ELSEVIER

Ecological Engineering 15 (2000) S157–S170

ECOLOGICAL ENGINEERING

www.elsevier.com/locate/ecoleng

Spatial and temporal patterns of carbon storage and species richness in three South Carolina coastal plain riparian forests

Laura A. Giese [a,*], W. Michael Aust [a], Carl C. Trettin [b], Randall K. Kolka [c]

[a] *Department of Forestry, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA*
[b] *USDA Forest Service, Southeastern Forest Experiment Station, Center for Forested Wetlands Research, Charleston, SC 29414, USA*
[c] *Department of Forestry, University of Kentucky, Lexington, KY 40546, USA*

Received 19 March 1999; received in revised form 1 June 1999; accepted 15 September 1999

Abstract

The distribution of organic matter within a floodplain is a controlling factor affecting water quality, habitat, and food webs. Accordingly, development of vegetation in the riparian zone can be expected to influence ecosystem functions, and organic matter storage patterns are believed to be indicators of functional recovery in disturbed riparian zones. Our objective was to compare the distribution and allocation of organic matter among microsites within the floodplain and with temporal changes (successional status) associated with community development. Three third order streams in the upper coastal plain of South Carolina were selected. Measurement transects were established across three floodplains of varying successional status, Meyer's branch; a mature riparian hardwood forest; Fourmile branch; a mid-successional riparian forest; and Pen Branch, an early successional riparian forest. Overall, measurements of aboveground biomass, soil carbon, and stand structure indicate that the early and mid successional stands are becoming more similar to the mature stand and that microsite differences within the braided, riparian stream systems are small.

Keywords: Carbon; Disturbance; Forest succession; Riparian; Wetland restoration

1. Introduction

In the last 15–20 years, riparian forests have become recognized as important components of the landscape and serve as a vital link between the aquatic environment and upland ecosystems. Riparian forests are especially critical to maintaining stream health and water quality, and providing the aquatic ecosystem with organic carbon, habitat, bank stabilization, and shade (Mitsch and Gosselink, 1993). Riparian forests also protect waterways from sediment, nutrients, and other surface and groundwater pollutants. Accordingly, maintenance of riparian vegetation or restoration

* Corresponding author. Tel.: + 1-540-2319929; fax: + 1-540-2313330.
E-mail address: lgiese@vt.edu (L.A. Giese).

PII: S0925-8574(99)00081-6

of degraded sites is critical to sustain inherent ecosystem functions and values.

Organic matter is a primary energy source, in forests it is derived from litter fall, root turnover, and microbial organisms. The relationship between forest productivity and organic matter pools (i.e. vegetation, soils, water) is complex. Vegetation has been found to be more important than microclimate, soil, successional processes, slope, aspect, and elevation in controlling soil organic carbon in an ecosystem (Van Cleve and Powers, 1995). Vegetation directly influences soil carbon accumulation and soil development through above- and below-ground net primary production (NPP) (Zak et al., 1990). Most of the retention of organic carbon in flooded ecosystems occurs in the floodplain. Plant nutrient supply is affected by detrital processes, which influence organic matter mineralization rates, which in turn is influenced by hydroperiod. Accordingly, this feedback mediates nutrient supplies for NPP and the status of soil organic matter.

Successional patterns of NPP and aboveground biomass have been established for upland forest ecosystems (Odum, 1960). A similar pattern of productivity increasing in a stepwise fashion with time can be found in riparian forests as succession proceeds to dominance by tree forms. Net primary productivity can vary depending principally on the species composition and condition of the floral community.

Riparian ecosystems are often considered to have a combination of high species diversity, high species densities, and high productivity (Mitsch and Gosselink, 1993). Species richness is generally low in the early stages of succession and increases as the 'climax' community is approached (Spellerberg, 1991). Odum's (Odum, 1960) classic study of old field succession in South Carolina observed an increase in species number from five dominant species to nearly 20 dominant species after a period of 7 years. In subsequent years, herbaceous species numbers increased, but annual productivity remained fairly constant. The inclusion of woody species shows a rapid increase in annual productivity with canopy closure followed by stabilization (Peet, 1982). There is little evidence that the addition of a new species in later successional stages results in higher productivity (Mooney and Gulmon, 1983).

In early stages of succession, subtle changes in landscape elevation (micro-topography) may influence herbaceous species establishment and growth, subsequently affecting the accumulation of organic matter. Micro-topography was found to influence the distribution of vegetation (frequency and density) across an elevation gradient (Zedler and Zedler, 1969; Huenneke and Sharitz, 1986). Microsite elevation is strongly correlated with seedling distribution in a floodplain swamp (Titus, 1990). Significant correlations between elevation gradients, and organic matter content and moisture have also been found (Zedler and Zedler, 1969; Titus, 1990). Additionally organic matter levels have been shown to influence species distribution where differences in elevation were not controlling. In a comparison between floodplain, transition, and upland, Johnson and Bell (1976) found biomass and NPP to be greatest in the floodplain zone and least in the transition zone. Conner et al. (1993) found an increase in stem wood production in dry and wet sections of a bottomland hardwood forest in Louisiana, but production remained relatively unchanged in a transitional area.

Achieving restoration of a riparian forest is difficult, especially if the successional processes have been altered. An additional challenge is determining whether a restoration effort is successful. Investigating the biotic–abiotic interactions in riparian forests may provide some insights to recovery processes. These interactions may operate as measures/indices of success. Relationships between vegetation, soil carbon, species richness, and micro-topography may show trends that suggest restoration is occurring and be used to evaluate restoration success. The comparison of these interactions/relationships through a forest chronosequence may provide a better understanding of restoration processes.

