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Biomass and carbon pools of disturbed riparian forests

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Abstract

Quantification of carbon pools as affected by forest age/development can facilitate riparian restoration and increase awareness of the potential for forests to sequester global carbon. Riparian forest biomass and carbon pools were quantified for four riparian forests representing different seral stages in the South Carolina Upper Coastal Plain. Three of the riparian forests were recovering from disturbance (thermal pollution), whereas the fourth represents a mature, relatively undisturbed riparian forest. Above and belowground carbon pools were determined from linear transects established perpendicular to the main stream channels and spanning the width of the riparian area. The objective of this study was to quantify the biomass and carbon pools in severely disturbed, early successional bottomland hardwood riparian forests and to compare these values to those of a less disturbed, mature riparian forest.

Aboveground biomass in all four riparian forests increased during the 2.5-year investigation period. The total carbon pool in these South Carolina Coastal Plain riparian forests increased with forest age/development due to greater tree and soil carbon pools. The mature riparian forest stored approximately four times more carbon than the younger stands. The importance of the herbaceous biomass layer and carbon pool declined relative to total aboveground biomass with increasing forest age. As stands grew older fine root biomass increased, but an inverse relationship existed between percentages of fine root biomass to total biomass. The root carbon pool increased with forest age/development due to a combination of greater fine root biomass and higher root percent carbon.

Aboveground net primary production (NPP) in young riparian forests rapidly approached and exceeded NPP of the more mature riparian forest. As a woody overstory became established (after ~8–10 years) annual litterfall rate as a function of NPP was independent of forest age and litterfall amount in the young riparian forests was comparable to mature riparian forests. Biomass in the riparian forest floor and carbon pool declined with increasing riparian forest development. Woody debris in these riparian forests comprised a relatively small carbon pool. An understanding of bottomland hardwood riparian forest carbon pools at different stages of succession allows us to assess how time since disturbance influences these pools, leading to a better understanding of the recovery processes.
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1. Introduction

Riparian forests may store large quantities of carbon because of their relatively high rates of productivity and/or the saturated conditions that can favor the storage of belowground carbon. For bottomland hardwood riparian forests the components of carbon pools (and key investigations) are:

1. aboveground biomass (Peet, 1981; Dunn and Sharitz, 1987; Kirkman et al., 1996; Thuille et al., 2000),
2. roots (Harris et al., 1977; Santantonio et al., 1977; Montague and Day, 1980; Cromack, 1981; Kozlowski, 1985; Raich and Nadelhoffer, 1989), litterfall (Kira and Shidei, 1967; Brown et al., 1978; Megonigal and Day, 1988; Conner, 1994; Delong and Brusven, 1994),
3. litterfall (Conner and Day, 1976, 1992; Mitsch, 1978; Brinson et al., 1981; Scott et al., 1985; Megonigal et al., 1997; Burke et al., 1999) and forest floor (Trettin et al., 1999),
4. woody debris (Day, 1982; Angermeier and Karr, 1984; Benke et al., 1985; Harmon et al., 1986; Chueng and Brown, 1995; Polit and Brown, 1996; Van Lear, 1996),
5. soil carbon (Megonigal and Day, 1988; Johnson, 1992; Collins and Wein, 1998; Trettin et al., 1999; Wojick, 1999; Garten and Wullschleger, 2000; Hoover et al., 2000; Thuille et al., 2000), and
6. submerged aquatic vegetation (SAV) (Hough and Wetzel, 1975; Dawson, 1980; Barko and Smart, 1983; Carpenter and Lodge, 1986).

Although bottomland hardwood forests are widely credited with carbon storage, few studies exist that have quantified the changes in carbon storage as affected by disturbance effects that alter the successional state of these riparian forests. The main objective of this project was to quantify the components of the above and belowground carbon pools in severely disturbed, early successional bottomland hardwood riparian forests and to compare these values to those of a less disturbed, mature riparian forest.

2. Site description

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 (latitude 33°N, longitude 82°W) (Fig. 1). Pen Branch and Fourmile Branch streams, third order tributaries of the Savannah River, were highly disturbed by thermal, elevated discharges from nuclear production processes between 1954–1989, and 1955–1985, respectively. These stream corridors experienced elevated temperatures (up to 70 °C) and increased discharge (1–2 orders of magnitude greater than base flow). The thermal discharge killed the bottomland hardwood vegetation and disrupted sediment erosion and deposition patterns. The third stream in this study, Meyer's Branch, represents a minimally disturbed, third order reference condition which has vegetation similar to that of the other two streams prior to thermal disturbance. Minor disturbances, such as selective logging in the 1940s occurred in Meyer's Branch, but it never received thermal effluent (Barton et al., 2000).

There are two treatment areas along Pen Branch: one area has been allowed to regenerate naturally (Pen Branch NR), whereas an adjacent area was regenerated artificially with bottomland hardwood plantings following site preparation with herbicides and prescribed burning (Pen Branch AR). The age of the riparian forests adjacent to Pen Branch, Fourmile Branch, and Meyer's Branch at the time this study began were 2 and 8, 12 years, and approximately 60 years, respectively.

Herbaceous vegetation and blackberry (*Rubus* spp.) was predominant in Pen Branch (AR) with some smooth alder (*Alnus serrulata* (Ait.) Willd.), and buttonbush (*Cephalanthus occidentalis* L.). Early successional species such as willow (*Salix* L. spp.), waxmyrtle (*Myrica cerifera* L.), smooth alder, and buttonbush dominated Pen Branch (NR). The woody component of the Fourmile Branch riparian forest was also dominated by willow with the addition of red maple (*Acer rubrum* L.), smooth alder, waxmyrtle, river birch (*Betula nigra* L.), sweetgum (*Liquidambar styraciflua* L.) and persimmon (*Diospyros virginiana* L.). Meyer's Branch represents a mature bottomland hardwood riparian forest with a mixed species composition including bald cypress (*Taxodium distichum* L.), swamp and water tupelo (*Nyssa sylvatica* Marsh. and *N. aquatica* L.), red maple, green ash (*Fraxinus pennsylvanica* Marsh.), Laurel oak (*Quercus laurifolia* Michx.), willow oak (*Q. phellos* L.), sweetgum,

