits a lower tolerance for high groundwater tables and surface flooding (Bonn and Roloff 2002). As a consequence *F. excelsior* trees are shallow-rooted to avoid permanently water-saturated soil conditions, which can lead to drought stress and root dieback during dry times. *Quercus robur* and *P. alba* develop cordate root systems characterised by a higher percentage of fine roots in deeper soil horizons (Bonn and Roloff 2002; Sitte et al. 2002). This may explain why CFR of *F. excelsior* was higher than for *Q. robur* and *P. alba*, which share similar site conditions. In contrast, the ecological amplitude of *Salix* species covers a wide range of wet soil conditions (Timoney and Argus 2006). The root system of *S. alba* is adapted to both permanently high groundwater tables, e.g. on gley soils, and to continuously changing groundwater tables including surface flooding with sediment deposition. *Salix alba* is known to provide roots with oxygen (Jackson and Attwood 1996) below water level and to form adventitious roots after stem burial by sediments (Koop 1987; Timoney and Argus 2006). These adaptations of the root system maintain living roots and stimulate growth of new roots in water-saturated soils, which might explain why *S. alba* had the lowest dead CFR and higher total CFR.

Carbon stock and drivers of aboveground biomass

Mean CAB was 123 t ha^{-1} and thus clearly lower than 222 t ha^{-1} reported by Cierjacks et al. (2011) for the same study area. Apart from methodological differences, this may be attributed to the inclusion of forest stands in diked floodplain forests with lower C stocks and relatively young forest stands along with the low DBH of our sample trees.

In contrast to CFR, mean CAB was higher in FRF than in DRF, but this difference was not significant (*t*-test, $P=0.08$). Similar results have been reported for unflooded mixed hardwood sites and flooded sites in Virginia, USA (Day and Megonigal 1993). In accordance with our results, the study from Virginia revealed a significantly higher belowground biomass in unflooded compared to flooded sites, whereas aboveground biomass was—albeit not significantly—lower at unflooded sites. Although the water gradient from swamp to mixed hardwood forest was clearly broader in the study by Day and Megonigal (1993), their findings highlight the relevance of fine roots in C cycling as they point to a possible trade-off between belowground and aboveground biomass production.

Higher CAB in FRF can be explained by higher NPP due to optimal water supply in the proximity of the river. Mitsch and Ewel (1979) proposed a relationship between drainage conditions and NPP in forested wetlands, with lowest NPP under very dry and wet drainage conditions and highest NPP at intermediate levels. Day and Megonigal (1993) generalised the relationship to a flooding gradient that implies lower NPP with no or continuous flooding, and highest NPP with periodic flooding. Although the groundwater table is generally lower adjacent to the main channel than at greater distances from the river, many trees easily avoid possible drought stress by forming deeper roots (Pregitzer and Friend 1996). Consequently, a high aboveground production can be maintained even during drier periods compared to trees with a shallower root system growing at high groundwater levels. In the latter case, temporary limitations in water supply may result in reduced stomatal conductance along with canopy dieback (Horton et al. 2001a) and lower storage of biomass in aboveground plant tissues.

In contrast to fine roots, the predictive power of the models for CAB was relatively low (10 %). However, the magnitude of the fluctuation in the groundwater table, the distance to the Danube River and the low groundwater table proved to explain most of the variation in CAB. Previous studies failed to predict this parameter by spatial gradients (Cierjacks et al. 2011). Here, we covered a larger lateral gradient (1,458 vs. 518 m) and thus a broader range of hydrological conditions, which presumably led to clearer results.