Spatial patterns of vegetation–soil relationships within a riparian forest, especially along a gradient perpendicular to the stream, are not well known. Understanding how spatial structure influences ecosystem processes may also provide insight to determining the recovery of disturbed riparian ecosystems. This study will address whether very highly disturbed ecosystems can re-develop net primary productivity and a similar species composition compared to an undisturbed reference system, and does tree planting with site preparation change this natural recovery pattern. Also, investigated is the influence of riparian forest age on spatial and temporal patterns of carbon storage and species richness in riparian forests.

2. Study area and methods

The study sites are located in riparian forests adjacent to three braided, blackwater streams on the Savannah River Site (SRS), National Environmental Research Park in South Carolina. Pen branch and Fourmile branch are third order tributaries of the Savannah river that received thermal, elevated discharge from nuclear production processes between 1954 and 1989, and 1955 and 1985, respectively. This disturbance resulted in the loss of vegetation (mainly the woody component), and sediment erosion and deposition (Kolka et al., 2000). The third stream system, Meyer's branch, represents a minimally disturbed, third order reference site. Selective logging occurred in Meyer's branch in the 1940s. The age of the riparian forests adjacent to Pen branch, Fourmile branch, and Meyer's branch at the time of the study are 7, 11, and approximately 60 years, respectively. There are two treatment areas along Pen branch. One area is considered a control and has been allowed to regenerate naturally. An adjoining area was herbicided followed by burning and then planting with bottomland hardwood species. This is referred to as the artificial regeneration area.

2.1. Species composition

The riparian areas on either side of the main stream channels range in width from 8 to 95 m. Early successional species of willow (*Salix* spp. L.), waxmyrtle (*Myrica cerifera* L.), smooth alder (*Alnus serrulata* (Ait.) Willd.), and buttonbush (*Cephalanthus occidentalis* L.) dominate the natural regeneration riparian area of Pen branch. The planted section (artificial regeneration) of Pen branch is dominated by herbaceous vegetation and blackberry (*Rubus* spp.), with some buttonbush and alder. The woody component of the Fourmile branch riparian forest is also dominated by willow, with the addition of red maple (*Acer rubrum* L.), alder, waxmyrtle, and loblolly pine (*Pinus taeda* L.). Meyer's branch represents a mature bottomland forest with a mixed species composition including bald cypress (*Taxodium distichum* L.), tupelo (*Nyssa* spp.), red maple, Virginia willow (*Itea virginica* L.), arrowwood (*Viburnum dentatum* L.), and dog-hobble (*Leucothoe axillaris* (Lam.) D. Don.) as the dominant species.

2.2. Soil descriptions

Soils in the riparian area of Pen branch include typic endoaquepts, typic fluvaquents, and thapto-histic fluvaquents (Azola, 1997). Adjacent upland soils were characterized as entisols and ultisols. In the Fourmile branch riparian forest, soils are generally thapto-histic fluvaquents which have a buried A or histic horizon. Adjacent upland soils are ultisols on the west side of the main channel (typic endoaquults, aquic hapludults) and entisols on the east side of the main channel (typic and aquic quartzipsamments). Most of the soils in the Meyer's branch riparian forest have an organic layer at least 18 cm deep and the histosols present (typic medisaprists) had several organic layers extending to an average of 102 cm. Other riparian soil types include humaqueptic endoaquepts and fluvaquents. The upland soils are very sandy (grossarenic hapludults, and arenic endoaquults).

2.3. Standing biomass

Transects were established perpendicular to the main stream channel and generally ran the width of the riparian area extending into the upland. The transects in this study were established in conjunction with the transects established for the hydrology project presented in this publication (Kolka et al., 2000). Transect length ranged from 3 to 94 m. Three transects were established within the natural regeneration area of Pen branch (PBC), three within the artificial regeneration area of Pen branch (PBD), six within the Fourmile branch (FM) riparian forest, and five within the Meyer's branch (MB) riparian forest. Along each transect, main plots were spaced at 15.2-m intervals originating at the main channel. The number of main plots and subplots for the riparian areas within each study site are provided in Table 1. At each main plot, the diameter, height, and species of all trees (dbh >4.0 cm) within a 0.013 ha circular plot were recorded. Diameter, height, and species were recorded for all shrubs (dbh <4.0 cm and height >0.5 m) within a 0.002 ha plot. Field sampling was conducted in June 1997. Aboveground biomass values for the trees and shrubs were estimated using dbh:biomass regressions from the literature (Clark et al., 1985; Muzika et al., 1987; Mader, 1990; Hauser, 1992; Gholz et al., 1999).

2.4. Herbaceous/species richness

Along each transect, subplots were spaced at 4.5 m on either side of the main plot with the main plot serving as a third subplot. Within each subplot, herbaceous vegetation (<0.5 m in height, regardless of growth form) was clipped from a 0.25 m^2 area. The species observed in each clip plot were recorded to determine species richness (# per 0.25 m^2). Micro-topography was subjectively rated at each subplot to be either wet, intermediate, or dry based on position in the landscape (ridge or swale). Field sampling was conducted in June and August 1997. All the clipped vegetation was oven dried at 60°C for at least 2 weeks and then weighed.