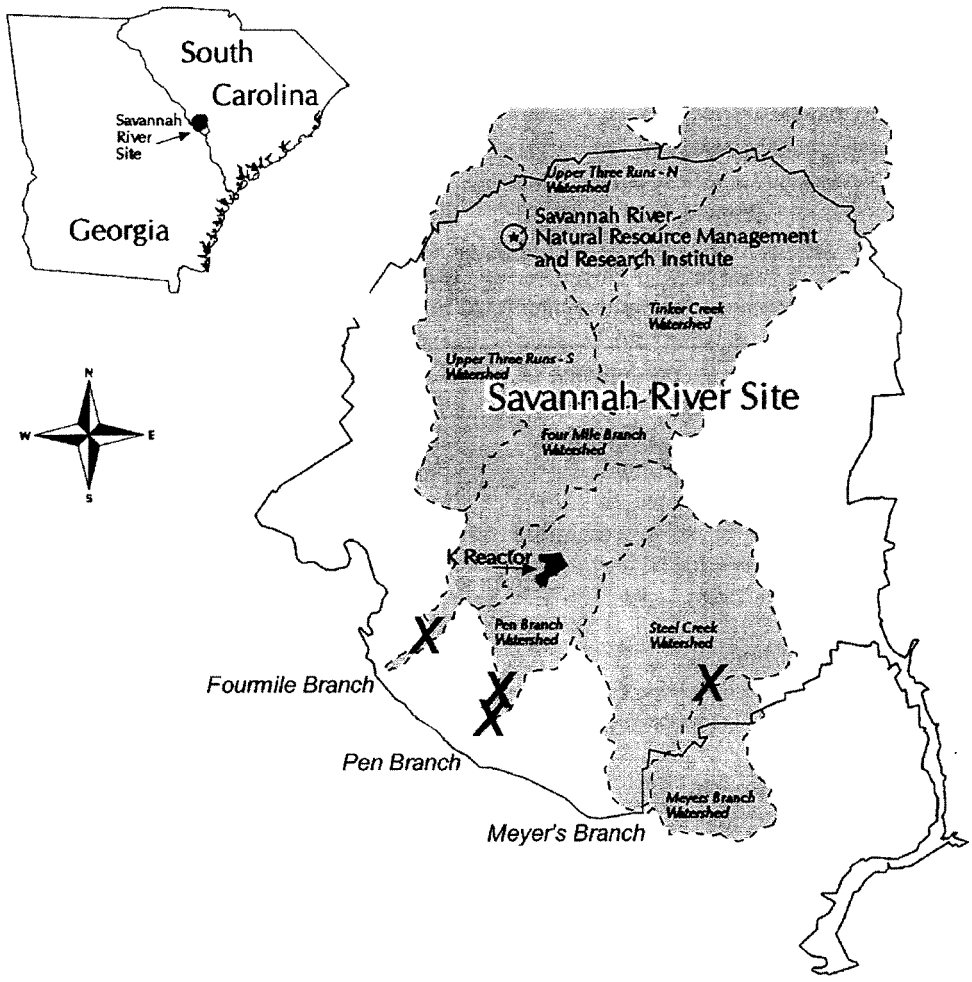

Fig. 1. Site map with the location of the four study sites (X) within the SRS, South Carolina. The shaded area depicts the watershed associated with each stream.

American elm (*Ulmus americana* L.), Virginia willow (*Itea virginica* L.), arrowwood (*Viburnum dentatum* L.), nannyberry (*Viburnum nudum* L.), spicebush (*Lindera benzoin* (L.) Blume.), smooth alder, and doghobble (*Leucothoe axillaris* (Lam.) D. Don.).

3. Methods

3.1. Woody aboveground carbon storage

In 1997 sampling transects were established perpendicular to the main stream channel, and these transects spanned the entire width of the riparian area on both sides of the stream. Transect locations were predetermined by an existing hydrology study (Kolka et al., 2000) so that we could take advantage of existing data sets and hydrologic monitoring equipment. Transect lengths ranged from 3 to 94 m originating on either side of the main stream channel. Three transects were established within the natural regeneration area of Pen Branch (NR), three within the artificial regeneration area of Pen Branch (AR), six within the Fourmile Branch riparian forest, and five within the Meyer's Branch riparian forest resulting in total transect lengths of 148, 176, 230, and 233 m, for each site, respectively. Along each riparian forest transect, 0.013 ha tree and 0.002 ha shrub subsampling plots (Wenger, 1984) were

established at 15.2 m intervals beginning at the main stream channel. There were 11, 12, 16 and 15 subsampling plots for Pen Branch (AR), Pen Branch (NR), Fourmile Branch, and Meyer's Branch, respectively. Within tree and shrub plots, the diameter at breast height (dbh), total height, and species of tree (dbh >4.0 cm) and shrub (dbh <4.0 cm and height >0.5 m) were recorded. Field sampling was conducted in June 1997 and then repeated 2.5 years later in November 1999. Aboveground biomass values for the trees and shrubs were estimated using existing dbh:biomass regressions developed for the species encountered on similar sites (Clark and Taras, 1976; Peet and Council, 1980; Clark et al., 1985; Muzika et al., 1987; Mader, 1990; Hauser, 1992; Zaebst, 1997; Gholz et al., 1999). These biomass estimates were converted to carbon storage estimates by assuming biomass was comprised of 50% carbon as is commonly conducted for tree and shrub estimates (Richter et al., 1995).