The relationship of CAB to hydrological parameters (fluctuation in the groundwater table, distance to low groundwater table) was best described by sigmoidal fitted functions (Fig. 5). Increased CAB was observed for thresholds of around 1 m of fluctuation in the groundwater table and 3.5 m depth to the low groundwater table. Assuming that an increased CAB indicates higher NPP, our findings support the hypothetical stress-subsidy relationship (Mitsch and Ewel 1979), which forecasts inhibition of NPP under extreme, i.e. too dry or too wet, conditions. Consequently, transpiration of riparian vegetation proved to be lowest both in cases where the groundwater table was below the rooting zone or in water-saturated soil conditions (Baird et al. 2005). The contrasting responses of biomass growth to the vertical gradient shown by Horton et al. (2001b), which revealed that groundwater tables deeper than 2.5–3 m below the soil surface during the growing season month of July resulted in growth depression expressed by canopy dieback, may be related to the climate of the semi-arid study area in Arizona, USA.

Conclusions

Our findings show that the hydrological regime in the soil of FRF tends to vary more than that in DRF. Consequently, CFR and CAB are related to the hydrological conditions which change along lateral and vertical gradients in floodplains.

Moreover, our study suggests that CFR was determined by specific adaptations of the studied tree species. Consequently, we provide evidence that spatial and hydrological gradients and tree species composition are powerful predictors of C stocks in riparian ecosystems. Despite pronounced differences between FRF and DRF, there is only weak support for the idea that the construction of the Marchfeld dike directly influenced C allocation in the floodplain forests within the time scale considered (110 years). Still, a possible species shift due to missing flooding in the long run as stated by Hohensinner et al. (2011) in the wake of river engineering measures may cause notable changes in fine root dynamics.

As in earlier studies, our data point to an inverse response of CFR and CAB to hydrological parameters. Due to higher groundwater tables at greater distances from the main river, trees tended to invest a higher proportion of C in the belowground biomass expressed by a denser root system and higher root turnover presumably to improve nutrient uptake from the given soil volume. Consequently, aboveground biomass allocation was reduced, which may be further exacerbated by higher drought sensitivity and related canopy dieback when longer drought periods occur during the growing season. Our study species responded differently to these conditions, which may show a species-specific plasticity in belowground versus aboveground biomass allocation.

Our study suggests fine roots are a more sensitive indicator of ecosystem C distribution than the more stable aboveground C stocks. The explained variance in calculated BRT models for CFR was generally much higher compared to our models of CAB. More research on underlying mechanisms of C allocation in riparian ecosystems is needed, in particular, by considering a broader moisture gradient that includes very dry and permanently wet sites. Moreover, future studies should also include productivity data at the ecosystem level to analyse the short-term pattern of C allocation in response, for example, to flooding, precipitation and temperature. Finally, our data imply that sites at greater distances from the main channel are more sensitive to sinking water tables in floodplain soil.

Acknowledgments This study was carried out as a part of the project “Carbon dynamics in soils and vegetation of riparian forests” funded by the Deutsche Forschungsgemeinschaft (DFG, grant number CI 175/1). We thank Torben Lübbe for helping with the field and laboratory work. We also thank Christian Fraissl and Christian Baumgartner (Donau-Auen National Park administration), Alfred Paul Blaschke from the TU Vienna for providing a groundwater model, the via donau – Österreichische Wasserstraßen-Gesellschaft mbH for providing the digital elevation model, Jörg Luster (Swiss Federal Institute for Forest, Snow and Landscape Research) for the pre-submission review and Kelaine Vargas for improving our English. Two anonymous reviewers helped to improve a former version of the manuscript.

References

Baird KJ, Stromberg JC, Maddock T (2005) Linking riparian dynamics and groundwater: an ecohydrologic approach to modeling groundwater and riparian vegetation. Environ Manag 36:551–564

Baker TT, Conner WH, Lockaby GB, Stanturf JA, Burke MK (2001) Fine root productivity and dynamics on a forested floodplain in South Carolina. Soil Sci Soc Am J 65:545–556

Bendix J, Hupp CR (2000) Hydrological and geomorphological impacts on riparian plant communities. Hydrol Process 14:2977–2990

BMU (2003) Hydrologischer Atlas von Deutschland (HAD). Bundesministerium für Umwelt, Naturschutz und Reaktorsicherheit (ed), Bonn/Berlin