Table 1
Number of main plots and subplots within the riparian component of the study areas

Study area	Riparian	
	Main plots	Sub-plots
Pen branch *Natural regeneration*	12	37
Pen branch *Artificial regeneration*	11	34
Fourmile branch	16	51
Meyer's branch	15	49

2.5. Net primary productivity

Estimation of total net annual primary productivity was determined by the mean annual increment method (Art and Marks, 1971) in which the woody biomass is divided by the age of the forest stand. The mean annual increment method generally underestimates the current woody production. Trees and shrubs were divided by the respective riparian forest age (7, 11 and 60 years for the two areas in Pen branch, the riparian forest along Fourmile branch, and the Meyer's branch riparian forest, respectively). For Meyer's branch 60 years was used as a conservative measure since the area supposedly was selectively harvested in the 1940s. The herbaceous strata were considered the annual increment.

2.6. Soil carbon

Bulk soil samples were collected from the O/A horizons in each riparian area and adjacent upland. The A-horizon is approximately 7.5–13 cm in depth in the Fourmile branch riparian forest and 7.5–15 cm in depth in the two areas of Pen branch (Azola, 1997). The O-horizon in the Meyer's branch riparian forest ranges from 20 – to 76 + cm. Samples were taken corresponding to a certain distance from the main channel (0–15.2, 15.2–30.3, 30.3–45.4, and 60.6 m) and associated with micro-topography assessments similar to the micro-topography ratings given for the herbaceous subplots. The carbon content of the soil was determined with a LECO gas analyzer.

2.7. Riparian forest similarity

Sorensen's index (Sorensen, 1948) was used to compare community similarity based on number of species only, whether common or rare Eq. (1).

Table 2
Aboveground biomass, mean annual productivity, species richness, and soil carbon for four riparian forests located at the SRS in SC[a]

	Pen branch natural regeneration	Pen branch artificial regeneration	Fourmile branch	Meyer's branch
	Aboveground biomass (kg ha^{-1})			
Herbaceous[b]	1205b (560)	4503a (2320)	1791b (1700)	505c (860)
Shrubs	6303 (7311)	833 (1442)	4609 (5963)	4694 (2639)
Trees (× 1000)	19.5b (7.8)	0.313b (0.5)	17.5b (15.0)	196.6a (105.6)
Total[c] (× 1000)	27.0b (10.0)	5.7b (1.9)	7.4b (6.4)	202.0a (106.0)
Mean annual productivity (kg ha^{-1} per year)[c,d]	4442 (1200)	4662 (1152)	3680 (923)	3859 (2395)
Herbaceous species richness[b,e]	2.35ab (1.22)	2.86ab (1.74)	2.23b (1.51)	2.96a (1.62)
Soil carbon[f] (%)	4.68b (1.26)	4.32b (1.96)	4.06b (2.27)	13.19a (2.44)

[a] Significant difference between letters a, b, and c; numbers in parentheses represent S.D.
[b] N for PBC, PBD, FM, and MB are 37, 34, 51, 49, respectively.
[c] Includes tree and shrub growth, and herbaceous growth.
[d] In PBC, PBD, FM, and MB for shrubs, trees, total biomass and annual productivity $N = 12, 11, 16, 15$, respectively.
[e] Species richness incorporates both June 1997 and August 1997 sample dates. N for PBC, PBD, FM, and MB are 63, 64, 99, 98, respectively.
[f] N for PBC, PBD, FM, and MB are 27, 48, 75, 66, respectively.

$$\text{Percent similarity} = \frac{\text{Number of areas being compared} \times \text{Number of species in common}}{\text{Total number of species in areas being compared}} \times 100 \qquad (1)$$

2.8. Statistical analysis

All comparisons were performed with analysis of variance (ANOVA) followed by multiple comparison procedures (Tukey and LSD). Regression was used to determine if there was a linear relationship between distance from the main stream channel and species richness, herbaceous biomass, and soil carbon. An alpha level of 0.05 was used for all statistical analyses.

3. Results

3.1. Standing biomass

Herbaceous biomass was not significantly different between the two sampling dates (June and August 1997), except in the Fourmile branch riparian forest (data not shown). Generally, the June sampling date had a higher biomass, therefore, these values were included in the calculation of total biomass. The planted riparian area of Pen branch had significantly greater herbaceous biomass than the other three riparian forests (Table 2). The Fourmile branch riparian forest and the natural regeneration area of Pen branch have greater herbaceous biomass than the Meyer's branch riparian forest.

Comparisons across the riparian forest chronosequence showed that total aboveground biomass was significantly greater in the Meyer's branch riparian forest than the other three riparian forests (Table 2). Between the four riparian forests, shrub biomass was not significantly different. However, tree biomass was significantly greater in the Meyer's branch riparian forest than the other three riparian forests.

3.2. Productivity

Mean annual productivity (Table 2) was not significantly different between the four riparian forests or the adjacent upland forests.

3.3. Carbon

Soil carbon was significantly higher in the riparian forest of Meyer's branch than the other three disturbed riparian forests (Table 2). Generally, the riparian forest had significantly more soil carbon than the adjacent upland except for the artificial regeneration area of Pen branch.

3.4. Herbaceous species richness

Species richness was only analyzed for the herbaceous component. Number of herbaceous species per subplot in each riparian forest ranged from 1 to 8 in the three disturbed riparian forests, and 0–7 in the Meyer's branch riparian forest. Species richness was significantly lower in the Fourmile branch riparian forest than the Meyer's branch riparian forest.

3.5. Riparian forest similarity

The combined tree and shrub data accounted for 8, 11, 15, and 25 species for the natural regeneration area of Pen branch, artificial regeneration area of Pen branch, Fourmile branch riparian forest and the Meyer's branch riparian forest, respectively. Five species were common to the three disturbed riparian areas (red maple, alder, buttonbush, waxmyrtle, and willow), and only two species were common to all four riparian forests (red maple and waxmyrtle). Red maple was more abundant in the mature riparian forest whereas, waxmyrtle was more prevalent in the three younger riparian forests.