3.2. Herbaceous carbon storage

Along each transect, 0.25 m^2 clip plots were spaced at 4.5 m intervals. There were 34, 37, 51, and 49 clip plots for Pen Branch (AR), Pen Branch (NR), Fourmile Branch, and Meyer's Branch, respectively. All vegetation <0.5 m in height (regardless of growth form) was collected and removed from each plot (Hall et al., 1993). Herbaceous vegetation was solely collected in Pen Branch (NR) and Fourmile Branch. In addition to herbaceous vegetation, two woody shrubs, *Rubus* in Pen Branch (AR) and some *L. axillaris* (Lam.) D. Don. in Meyer's Branch, were included in the herbaceous layer sampling to expedite the process since they were exceptionally abundant. These species were not sampled in the herbaceous layer for Pen Branch (NR) or Fourmile Branch either because they were not present or not exceptionally abundant. Sampling was conducted four times: June and August 1997 and 1998 (same general area with no overlap of clip plot area to avoid influence from previous sampling). Each sample of clipped vegetation was dried at 60 °C and periodically measured until a constant weight was achieved.

3.3. Net primary productivity

Total net annual primary productivity was estimated by the mean annual increment method (Art and Marks, 1971) in which woody biomass is divided by age of the forest stand. The mean annual increment method is not an exact estimate of current annual woody production, but it is allows interpretation of chronosequence data. Tree and shrub biomass were divided by the respective riparian forest age. Two ages were used for each site because the repeated measures for the areas were 2.5 years apart (2 and 4.5, 8 and 10.5, 12 and 14.5, 60 and 62.5 years for the Pen Branch (AR), Pen Branch (NR), Fourmile Branch, and Meyer's Branch riparian forests, respectively). The herbaceous stratum was considered to be an annual increment. Shrub biomass was divided by forest stand age, but this will underestimate shrub NPP in the older Meyer's Branch riparian forest because it does not account for the loss of shrub biomass as the stand age increases.

3.4. Litterfall

Eight litter traps (0.187 m^2 each) per site were placed randomly in each riparian area. Collectors were elevated approximately 0.6 m to prevent inundation during flood events. Litter was collected biweekly from September to November and approximately every 2 months for 1 year (September 1997–August 1998) thereafter for a total of 10 collection periods. Litter was separated by component (leaves, stems, miscellaneous [e.g., seeds, flowers, and insects]). Samples were dried at 60 °C and periodically measured until a constant weight was achieved for each component (leaves, twigs, and miscellaneous). For all four sites, only tree and shrub litterfall components were included. In Pen Branch (AR), herbaceous vegetation tended to engulf the litter traps, but care was taken to not include herbaceous material in the sample.

3.5. Forest floor

Forest floor samples consisting of the Oi (leaves, twigs) and Oe (fragmented leaves and twigs) layers combined were collected from fifteen 0.25 m^2 areas placed randomly within each riparian forest. Forest floor samples were collected in early May 1998 to emulate what would be remaining of the previous season's litterfall. Samples were separated into two categories: leaves, and twigs and miscellaneous. Litter samples were dried at 60 °C and periodically measured until a constant weight was achieved.

3.6. Woody debris

Woody debris was inventoried using a line-intersect method (Wenger, 1984). From randomly selected azimuths, 10–20 m transects originated from vegetation plot centers in each riparian area. Woody debris was tallied along these transects and recorded as fine (1–2.5 cm), medium (2.5–10 cm), and large (>10 cm) diameter. The median diameters of the fine and medium size classes, the actual diameter of the large size class, and average relative density for mixed hardwoods (Harmon et al., 1980; Phillips, 1981) were used to convert woody debris to biomass. Penetrometer readings were taken on medium and large pieces to determine their soundness (Scheungrab, personal communication). A sound/rotten designation was given subjectively to fine woody debris.

3.7. Fine roots

Sampling for fine roots was conducted in June 1999. Two 5 cm diameter × 20 cm length metal cores were inserted into the soil near, but not within, each clip plot (Hall et al., 1993). Samples (soil and roots) were refrigerated until fine roots could be washed/separated from the soil with a jet of water on a sieve (pore openings $\leq$2 mm). Only roots $\leq$5 mm were retained. Roots were rated subjectively as live or dead. Live roots were considered resilient, flexible and fleshy. Roots were classified dead if they were limp and crumbled easily. Fine roots were dried at 60 °C and periodically measured until a constant weight was achieved. It is important to recognize that the belowground biomass associated with larger roots has not been included in the samples collected from each riparian forest.

3.8. Soil carbon

Bulk soil samples were collected from the O and A horizons in each riparian area (James and Wells, 1990). The A horizon was 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 histic O horizon in the Meyer's Branch riparian forest ranged from 20 to 76+ cm. Carbon content of the soil samples was determined via infrared analysis (LECO Total Carbon Analyzer, CR12, LECO Corp., Saint Joseph, MI).

3.9. Stream vegetation—SAV

Stream plots were an extension of the terrestrial transects. SAV biomass was sampled based on stream width (<500 cm: three points; >500 cm: five points). Each sample size was 177 cm^2 (15 cm diameter). Canopy coverage over the stream was determined subjectively as no canopy (open), partial, or full canopy. Other stream measurements included: water depth at each point, percent SAV cover at each point, percent SAV cover across stream reach, and bank to bank stream width. Sampling occurred four times: August and December 1997, and May and August 1998. Samples were dried at 60 °C and periodically measured until a constant weight was achieved. One species (*Egeria densa* Planchon.) dominated the streams at both Pen Branch sites. No SAV was observed in Meyer's Branch during the sampling times.

3.10. Carbon laboratory analyses

Samples were collected for all herbaceous vegetation, roots, soil, litterfall, and forest floor. These samples were dried, stored, and analyzed for carbon content. Carbon content was determined via infrared analysis (LECO Total Carbon Analyzer, CR12, LECO Corp., Saint Joseph, MI). Three replicates of the respective sample were analyzed for carbon content and means were calculated for the replicates for use in statistical analyses. All aboveground woody components were assumed to have 50% carbon component as suggested by Richter et al. (1995).