BMU (2009) Auenzustandsbericht. Flussauen in Deutschland. Bundesministerium für Umwelt, Naturschutz und Reaktorsicherheit (ed), Berlin

Bonn S, Roloff A (2002) Konkurrenzdynamik und Ökophysiologie der wichtigsten Baumarten in Hartholzauenwäldern an der mittleren Elbe. Roloff A, Bonn S (eds) Ergebnisse ökologischer Forschung zur nachhaltigen Bewirtschaftung von Auenwäldern an der Mittleren Elbe. Forstwiss Beitr Tharandt/Contrib For Sci 17:7–59

Brinson MM, Lugo AE, Brown S (1981) Primary productivity, decomposition and consumer activity in freshwater wetlands. Annu Rev Ecol Syst 12:123–161

Burke MK, Chambers JL (2003) Root dynamics in bottomland hardwood forests of the Southeastern United States Coastal Plain. Plant Soil 250:141–153

Burke MK, Raynal DJ (1994) Fine root growth phenology, production, and turnover in a northern hardwood forest ecosystem. Plant Soil 162:135–146

Cabezas A, Comín FA (2010) Carbon and nitrogen accretion in the topsoil of the Middle Ebro River floodplains (NE Spain): implications for their ecological restoration. Ecol Eng 36:640–652

Cavalcanti GG, Lockaby BG (2005) Effects of sediment deposition on fine root dynamics in riparian forests. Soil Sci Soc Am J 69:729–737

Chave J, Muller-Landau HC, Baker TR, Easdale TA, ter Steege H, Webb CO (2006) Regional and phylogenetic variation of wood density across 2456 neotropical tree species. Ecol Appl 16:2356–2367

Cierjacks A, Kleinschmit B, Babinsky M, Kleinschroth F, Markert A, Menzel M et al (2010) Carbon stocks of soil and vegetation on Danubian floodplains. J Plant Nutr Soil Sci 173:644–653

Cierjacks A, Kleinschmit B, Kowarik I, Graf M, Lang F (2011) Organic matter distribution in floodplains can be predicted using spatial and vegetation structure data. River Res Appl 27:1048–1057

Conner WH, Gosselink JG, Parrondo RT (1981) Comparison of the vegetation of three Louisiana swamp sites with different flooding regimes. Am J Bot 68:320–331

Day FP, Megonigal JP (1993) The relationship between variable hydroperiod, production allocation, and belowground organic turnover in forested wetlands. Wetlands 13:115–121

Day FP, West SK, Tupacz EG (1988) The influence of groundwater dynamics in a periodically flooded ecosystem, the Great Dismal Swamp. Wetlands 8:1–13

Day FP, Weber EP, Hinkle CR, Drake BG (1996) Effects of elevated atmospheric CO_2 on fine root length and distribution in an oak-palmetto scrub ecosystem in Central Florida. Glob Chang Biol 2:143–148

De'ath G, Fabricius KE (2000) Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81:3178–3192

Elderd BD (2003) The impact of changing flow regimes on riparian vegetation and the riparian species *Mimulus guttatus*. Ecol Appl 13:1610–1625

Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. J Anim Ecol 77:802–813

Erwin KL (2009) Wetlands and global climate change: the role of wetland restoration in a changing world. Wetl Ecol Manag 17:71–84

Fierke MK, Kauffman JB (2005) Structural dynamics of riparian forests along a black cottonwood successional gradient. For Ecol Manag 215:149–162

Fox J (2008) Applied regression analysis and generalized linear models. Sage Publications, Los Angeles

Friedman JM, Osterkamp WR, Lewis WM (1996) The role of vegetation and bed-level fluctuations in the process of channel narrowing. Geomorphology 14:341–351

Giese LA, Aust WM, Trettin CC, Kolka RK (2000) Spatial and temporal patterns of carbon storage and species richness in three South Carolina coastal plain riparian forests. Ecol Eng 15:S157–S170