Herbaceous species similarity was calculated for the four riparian forests. The two areas in Pen branch had 23 common species and 68% similarity. The Fourmile branch riparian forest and natural regeneration area of Pen branch had 24 species in common and 64% similarity. Only 21 species and 54% similarity was found between the Fourmile branch riparian forest and the artificial regeneration area of Pen branch. The Meyer's branch riparian forest had 26, 20, and 15 species in common with the Fourmile branch riparian forest, the natural regeneration area of Pen branch, and the artificial regeneration area of Pen branch, respectively. The Meyer's branch riparian forest had 58% similarity to the Fourmile branch riparian forest, 50% similarity to the natural regeneration area of Pen branch, and 36% similarity to the artificial regeneration area of Pen branch.

3.6. Micro-topography

Micro-topography appears to influence herbaceous biomass (Table 3). There was significantly higher herbaceous biomass in the 'wet' areas of the Fourmile branch riparian forest than the 'dry' areas. However, there was no significant difference in herbaceous biomass between 'wet', 'intermediate' and 'dry' areas in either the natural or artificial regeneration riparian areas of Pen branch and no significant difference between the 'wet' and 'intermediate' areas in the Meyer's branch riparian forest. Although not significant, there appears to be several trends. In the Pen branch artificial regeneration area and the Meyer's branch riparian forest herbaceous biomass increases as micro-topography becomes drier. Contrastingly, in the riparian forest of Fourmile branch herbaceous biomass decreases from 'wet to dry' areas.

Micro-topography also appears to influence species richness. In general, the 'intermediate' areas express greater herbaceous species richness. In the Fourmile branch riparian forest, species richness was significantly more in the 'intermediate' areas than either the 'wet' or 'dry' areas. There was no micro-topography effect on species richness in the natural regeneration area of Pen branch or the Meyer's branch riparian forest.

The percent carbon in the soil appears to be influenced by micro-topography. In the Fourmile branch riparian forest there was significantly more carbon in the soil of 'wet' areas, but significantly more soil carbon in the 'dry' areas of the artificial regeneration area of Pen branch. Again, there was no difference in soil carbon based on micro-topography in the natural regeneration area of Pen branch or the Meyer's branch riparian forest. In general, the percent carbon in the soil follows micro-topography trends similar to the herbaceous biomass.

Table 3
Differences in herbaceous biomass, species richness and percent soil carbon due to micro-topography; wet (W), intermediate (I), and dry (D)[a]

Study area	Herbaceous biomass (g)			Species richness			Soil carbon (%)		
	W	I	D	W	I	D	W	I	D
Pen branch natural regeneration	27.3 (23)	39.6 (25)	29.1 (18)	2.2 (1.2)	1.9 (1.2)	2.6 (1.2)	N/A[b]	3.4 (0.2)	4.8 (0.6)
Pen branch artificial regeneration	95.2 (58)	115.2 (45)	135.3 (53)	2.8 (1.8)	3.4 (1.8)	2.2 (1.3)	3.0b (1.5)	4.5ab (0.1)	5.75a (1.5)
Fourmile branch	47.0a (37)	41.5ab (32)	25.8b (34)	2.0ab (0.9)	2.9a (1.6)	2.0b (1.7)	5.0a (2.7)	N/A	2.9b (0.6)
Meyer's branch	7.6 (7)	16.0 (19)	N/A	2.6 (1.6)	3.7 (2.0)	N/A	13.0 (3.0)	13.5 (1.5)	N/A

[a] Significant difference between letters a and b; numbers in parentheses are S.D.
[b] N/A, no sample obtained or sample size too small.

Table 4
Regression analysis for dependent variables herbaceous biomass, species richness, and soil carbon, and independent variable distance[a]

Study area	Herbaceous biomass				Species richness				Soil carbon (%)			
	Intercept	Slope	P-value	r^2	Intercept	Slope	P-value	r^2	Intercept	Slope	P-value	r^2
Pen branch natural regeneration	29.4	0.40	0.481	0.01	2.2	0.02	0.620	0.00	5.6	−0.46	0.120	0.09
Pen branch artificial regeneration	126.2	−2.13	0.104	0.04	3.2	−0.05	0.213	0.02	3.5	0.40	0.118	0.05
Fourmile branch	42.5	−1.16	0.317	0.01	2.7	−0.10	0.046	0.04	4.8	−0.30	0.225	0.02
Meyer's branch	−0.3	1.80	2.4E−07	0.24	3.5	−0.07	0.037	0.04	11.3	0.77	0.004	0.12

[a] Equation example, herbaceous biomass = intercept + slope × distance from main channel.

3.7. Spatial effects on vegetation

There was no significant linear relationship between distance from main channel and herbaceous biomass, species richness, or percent carbon in the soil in either of the Pen branch riparian areas (Table 4). There was a slightly significant linear relationship between distance from the main channel and species richness in the Fourmile branch riparian forest. All three dependent variables were significant with distance from the main channel in the Meyer's branch riparian forest.

4. Discussion

As riparian forests recover from disturbance abiotic–biotic interactions should develop towards a facsimile of their original state and reflective of undisturbed systems. This assumption may not be reasonable if the substrate in the disturbed riparian forests has been severely altered. Consequently, successional processes may no longer be operating at the same scale. A critical factor for successful restoration is the establishment of original/appropriate hydrology followed by edaphic and biotic components (Clewell and Lea, 1990). Aboveground biomass, organic carbon, and species richness may serve as criterion for evaluating restoration.