3.11. Statistical analysis procedures

The unique nature of the thermal disturbances prevented true replication, therefore, the transects within each site served as pseudo-replicates. The four sites (Pen Branch (AR), Pen Branch (NR), Fourmile Branch and Meyer's Branch) that represent different seral stages were interpreted as treatments. Data from the various biomass and carbon pools were interpreted via analysis of variance (ANOVA) for a completely randomized design (SAS Institute, 1996). When treatment differences were detected, the Tukey's multiple range test was used to test treatment mean differences. A significance level (α) of 0.05 was used for all tests.

4. Results and discussion

4.1. Aboveground biomass

The prescribed burning site preparation measures used in the artificial regeneration section of Pen Branch resulted in a lush herbaceous cover and relatively few of the planted seedlings survived. Therefore, the woody vegetation in Pen Branch (AR) is primarily natural regeneration, which is younger than in the natural regeneration site. Subsequently, Pen Branch (AR) actually represents the 'youngest' seral stage. The Pen Branch (NR) and Fourmile Branch riparian forests were relatively similar in successional development, as displayed by the increase in shrub and tree species and coverage, a nearly closed canopy, and the decline in herbaceous cover. Although Meyer's Branch was a relatively mature riparian forest with a closed canopy, it still exhibited an increase in biomass over 2.5 years and represents a later seral stage, but not necessarily the 'climax' stage. Aboveground biomass in all four riparian forests increased over a 2.5-year period (Fig. 2).

With increasing forest development, herbaceous biomass declined and became a very small portion of the total aboveground biomass (Fig. 3 and Table 1). Herbaceous biomass in the 'youngest' seral stage, Pen Branch (AR), was significantly greater than that of the other three riparian forests. Herbaceous biomass data obtained for several riparian forests recovering from thermal disturbance as well as an undisturbed riparian forest illustrates a general decline in herbaceous biomass with increasing forest age/development (Sharitz et al., 1974; Muzika et al., 1987).

The abundance of *Rubus*, which was included in the herbaceous component, generated a significantly greater percent carbon in herbaceous vegetation of Pen Branch (AR) than the percent carbon in herbaceous vegetation of Pen Branch (NR) and Fourmile Branch (Table 2). The percent carbon in herbaceous vegetation in Meyer's Branch was not significantly different than Pen Branch (AR) due to the inclusion of a woody shrub in the herbaceous layer of both sites. However, the percent carbon in the Meyer's Branch herbaceous vegetation was significantly

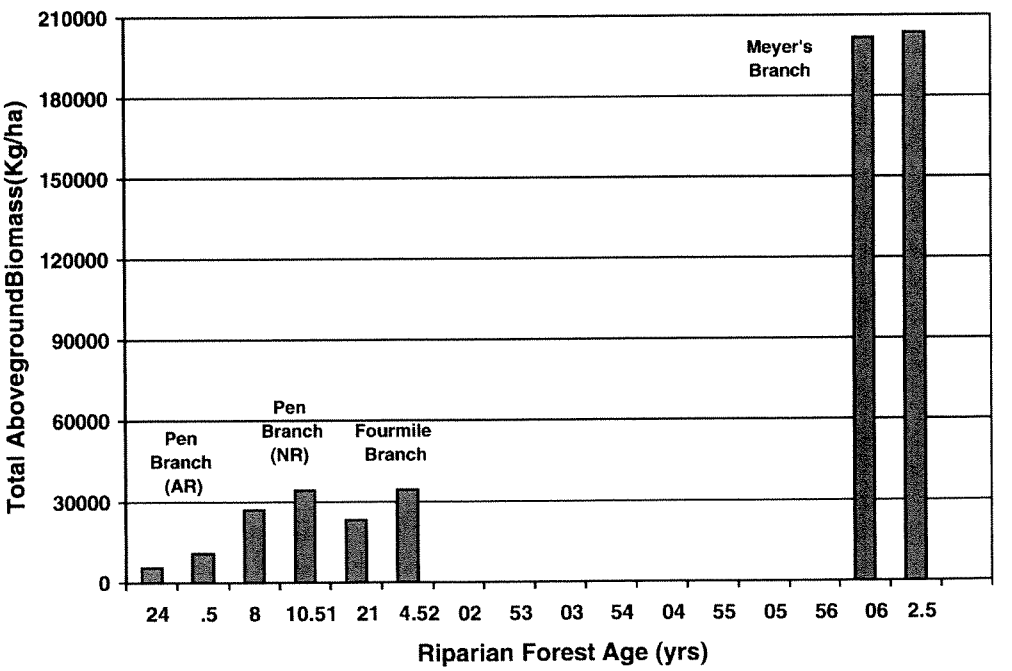

Fig. 2. Total aboveground biomass (tree, shrub and herb) for several South Carolina Coastal Plain riparian forests of differing ages. *X*-axis is not linear.