Giese LAB, Aust WM, Kolka RK, Trettin CC (2003) Biomass and carbon pools of disturbed riparian forests. For Ecol Manag 180:493–508

Grier CC, Vogt KA, Keyes MR, Edmonds RL (1981) Biomass distribution and above- and belowground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. Can J For Res 11:155–167

Haubenberger G, Weidinger H (1990) Gedämmte Au - Geflutete Au. Vergleichende Grundlagenforschung zur forstökologischen Beurteilung abgedämmter und gefluteter Auwaldstandorte östlich von Wien. Magistratsabteilung 49, Forstamt und Landwirtschaftsbetrieb der Stadt Wien (ed), Vienna, Austria

Hazlett PW, Gordon AM, Sibley PK, Buttle JM (2005) Stand carbon stocks and soil carbon and nitrogen storage for riparian and upland forests of boreal lakes in Northeastern Ontario. For Ecol Manag 219:56–68

Hohensinner S, Jungwirth M, Muhar S, Schmutz S (2011) Spatio-temporal habitat dynamics in a changing Danube River landscape 1812–2006. River Res Appl 27:939–955

Horton JL, Kolb TE, Hart SC (2001a) Physiological response to groundwater depth varies among species and with river flow regulation. Ecol Appl 11:1046–1059

Horton JL, Kolb TE, Hart SC (2001b) Responses of riparian trees to interannual variation in ground water depth in a semi-arid river basin. Plant Cell Environ 24:293–304

IPCC JJ (2001) Climate change 2001. Impacts, adaptation and vulnerability; contribution of Working Group II to the third assessment report of the Intergovernmental Panel on Climate Change. Cambridge Univ Press, Cambridge

Jackson MB, Attwood PA (1996) Roots of willow (*Salix viminalis* L.) show marked tolerance to oxygen shortage in flooded soils and in solution culture. Plant Soil 187:37–45

Jackson RB, Mooney HA, Schulze ED (1997) A global budget for fine root biomass, surface area, and nutrient contents. Proc Natl Acad Sci USA 94:7362–7366

Jacobson RB, O'Connor JE, Oguchi T (2003) Surficial geologic tools in fluvial geomorphology. In: Kondolf GM, Piégay H (eds) Tools in fluvial geomorphology. Wiley, Chichester, pp 25–57

Kiley DK, Schneider RL (2005) Riparian roots through time, space and disturbance. Plant Soil 269:259–272

Koop H (1987) Vegetative reproduction of trees in some European natural forests. Vegetatio 72:103–110

Kramer H, Akça A (2002) Leitfaden zur Waldmeßlehre, 4. Aufl. Sauerländer's Verlag, Frankfurt am Main

Lehtonen A, Mäkipää R, Heikkinen J, Sievänen R, Liski J (2004) Biomass expansion factors (BEFs) for scots pine, norway spruce and birch according to stand age for boreal forests. For Ecol Manag 188:211–224

McClaugherty CA, Aber JD, Melillo JM (1982) The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. Ecology 63:1481–1490

McTammany ME, Webster JR, Benfield EF, Neatrour MA (2003) Longitudinal patterns of metabolism in a southern Appalachian River. J N Am Benthol Soc 22:359–370

Megonigal JP, Day FP (1992) Effects of flooding on root and shoot production of bald cypress in large experimental enclosures. Ecology 73:1182–1193

Meinen C, Hertel D, Leuschner C (2009) Biomass and morphology of fine roots in temperate borad-leaved forests differing in tree species diversity: is there evidence of below-ground overyielding? Oecologia 161:99–111

Merritt DM, Cooper DJ (2000) Riparian vegetation and channel change in response to river regulation: a comparative study of regulated and unregulated streams in the Green River Basin, USA. Regul Rivers Res Manag 16:543–564

Mitsch WJ, Ewel KC (1979) Comparative biomass and growth of cypress in Florida wetlands. Am Midl Nat 101:417–426