Table 5
Herbaceous biomass at several undisturbed and thermally recovering riparian forests on the SRS, SC

Study Area	Herbaceous biomass (kg ha^{-1})	Reference
Pen branch-thermal 20 years	2230	Sharitz et al., 1974
Steel creek-5 years post thermal natural regeneration	3400	Sharitz et al., 1974
Pen branch-7 years post thermal artificial regeneration	4468	This study
Pen branch-7 years post thermal natural regeneration	1295	This study
Fourmile branch-11 years post thermal	1462	This study
Steel creek-15 years post thermal	900	Muzika et al., 1987
Meyer's branch-mature undisturbed (1983)	150	Muzika et al., 1987
Meyer's branch-mature undisturbed (1997)	520	This study
Upper Three Runs creek-mature undisturbed	1340	Sharitz et al., 1974

The planted riparian area of Pen branch has the greatest herbaceous biomass which probably is a reflection of the site preparation. The burning and herbicide treatment opened the canopy and allowed for the rapid establishment of herbaceous species. The herbaceous biomass in the mature riparian forest of Meyer's branch is less than the other three riparian forests, but 3.5 times greater than the annual herbaceous biomass found by Muzika et al. (1987) in Meyer's branch. Although Muzika's study was in the same general area as this study, she sampled 13 years earlier as well as later in the growing season, which could account for differences in herbaceous biomass. The herbaceous biomass in the two riparian areas of Pen branch, and the Fourmile branch riparian forest is > 15 year recovering riparian forests (Muzika et al., 1987) which is reflective of changes in stand structure proceeding towards a closed canopy. Reviewing chronological herbaceous biomass data from studies conducted at SRS there is a general decrease in herbaceous biomass with time (Table 5).

Herbaceous and shrub biomass were found to be higher in a floodplain–upland transition zone as a result of low tree biomass (Johnson and Bell, 1976) which is similar to the artificial regeneration area of Pen branch. In a bottomland hardwood and bald cypress–water tupelo swamp, Conner and Day (1976) found herbaceous biomass to be 2000 and 200 kg ha^{-1} per year, respectively. Bottomland hardwood herbaceous biomass values are comparable to the early successional sites in this study while the cypress-tupelo swamp biomass is similar to the undisturbed site (Meyer's branch).

The establishment of woody species is probably being prevented by competition with the rich herbaceous flora in the artificial regeneration area of Pen branch. This is similar to the sediment deposition and dense herb cover that have inhibited bald cypress regeneration in the disturbed Steel creek floodplain (Dunn and Sharitz, 1987). Whereas the mature riparian forest of Meyer's branch has significantly higher tree biomass than the three disturbed systems, there are no major differences in tree biomass between the disturbed riparian forests. Although not significantly different, shrub biomass tends to be lowest in the artificial regeneration area of Pen branch, comparable between the Fourmile branch riparian forest and the Meyer's branch riparian forest, and greatest in the natural regeneration area of Pen branch. Since the Fourmile branch riparian forest is only a couple years older, the contradictory pattern in shrub biomass between it and the natural regeneration area of Pen branch could be exhibiting a stand structure transition or be influenced by differing hydroperiods (Johnson and Bell, 1976; Mitsch and Ewel, 1979). Tied to changes in plant community structure Wigginton et al., 2000 also found a marked decline in herbaceous material and a considerable increase in woody foliage in the forest floor with later seral stages.

The total aboveground biomass and mean annual productivity in the mature riparian forest of Meyer's branch is comparable to other undisturbed coastal plain riparian forests (Table 6) and has the greatest total biomass of the four forests studied. Disturbed sites have similar productivity to undisturbed sites, but much lower aboveground biomass. The 11-year-old riparian forest of Fourmile branch has less total biomass than the 7-year-old natural regeneration area of Pen branch. This contradiction may occur because Fourmile has a flashier hydroperiod and more swale microtopography that tends to pond water, whereas the natural regeneration area of Pen branch is generally drier and soils are better aerated. A 7 and 8-year-old post harvest riparian forest along the Santee river, SC had woody biomass of 55.8 kg ha^{-1} (Bates, 1989), which is higher than the disturbed riparian forests in this study. The lower biomass is probably due to the intensity, duration, and scale of the thermal disturbance (Reiners, 1983; De Steven and Sharitz, 1997) that occurred at these sites.

Mean annual productivity was not significantly different between the four riparian forests and this may be because the value does not include litterfall (Table 2). The herbaceous component in the artificial regeneration area of Pen branch appears to overcome the lack of woody vegetation. Bates (1989) found productivity rates of 9090 kg ha^{-1} per year for a 7 and 8-year-old post harvest riparian forest. This is at least twice the productivity found at all four sites in this study. Again the severity of the disturbance that occurred at SRS likely removed an available seed source as well as disrupted a suitable substrate for growth. Scott et al. (1985) also observed how disturbance affects productivity. They found higher aboveground NPP at a least disturbed site compared to an intermediate disturbed site because the least disturbed site had a greater density of trees. Brown and Peterson (1983) found that not all riparian forest are highly productive, however the sites in this study appear to be moderately productive systems (Table 6).

The herbaceous layer production (1660 kg ha^{-1} per year) in the 7 and 8-year-old floodplain forest of the Santee river (SC) was highest in mid-spring, coinciding with seasonal flood water recession (Bates, 1989). Similar patterns in herbaceous vegetation were found at SRS with the June sampling higher than the August sampling.