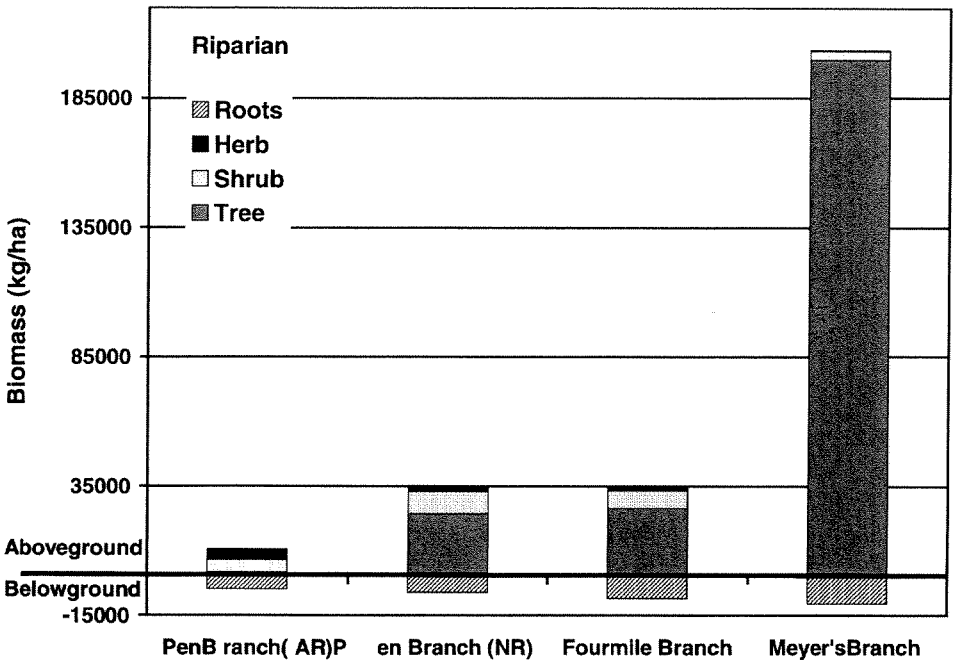

Fig. 3. Tree, shrub, herb, and fine root biomass for four riparian forests of differing stand age in the South Carolina Coastal Plain. Tree and shrub calculations are from the November 1999 data, herb values are the mean of the four sample dates (June and August 1997 and 1998), and root values are from the June 1999 data.

Table 1
The above and belowground biomass, below/aboveground biomass ratio, and NPP with and without litterfall for four riparian forests in the South Carolina Coastal Plain

		kg ha^{-1}			
		Pen Branch (AR)	Pen Branch (NR)	Fourmile Branch	Meyer's Branch
Trees	1997	313	19487	17510	196558
	1999	1731	24414	26516	199847
Shrubs	1997	833	6303	4609	4694
	1999	4702	8629	6713	3378
Herbs[a]	1997	4468	1295	1462	520
	1998	3800	945	735	370
Fine roots		4770	6010	8460	10590
Below/aboveground biomass ratio[b]	1997	1.18	4.54	2.78	20.00
	1999	2.17	5.55	4.00	20.00
		kg ha^{-1} per year			
		Pen Branch (AR)	Pen Branch (NR)	Fourmile Branch	Meyer's Branch
NPP[c] w/o litterfall		5720	407	3422	3682
NPP w/litterfall[d]		6004	10317	7649	8947

[a] Herbaceous biomass was the mean for the sampling year.
[b] Below/aboveground biomass ratio: root/(tree + shrub + herb).
[c] NPP includes trees (1999), shrubs (1999), and herbaceous mean.
[d] Annual litterfall was collected September 1997–August 1998.

Table 2
Percent carbon and carbon pools for the herb and root components of four riparian forests in the South Carolina Coastal Plain[a]

Study area	Herbs		Roots	
	Percent carbon	Carbon pool (g C m^{-2})	Percent carbon	Carbon pool (g C m^{-2})
Pen Branch (AR)	46 (2) a	213 (97) a	41 (5) b	185 (105) c
Pen Branch (NR)	44 (3) bc	62 (43) b	46 (3) a	277 (182) bc
Fourmile Branch	43 (4) c	62 (53) b	44 (6) ab	304 (211) b
Meyer's Branch	45 (2) ab	16 (15) c	46 (5) a	436 (242) a

[a] Within a column, letters different from each other are significantly different ($\alpha = 0.05$). Standard deviations are in parentheses. Sample size (N) for Pen Branch (AR), Pen Branch (NR), Fourmile Branch, and Meyer's Branch, respectively, are 53, 40, 60, 40 and 54, 40, 86, 44 for riparian herbs and roots, respectively.

greater than the percent carbon in herbaceous vegetation in Fourmile Branch. The predominant herb (*Commelina virginica* L.) in Fourmile Branch has a rhizomatous growth form that may require less structural carbon and therefore possesses a lower percent carbon. A combination of greater herbaceous biomass and higher percent carbon resulted in Pen Branch (AR) having a significantly greater herbaceous carbon pool compared to the other three riparian forests (Table 2). Both Pen Branch (NR) and Fourmile Branch riparian forests have significantly greater herbaceous carbon pools than the Meyer's Branch riparian forest even with the inclusion of a woody shrub in Meyer's Branch. This implies that despite apparent statistical differences in the percent carbon of herbaceous species (data not shown), the herbaceous carbon pool decreases with forest age/development in riparian forests.

The tree and shrub biomass increased in each site over a 2.5-year period, except for a decrease in shrub biomass in Meyer's Branch (Table 1). Both tree and shrub biomass increased significantly in Pen Branch (AR) over the 2.5 years suggesting that this site is following successional patterns toward a forest community. The larger tree and shrub biomass of the Meyer's Branch riparian forest was the result of the large age difference between Meyer's Branch and the other three riparian forests (Fig. 3 and Table 1). Aboveground biomass in Meyer's Branch is comparable to values reported for other forested wetlands (Johnson and Bell, 1976; Conner and Day, 1976, 1982; Schlesinger, 1976; Day and Dabel, 1978; Mitsch and Ewel, 1979; Mullholland, 1979; Brown, 1981; Muzika et al., 1987; Mitsch et al., 1991).

4.2. Fine roots

There was an increase in fine root biomass with increasing forest age (Fig. 3), however, an inverse relationship was observed between percentage of fine root biomass to total biomass and riparian forest age. Fine root biomass comprised 31, 15, 20 and 5% of the total biomass for Pen Branch (AR), Pen Branch (NR), Fourmile Branch, and Meyer's Branch, respectively, all of which were in the range found by Harris et al. (1977) and Montague and Day (1980). Fine root biomass in Meyer's Branch was significantly greater than that in the other three riparian forests, and fine root biomass in Fourmile Branch was significantly greater than that in both Pen Branch riparian forests. Fine root biomass in the three younger riparian forests was one-fourth to one-half that found in other mature forested wetlands, while fine root biomass in Meyer's Branch was only slightly less than the other mature forested wetlands (Montague and Day, 1980). Fine root biomass increased with forest development, which supports the proposition by Nadelhoffer et al. (1985) that fine root production increases in direct proportion to aboveground production.