Nadelhoffer KJ, Raich JW (1992) Fine root production estimates and belowground carbon allocation in forest ecosystems. Ecology 73:1139–1147

Naiman RJ, Décamps H (1997) The ecology of interfaces: riparian zones. Annu Rev Ecol Syst 28:621–658

Persson H (1980a) Death and replacement of fine roots in a mature scots pine stand. Ecol Bull (Stockholm) 32:251–260

Persson H (1980b) Spatial distribution of fine-root growth, mortality and decomposition in a young scots pine stand in Central Sweden. Oikos 34:77–87

Piégay H, Schumm SA (2009) System approaches in fluvial geomorphology. In: Kondolf GM, Piégay H (eds) Tools in fluvial geomorphology. Wiley, Chichester, pp 105–134

Pregitzer KS, Friend AL (1996) The structure and function of *Populus* root systems. In: Stettler RF, Bradshaw HD Jr, Heilman PE, Hinckley TM (eds) Biology of *Populus* and its implications for management and conservation. NRC Res Press, Ottawa, pp 331–354

R Development Core Team (2012) R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org, Accessed 09 January 2012

Raich JW, Nadelhoffer KJ (1989) Belowground carbon allocation in forest ecosystems: global trends. Ecology 70:1346–1354

Rotkin-Ellman M, Addy K, Gold AJ, Groffman PM (2004) Tree species, root decomposition and subsurface denitrification potential in riparian forests. Plant Soil 263:335–344

Sali-Bazze M (1981) Entwicklung und Altersstellung von Böden der Donau- und Marchauen im Gebiet von Orth an der Donau und Marchegg / Baumgarten. Dissertation, Universität für Bodenkultur in Wien

Samaritani E, Shrestha J, Fournier B, Frossard E, Gillet F, Guenat C et al (2011) Heterogeneity of soil carbon pools and fluxes in a channelized and a restored floodplain section (Thur River, Switzerland). Hydrol Earth Syst Sci 15:1757–1769

Schachtschabel P, Blume HP, Brümmer G, Hartge KH, Schwertmann U (1998) Lehrbuch der Bodenkunde. Ferdinand Enke Verl, Stuttgart

Schapire R (2002) The boosting approach to machine learning–an overview. In: Denison DD, Hansen MH, Holmes C, Mallick B, Yu B (eds) MSRI Workshop on nonlinear estimation and classification (2002). Springer, New York, pp 149–172

Simm DJ, Walling DE (1998) Lateral variability of overbank sedimentation on a Devon flood plain. Hydrol Sci J 43:715–732

Sitte P, Weiler EW, Kadereit JW, Bresinsky A, Körner C (2002) Strasburger. Lehrbuch der Botanik. 35. Aufl. Spektrum Akad Verl, Heidelberg

Timoney KP, Argus G (2006) Willows, water regime, and recent cover change in the Peace-Athabasca Delta. Ecoscience 13:308–317

Tockner K, Schiemer F, Ward JV (1998) Conservation by restoration: the management concept for a river–floodplain system on the Danube River in Austria. Aquat Conserv Mar Freshw Ecosyst 8:71–86

Vogt KA, Vogt DJ, Palmiotto PA, Boon P, O'Hara J, Asbjornsen H (1996) Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant Soil 187:159–219

Vogt KA, Vogt DJ, Bloomfield J (1998) Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. Plant Soil 200:71–89

Williams CA, Cooper DJ (2005) Mechanism of riparian cottonwood decline along regulated rivers. Ecosystems 8:1–14

Zentralanstalt für Meteorologie und Geodynamik (2002) Klimadaten von Österreich 1971–2000. http://www.zamg.ac.at/fix/klima/oe7100/klima2000/klimadaten_oesterreich_1971_frame1.htm. Accessed 01 November 2011

Zianis D, Muukkonen P, Mäkipää R, Mencuccini M (2005) Biomass and stem volume equations for tree species in Europe. Silva Fenn Monogr 4:1–63

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14