Herbaceous species richness in the mature riparian forest of Meyer's branch was greater than the three disturbed riparian forests at the 0.25 m^2 scale (Table 2). Sharitz et al. (1974) studied thermal and post-recovery sites at the SRS and found higher plant species number in the 5-year post-thermal site than directly after disturbance. In an old-field succession in a former bottomland hardwood forest, Battaglia et al. (1995) found that the number of species increases up to year 3, but decreases in years 4 and 5. Successional patterns in an Indiana bottomland exhibited a considerable influx of woody species by year 10, however many of the woody species that would become important components of later seral stages were present at 2 years after the former agricultural field was abandoned (Hopkins and Wilson, 1974).

As predicted by successional theory, the number of tree and shrub species increased with forest

Table 6
Aboveground biomass and production of coastal plain riparian forests and similar forested wetlands (adapted from Conner, 1994 and modified from Zaebst, 1997)

Forest type/location	Aboveground biomass (kg ha^{-1} × 1000)	Annual productivity (stem growth only) (kg ha^{-1} per year × 1000)	Reference
Cypress–water tupelo/LA	375	5.0	Conner and Day, 1976
Cypress–water tupelo/FL	190	2.89	Mitsch and Ewel, 1979
Floodplain swamp/NC	267	5.85	Mullholland, 1979
Floodplain swamp/FL	284	10.86	Brown, 1981
Bottomland hardwood/LA	165	8.0	Conner and Day, 1976
Dismal swamp-bottomland hardwood/VA	189	–	Day and Dabel, 1978
Dismal swamp-maple/gum/VA	190	–	Day and Dabel, 1978
Cypress swamp/LA	278	–	Conner and Day, 1982
Cypress-hardwood/FL	154	3.36	Mitsch and Ewel, 1979
Dismal swamp-cypress/VA	339	--	Day and Dabel, 1978
Okefenokee swamp/GA	307	3.53	Schlesinger, 1978
Cypress-hardwood/SC	202	3.35	This study
Meyer's branch Cypress-hardwood/SC	348	13.4	Muzika et al., 1987
Naturally recovering bottomland hardwood/SC 15 years post disturbance	26	2.85	Muzika et al., 1987
Naturally recovering bottomland hardwood/SC 11 years post disturbance-FM	7.4	1.89	This study
Naturally recovering bottomland hardwood/SC 7 years post disturbance-PBC	27	3.24	This study
Restored bottomland hardwood/SC 7 years post disturbance-PBD	5.7	0.16	This study

age at our sites. Sharitz et al. (1974) found similar increase in woody species numbers following thermal disturbance. The Meyer's branch riparian forest had 15–20 herbaceous species common to the disturbed riparian areas of Pen branch and 36–50% similarity (note that the natural regeneration area of Pen branch had 37 subplots used for species identification and the Meyer's branch riparian forest had 49 subplots, therefore if more subplots were established in the natural regeneration area of Pen branch, there is the possibility to find more species in common). However, several factors (hydroperiod, substrate) inherent to each site could impede establishment of certain species and limit species diversity. Sixteen common species and approximately 30% similarity were found between an undisturbed site and a 5-year post thermal recovery site on the SRS (Sharitz et al., 1974). The slightly lower similarity may be due to the inclusion of trees species in their study. Herbaceous species similarity is fairly high between the two riparian areas of Pen branch. The natural regeneration area of Pen branch has greater similarity to the riparian forest in Fourmile branch and the Meyer's branch riparian forest than the artificial regeneration area of Pen branch possibly due to the site preparations conducted in the latter. Sharitz et al. (1974) also found species similarity to be high between thermally affected areas. However, the Fourmile branch riparian forest has greater species similarity to the mature riparian forest of Meyer's branch than to either areas of Pen branch which may suggest that the riparian forest of Fourmile branch is further along in succession than the Pen branch sites. The fewer sample plots in Pen branch compared to Fourmile branch and Meyer's branch (Table 1) may also influence herbaceous species similarity.

Micro-topography interacting with the hydroperiod in these riparian forests forms a heterogeneous environment. The slight variation in elevation results in changes in vegetation composition due to an anaerobic gradient (Wharton et al., 1982). However, the effect of micro-topography was not apparent in the natural regeneration area of Pen branch and the Meyer's branch riparian forest. In Meyer's branch, micro-topography is very subtle, unlike the ridge and swale landscape in the Pen branch and Fourmile branch riparian forests. Although the stream system is braided in the natural regeneration riparian area of Pen branch, most of the herbaceous plots were 'dry'. Micro-topography seemed to have the greatest effect in the Fourmile branch riparian forest. The 'wet' areas had a few dominant herbaceous species, which produced more biomass and possibly contributed more carbon to the soil than either the 'intermediate' or 'dry' areas (Table 3). There appears to be a distinct interaction between the amount of herbaceous biomass and percent carbon in the soil as evident also in the artificial regeneration area of Pen branch. Here the reverse occurred in that more herbaceous biomass and higher percent soil carbon was observed in the 'dry' areas.

There appears to be little spatial gradient influence on herbaceous biomass, herbaceous species richness or percent carbon in the soil in the three disturbed riparian forests. There is a slightly significant decrease in species richness with increasing distance from the Fourmile branch main channel. The braided landscape probably interferes with the distribution of sediment and organic matter deposited in the riparian areas during flooding. The Meyer's branch riparian forest showed a significant increase in herbaceous biomass and percent carbon in the soil with increasing distance from the main channel. In sampling the herbaceous component in Meyer's branch, a prevalent woody species which was abundant along the upland/wetland boundary was included, and this may have significantly increased the amount of herbaceous biomass.