The numbers of roots from woody species increases with forest age/development, and roots from woody species generally have a greater percent carbon than roots of herbaceous species. The percent carbon in fine roots at Pen Branch (NR) and Meyer's Branch was significantly greater than the percent carbon in those at Pen Branch (AR) (Table 2). The percent carbon of the fine roots in Fourmile Branch also was greater than the Pen Branch (AR) fine root percent carbon, which implies that the predominance of roots associated with

trees and shrubs have higher percent carbon than herbaceous roots. Greater fine root biomass combined with a higher percent carbon in fine roots result in Meyer's Branch having a significantly greater root carbon pool than the other three riparian forests (Table 2). The fine root carbon pool in Fourmile Branch was significantly greater than the Pen Branch (AR) fine root carbon pool. Based on these data the fine root carbon pool increases with forest age/development.

4.3. Aboveground/belowground ratio

The ratio of aboveground biomass to belowground biomass increased with increasing forest age/development (Table 1) in the riparian forests. Herb-dominated riparian communities appear to have equivalent amounts of aboveground and belowground biomass. The increase in fine root biomass over time was much smaller compared to the amount that tree/shrub/herb biomass increased with stand development. The woody species that became established allocated more resources into aboveground biomass than belowground, thereby lowering the ratio. However, including the biomass of the larger roots would affect this ratio. Richter et al. (1995) found that larger roots accounted for approximately 5% of the total ecosystem biomass for 34-year-old loblolly pine (*Pinus taeda* L.) stands in Georgia. Mature upland forests adjacent to our riparian forests had comparable above/belowground ratios and were comparable to the mature riparian forest (data not shown). Therefore, this biomass ratio may be representative of forest age.

4.4. Net primary productivity

Forest age/development patterns influenced net primary production (NPP) in these riparian forests. A drop in production during later stages of succession can be attributed to developing forest structure (Table 1; NPP w/o litterfall). In general, NPP in young riparian forests exceeded NPP of the more mature riparian forests. NPP of trees, shrubs, and herbs combined was greater in both Pen Branch riparian forests than either Fourmile Branch or Meyer's Branch riparian forest (Table 1). Similar to findings by Mitsch (1978) and Johnson and Bell (1976), herbaceous vegetation in this study comprised a very small portion of the NPP except for Pen Branch (AR).

Annual litterfall comprised approximately 55–59% of the NPP in the naturally recovering or relatively mature riparian forests. In the herbaceous dominated riparian forest of Pen Branch (AR), annual litterfall only comprised approximately 5% of total NPP. Including litterfall as a component of NPP changed the pattern between the four riparian forests. NPP in the Pen Branch (NR) riparian forest exceeded NPP in the other three riparian forests and this may be indicative of the *Salix* dominated seral stage in Pen Branch (NR). Comparing NPP (with litterfall) in Pen Branch (AR) to the other riparian forests may be inappropriate because it is dominated by herbaceous vegetation. Litterfall production was likely influenced by the 'flashy' hydroperiod in the Fourmile Branch riparian forest and saturated conditions in the Meyer's Branch riparian forest which certainly impact the productivity of these sites.

4.5. Litterfall

Establishment of woody species occurred within 8–10 years, and possibly sooner, after thermal disturbance. The litterfall amount in these young riparian forests is comparable to mature riparian forests. Annual litterfall was significantly less in Pen Branch (AR) than the other three riparian forests due to the lack of woody species in the overstory (Table 3). In all four sites leaves comprise the greatest amount of annual litterfall biomass. Once the herbaceous stage of succession is surpassed and a woody overstory becomes established, annual litterfall rates are independent of forest age.

The annual foliar percent carbon for the mix of riparian species was less than 50% (Table 3). The foliar percent carbon determined during the peak fall litterfall period of a subsequent year was greater than 50% (percent carbon during the first year's peak litterfall period was less than 50%). This implies that percent carbon changes during the year (season) possibly due to current and antecedent climatic factors (i.e., leaching during precipitation events). Alternatively, since various species drop their leaves at different times of the year, the mix of riparian litterfall species is different during the fall than other seasons. A combination of both of these factors is

Table 3
Annual litterfall biomass, percent carbon and annual carbon pool for four riparian forests representing different successional stages in the Coastal Plain of South Carolina

	Leaves	Twigs	Miscellaneous	Total
		Biomass (g m^{-2})		
Pen Branch (AR)	19	3	6	28 b
Pen Branch (NR)	448	129	24	601 a
Fourmile Branch	344	56	19	423 a
Meyer's Branch	448	26	28	526 a
		Percent carbon[a,b]		
Pen Branch (AR)	NS (51.7)	49.8	46.9	–
Pen Branch (NR)	47.9 (51.6)	51.2	51.8	48.3[c]
Fourmile Branch	48.9 (52.9)	50.7	46.8	48.1
Meyer's Branch	48.0 (50.7)	49.4	50.1	45.8
		Carbon pool (g C m^{-2})		
Pen Branch (AR)	9 b	1 b	3 b	13 b
Pen Branch (NR)	215 a	66 a	12 ab	293 a
Fourmile Branch	168 a	29 ab	9 ab	206 a
Meyer's Branch	215 a	14 ab	14 a	242 a

[a] Annual percent carbon is based on the mean of 10 sampling dates.
[b] Values in parentheses are mean foliar percent carbon during the peak litterfall period in the fall.
[c] Total percent carbon is the weighted mean leaf, twig and miscellaneous. No total was calculated for Pen Branch (AR) because there was no percent carbon value for leaves.

possibly playing a role in carbon concentration of litterfall.

Annual litterfall carbon pools in these riparian forests range from 206 to 293 g m^{-2} after the establishment of the woody stage of succession (Table 3). Although twigs generally have a higher percent carbon, the leaf carbon pool comprises the greatest percentage of the annual litterfall carbon pool. Therefore, management tools that enhance foliar production (i.e., fertilization, stand spacing, control of water balance, species selection) will increase the litterfall carbon pool.

4.6. Forest floor

Although not statistically significant, total forest floor biomass decreased with increasing forest age (i.e., Pen Branch (NR) riparian forest > Fourmile Branch riparian forest > Meyer's Branch riparian forest) (Table 4). Even though the forest floor biomass was slightly lower than findings by Trettin et al. (1999), the forest floor carbon pool was similar to findings by Trettin et al. (1999). Hydroperiod, species composition, and decomposition rate are some of the more apparent factors that affect forest floor biomass.

Table 4
Mean riparian forest floor biomass (leaves and twigs), foliar percent carbon, and forest floor carbon pool for three riparian forests in the South Carolina Coastal Plain[a]

Site	Biomass (g m^{-2})			Carbon	
	Leaves	Twigs and miscellaneous	Total	Leaves (%)	Total (g m^{-2})
Pen Branch (NR)	59 [15] a	40 [15] a	99	25 (5) [14] a	35 [14] a
Fourmile Branch	64 [15] a	24 [15] a	88	32 (8) [9] a	32 [9] a
Meyer's Branch	45 [15] a	20 [15] a	65	39 (4) [8] a	28 [8] a

[a] Standard deviations are in parentheses. Sample sizes are in brackets. Within a column, means with different letters are significantly different. Assumed 50% carbon for twigs and miscellaneous.

Table 5
Carbon pools by component for four South Carolina Coastal Plain riparian forests[a]

Component	Pen Branch (AR)	Pen Branch (NR)	Fourmile Branch	Meyer's Branch
		Aboveground (kg ha^{-1} (%))		
Trees				
1997	156 (0.6)	9744 (16)	8755 (17)	98279 (82)
1999	866 (3.0)	12207 (30)	13258 (35)	99924 (83)
Shrubs				
1997	416 (1.6)	3152 (8)	2304 (7)	2347 (2)
1998	2351 (8.5)	4314 (11)	3356 (9)	1689 (1)
Herbs	2134 (8.5)	615 (2)	616 (2)	159 (0.0)
Woody debris	1.3 (0.0)	1.2 (0.0)	0.9 (0.0)	1.4 (0.0)
Litterfall	130 (0.0)	2930 (8)	2060 (6)	2420 (2)
Forest floor[b]	NS	350 (0.9)	320 (0.8)	280 (0.2)
Belowground				
Soil carbon[c]	20261 (81)	17470 (48)	15840 (49)	12038 (10)
Fine roots	1850 (7.4)	2770 (8)	3040 (9)	4360 (4)
Above/below, 1997	0.21	0.78	0.72	6.3
Ground ratio, 1999	0.24	0.96	1.01	6.3
Instream				
SAV	212 (0.8)	93 (0.2)	0	0
Total				
1997	25.1	37.1	32.9	120.0
1999	27.8	40.8	38.5	121.0

[a] Assume 50% carbon for trees, shrubs, woody debris and SAV (Turner et al., 1995; Meyer, 1986).
[b] No forest floor was sampled in Pen Branch (AR) because it was negligible.
[c] Soil carbon was calculated for the top 10 cm.

4.7. Woody debris

Woody debris comprised a relatively small part of the total carbon pool (Table 5). Mean woody debris biomass was 0.26, 0.23, 0.18, and 0.28 g m^{-2} for Pen Branch (AR), Pen Branch (NR), Fourmile Branch, and Meyer's Branch, respectively. High annual litterfall input of twigs in Pen Branch (NR) accounted for the greater woody debris biomass in Pen Branch (NR) compared to Fourmile Branch. In each riparian forest the amount of fine woody debris (1–2.5 cm) was significantly greater than medium sized woody debris (2.5–10 cm). No large woody debris (>10 cm) was found in Pen Branch (NR), however, several large pieces intersected the transect in Pen Branch (AR), probably remnants from the pre-disturbance forest. Meyer's Branch logically had the greatest number of large woody debris pieces due to its more mature forest composition, closely followed by Fourmile Branch. There was no significant difference in the biomass contribution between the fine and medium sized woody debris for all sites. The majority of the woody debris was considered sound and had undergone little decay.

4.8. Soil carbon

There is a web of interrelationships between hydroperiod, species composition, and soil carbon amount in a riparian forest. Species litterfall dynamics (leaves, twigs, fruits, and flowers) have an effect on organic matter and carbon incorporation into the soil, and these components in conjunction with root dynamics affect the carbon pool. Forest maturity and the intrinsic balance (resistant and resilient to change) of nutrient cycling processes affect soil organic matter and carbon percentages and quantities. The more mature riparian forest had significantly greater percent soil carbon (%C) and organic matter (%OM) than the three younger riparian forests (Meyer's Branch: 11.4%C

and 30.3%OM; Fourmile Branch: 4.0%C and 10.7%OM; Pen Branch (NR): 4.7%C and 12.9%OM; Pen Branch (AR): 4.2%C and 12.3%OM) due to the high litterfall inputs (leaves and twigs) and predominantly saturated conditions in Meyer's Branch. The organic matter (%) in these riparian forests is comparable to other Coastal Plain forested wetlands (Wharton et al., 1982; Axt and Walbridge, 1999).

4.9. Submerged aquatic vegetation

The main stream channels of each site were similar having sandy substrates, base flow rates of 12–38 cm s^{-1}, and widths ranging from 5.5 to 9.2 m. With the exception of possible differences in water chemistry in each stream, the only major difference between the streams was the age of the adjacent riparian forest. SAV was abundant in the two younger riparian forests (Pen Branch AR and NR). The closed canopy and subsequent shading at Meyer's Branch appears to have prevented the growth of SAV.

Water depth, clarity, and the amount of suspended particulates are several factors that could influence light penetration and affect the proliferation of SAV (Barko and Smart, 1981). The amount of SAV biomass in Pen Branch (AR) (43.6 g m^{-2}) was approximately 2.5 times greater than the SAV biomass in Pen Branch (NR) (16.8 g m^{-2}) and the difference was significant ($P = 0.0180$). Pen Branch (NR) is immediately upstream from Pen Branch (AR) so stream characteristics are as similar as possible. Pen Branch (AR) had greater tree, shrub, and foliar biomass than Pen Branch (NR); therefore, it is probable that the canopy shading was the controlling factor for the SAV.