The percentage of soil carbon in the mature riparian forest is approximately triple the carbon in the three younger riparian forests. Elevated flows in the disturbed riparian forest lead to the deposition of mineral sediment and may account for the lower percentage of soil carbon. Age and hydrologic factors influence the accumulation of organic matter in the riparian area. Wigginton et al. (2000) found forest floor organic matter and carbon content increased rapidly during early succession and declined thereafter, and soil carbon content increased with successional stage. In the early stages of old field succession on bottomlands, Hopkins and Wilson (1974) observed an increase in soil carbon in year 2 due to the rapid decomposition of annuals, followed by a decrease the third year due to a change in species which remain erect throughout the winter. The disturbed riparian areas in our study were rapidly colonized by herbaceous flora, and carbon accumulation is beginning to occur.

5. Conclusions

The severity of disturbance influences the ability of a community to return to a pre-disturbance condition. Site conditions and succession processes may be altered to the extent that recovery is not eminent. The structure of a riparian forest is not only reliant on successional processes, but often influenced by micro-topography. Small changes in elevation affects hydroperiod and subsequently herbaceous biomass, species richness, and percent carbon in the soil. The percentage of carbon in the soil suggests that the disturbed riparian forests are beginning to accumulate this essential component. Successional processes are slowly occurring in the disturbed riparian forests. If the hydrology has been altered, pre-disturbance species composition or a species composition similar to the mature riparian forest will not occur. However, the disturbed riparian forests appear to be providing functions comparable to the mature riparian forest if organic matter is a reliable indicator. The biotic–abiotic interactions and successional processes are indications of recovery, i.e. the disturbed riparian forests may be progressing toward a riparian forest similar to the mature riparian forest.

Acknowledgements

The authors wish to acknowledge the financial and logistical support of the US Forest Service — Center for Forested Wetlands Research, Savannah River National Resource Management and Research Institute, the Savannah River Site-National Environmental Research Park, and Virginia Polytechnic Institute and State University. Also, recognition of those who helped in the field, Cary Coppock; William Casey; Frederick James; Julian Singer and especially Rex Overacre.

References

Art, H.W., Marks, P.L., 1971. A summary table of biomass and net annual primary production in forest ecosystems of the world. In: 15th International Union Forest Res. Organ. Congress on Forest Biomass Studies: Growth and Yield, Sec. 25, pp. 3–32.

Azola, T., 1997. Soil taxonomic descriptions of three floodplains in the upper coastal plain of South Carolina. Undergraduate Student Research Project, School of Forestry and Wildlife Resources, Virginia Polytechnic Institute and State University, Blacksburg, VA, p. 41.

Bates, R.D., 1989. Biomass and primary productivity on an early successional floodplain forest site. In: Sharitz, R.R., Gibbons, J.W. (Eds.), Freshwater Wetlands and Wildlife, Conf-8603101, DOE Symposium Series No. 61, USDOE Office of Scientific and Technical Information, Oak Ridge, TN, pp. 375–383.

Battaglia, L.L., Keough, J.R., Pritchett, D.W., 1995. Early secondary succession in a southeastern US alluvial floodplain. J. Veg. Sci. 6, 769–776.

Brown, S., 1981. A comparison of the structure, primary productivity, and transpiration of cypress ecosystems in Florida. Ecol. Monogr. 51 (4), 403–427.

Brown, S., Peterson, D.L., 1983. Structural characteristics and biomass production of two Illinois bottomland forests. Am. Midl. Nat. 110 (1), 107–117.

Clark III, A., Phillips, D.R., Frederick, D.J., 1985. Weight, volume, and physical properties of major hardwood species in the Gulf and Atlantic coastal plains. USDA Forest Service, Southeastern Forest Experiment Station, Asheville, NC Research Paper 250, p. 66.

Clewell, A.F., Lea, R., 1990. Creation and restoration of forested wetland vegetation in the southeastern United States. In: Kusler, J.A., Kentula, M.E. (Eds.), Wetland Creation and Restoration: The State of the Science. Island Press, Washington, DC, pp. 195–232.

Conner, W.H., 1994. Effect of forest management practices on southern forested wetland productivity. Wetlands 14 (1), 27–40.

Conner, W.H., Day, J.W. Jr, 1976. Productivity and composition of a bald cypress-water tupelo site and a bottomland hardwood site in a Louisiana swamp. Am. J. Bot. 63, 1354–1364.

Conner, W.H., Day Jr., J.W., 1982. The ecology of forested wetlands in the southeastern United States. In: Gopal, B., Turner, R.G., Wetzel, R.G., Whigham, D.F. (Eds.), First Int. Wetlands Conf. on Wetlands Ecology and Management, 10–17 September 1980, New Delhi, India, INTECOL and NIE, pp. 69–87.

Conner, W.H., Day, J.W. Jr, Slater, W.R., 1993. Bottomland hardwood productivity: case study in a rapidly subsiding, Louisiana, USA, watershed. Wetl. Ecol. Manage. 2 (4), 189–197.

Day Jr., F.P., Dabel, C.V., 1978. Phytomass budgets for the Dismal Swamp ecosystem. VA J. Sci., 220–224.

De Steven, D., Sharitz, R.R., 1997. Differential recovery of s deepwater swamp forest across a gradient of disturbance intensity. Wetlands 17 (4), 476–484.

Dunn, C.P., Sharitz, R.R., 1987. Revegetation of a *Taxodium–Nyssa* forested wetland following complete vegetation destruction. Vegetatio 72, 151–157.

Gholz, H.L., Guerin, D.N., Cropper Jr., W.P., 1999. Phenology and productivity of saw palmetto (*Serenoa repens*) in a north Florida slash pine plantation. Can. J. For. Res., in press.

Hauser, J.W., 1992. Effects of hydrology-altering site preparation and fertilization-release on plant diversity and productivity in pine plantations in the coastal plain of Virginia. M.S. thesis, School of Forestry and Wildlife Resources, Virginia Polytechnic Institute and State University, Blacksburg, VA.

Hopkins, W.E., Wilson, R.E., 1974. Early oldfield succession on bottomlands of southeastern Indiana. Castanea 39, 57–71.

Huenneke, L.F., Sharitz, R.R., 1986. Microsite abundance and distribution of woody seedlings in a South Carolina cypress–tupelo swamp. Am. Midl. Nat. 115 (2), 328–335.

Johnson, F.L., Bell, D.T., 1976. Plant biomass and net primary production along a flood-frequency gradient in the streamside forest. Castanea 41 (2), 156–165.
Kolka, R.K., Singer, J.H., Coppock, C.R., Casey, W.P., Trettin, C.C., 2000. Influence of restoration and succession on bottomland hardwood hydrology. Ecol. Eng.
Mader, S.F., 1990. Recovery of ecosystem functions and plant community structure by a tupelo-cypress wetland following timber harvesting. Ph.D. dissertation, Department of Forestry, North Carolina State University, Raleigh, NC, p. 276.
Mitsch, W.J., Ewel, K.C., 1979. Comparative biomass and growth of cypress in Florida wetlands. Am. Midl. Nat. 101, 417–426.
Mitsch, W.J., Gosselink, J.G., 1993. Wetlands, second ed. Van Nostrand Reinhold, New York, p. 722.
Mooney, H.A., Gulmon, S.L., 1983. The determinants of plant productivity-natural versus man-modified communities. In: Mooney, H.A., Gulmon, S.L. (Eds.), Disturbance and Ecosystems Components of Response, vol. 4. Springer, Berlin, pp. 146–158.
Mullholland, P.J., 1979. Organic carbon export from upland and forested wetland watersheds. Limnol. Oceanogr. 24, 960–966.
Muzika, R.M., Gladden, J.B., Haddock, J.D., 1987. Structural and functional aspects of succession in southeastern floodplain forests following a major disturbance. Am. Midl. Nat. 117 (1), 1–9.
Odum, E.D., 1960. Organic production and turnover in old field succession. Ecology 41, 34–39.
Peet, R.K., 1982. Changes in biomass and production during secondary forest succession. In: Shugart, H.H., Botkin, D.F., West, D. (Eds.), Forest Succession: Concept and Application. Springer, Berlin, p. 262.
Reiners, W.A., 1983. Disturbance and basic properties of ecosystem energetics. In: Mooney, H.A., Gulmon, S.L. (Eds.), Disturbance and Ecosystems Components of Response, vol. 3. Springer, Berlin, pp. 83–98.
Schlesinger, W.H., 1978. Community structure, dynamics, and nutrient ecology in the Okefenokee cypress swamp-forest. Ecol. Monogr. 48, 43–65.
Scott, M.L., Sharitz, R.R., Lee, L.C., 1985. Disturbance in a cypress–tupelo wetland: an interaction between thermal loading and hydrology. Wetlands 5, 53–68.
Sharitz, R.R., Irwin, J.E., Christy, E.J., 1974. Vegetation of swamps receiving reactor effluents. Oikos 25, 7–13.
Sorensen, T.A., 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of the vegetation on Danish commons. K. dan. Vidensk. Selsk. Biol. Skr. 5, 1–34.
Spellerberg, I.F., 1991. Monitoring Ecological Change. Cambridge University Press, Cambridge, p. 334.
Titus, J.H., 1990. Microtopography and woody plant regeneration in a hardwood floodplain swamp in Florida. Bull. Torr. Bot. Club 117 (4), 429–437.
Van Cleve, K., Powers, R.F., 1995. Soil carbon, soil formation, and ecosystem development. In: McFee, W.W., Kelly, J.M. (Eds.), Carbon Forms and Functions in Forest Soils. Soil Science Society of America, Madison, WI, pp. 155–200.
Wharton, C.H., Kitchens, W.M., Sipe, T.W., 1982. The ecology of bottomland hardwood swamps of the Southeast: a community profile. US Fish and Wildlife Service, Biological Services Program, FWS/OBS-81/37, Washington, DC.
Wigginton, J.D., Lockaby, B.G., Trettin, C.C., 2000. Soil organic matter formation and sequestration across a forested floodplain chronosequence. Ecol. Eng.
Zaebst, T.W., 1997. Recovery status of a cypress (*Taxodium distichum*)–water tupelo (*Nyssa aquatica*) wetland 7 years after harvest disturbance. M.S. thesis, Department of Forestry, School of Forestry and Wildlife Resources, Virginia Polytechnic Institute and State University, Blacksburg, VA, p. 172.
Zak, D.R., Grigal, D.F., Gleeson, S., Tilman, D., 1990. Carbon and nitrogen cycling during old-field succession: constraints on plant and microbial biomass. Biogeochemistry 11, 1111–1129.
Zedler, J.B., Zedler, P.H., 1969. Association of species and their relationships to microtopography within old fields. Ecology 50 (3), 432–442.