4.10. Carbon pools

The total carbon pool in the mature riparian forest (Meyer's Branch) was conspicuously greater than the three younger riparian forests (Table 5) primarily due to greater tree and soil carbon pools. Riparian forest total carbon pools increase with forest age/development (Table 5). The herbaceous carbon pool decreased with increasing forest age. In the herb-dominated community, the above- to belowground carbon pool ratio was very small. As woody species initially become established, the ratio approached 1, implying a balance between above- and belowground carbon pools. With riparian forest maturity, the aboveground carbon pool increased substantially resulting in an above- to belowground ratio >1.

The litterfall carbon pools in the young riparian forests were comparable to those in the mature riparian forest. However, the litterfall carbon pools for all of the sites contributed a small percentage of the total riparian forest carbon pool (Table 5). The forest floor carbon pool decreased slightly with forest age and constituted a very small percentage of the total carbon pool. The woody debris carbon pool was comparable between the four riparian forests; however its percentage was negligible. Even the more mature riparian forest was not at a successional stage to contribute a significant amount of woody debris.

Within the first 10 cm of soil depth, the soil carbon pool decreased with increasing riparian forest age. However, the organic horizon of Meyer's Branch extended to 60+ cm, indicating that the soil carbon pool in Meyer's Branch is substantially greater than in the younger riparian forests. The root carbon pool increased with increasing forest development, and if the larger woody roots were included; the root carbon pool would be even greater with increasing forest development.

SAV was only found in the stream adjacent to the two youngest riparian forests and comprised a very small portion of the total carbon pool. However, since the SAV is the only living vegetation actually located in the stream, it may have a much more important influence of stream chemistry, sediment deposition, and macroinvertebrates (National Research Council, 1995; Mitsch and Gosselink, 2000) than its actual percentage indicates.

5. Conclusion

The biomass and carbon pools in disturbed riparian forests demonstrate distinct patterns. With increasing forest development, aboveground components (herbs, shrubs, trees, and SAV) in these riparian forests responded to traditional ecological processes. The biomass and carbon pools associated with litterfall, including forest floor and woody debris, and belowground components (fine roots and soil) may be more influenced by a combination of the species mix of a bottomland hardwood community and hydroperiod.

The total carbon pool in riparian forests increases with forest age/development due to greater tree and soil carbon pools. The mature riparian forest stored approximately four times more carbon than the younger (8–14 years old) stands. The ratio of above- to belowground carbon pools is small in herb-dominated communities, approaches 1 with the onset of a woody component, and continues to increase with riparian forest maturity. This ratio may be a valid indicator of changes in carbon pool magnitude during riparian forest succession.

With forest development, the herbaceous biomass and herbaceous carbon pool comprised a very small portion of the total aboveground biomass and generally declined with increasing forest age/development. Herbaceous species composition changed with seral stage and differences in percent carbon may influence carbon pool magnitude. Whether differences in percent carbon are ecologically significant depends on scale of interest. The subtle differences in percent carbon may play a role in plant evolutionary strategy as well as influence carbon sequestration potential.

An increase in fine root biomass occurred with increasing forest age, however, an inverse relationship between the percentages of fine root biomass to total biomass with increasing riparian forest age was observed. The combination of greater fine root biomass and higher root percent carbon in a relatively mature riparian forest contributed to a greater root carbon pool than younger riparian forests. Overall, the root carbon pool increased with forest age/development. This finding is important because it supports the premise that carbon storage by forests can be significantly increased by management practices that favor belowground carbon storage.

Riparian forest productivity was independent of forest age (seral stage) particularly with the inclusion of woody species providing substantial amounts of litterfall. NPP without litterfall in the young riparian forests rapidly approached and exceeded NPP of the more mature riparian forests. Including litterfall as a component of NPP changed the balance between riparian forests.

Establishment of woody species occurred within 8–10 years after thermal disturbance, and litterfall amount in young riparian forests rapidly becomes comparable to mature riparian forests. With the rapid recovery of litterfall, incorporation and recycling of nutrients to the riparian ecosystem from seasonal litterfall will provide the resources necessary for maintaining a healthy and productive forest. The forest floor appears to stabilize after 10–12 years, demonstrating equilibrium between the inputs and outputs to the forest floor and suggesting that nutrient cycling processes within each site are functioning. Since litterfall recovers at a young age, it may be used as an index for riparian restoration demonstrating that a riparian forest is on a trajectory toward a functioning mature riparian forest.

Woody debris in riparian forests was a function of forest development; however, it does not significantly contribute to the total riparian forest carbon pool. Theoretically, mature riparian forests should have a greater amount of terrestrial woody debris than younger riparian forests, but this was not observed in these riparian forests. The more mature riparian forest did have a greater amount of larger pieces of woody debris; but overall, all four sites had comparable estimates of woody debris biomass. Meyer's Branch is not at a maturity level to significantly contribute to woody debris biomass. Although woody debris in these riparian forests comprised a relatively small carbon pool, which may not be reflective of its importance in furnishing critical forest functions.

Several integrated factors such as light, water chemistry, and substrate control the establishment of SAV, and forest development (successional stage) appears to be a factor. Canopy closure associated with mature riparian forests is one of the main factors that influence the growth of SAV. Although the SAV constituted a small percentage of the total riparian forest carbon pool, it should not be overlooked for it plays an important role in the proper functioning of other riparian forest processes, particularly because it may influence stream hydrology and aquatic biota.

Riparian forest soils act as more persistent carbon sinks than vegetation, and therefore management practices that affect soil stability and fertility will aid carbon storage. Management practices that reduce soil erosion, restore natural vegetation, and increase fertilizer efficiency are strategies for soil carbon storage. Since biological processes also drive soil carbon storage, bioengineering opportunities should be researched and incorporated.

Although riparian forests are distinctly tied to their hydroperiod, increases in total biomass follow

traditional patterns of forest development/succession. After a major disturbance, the riparian forest restoration process is immediately set in motion. Forward succession is evident even though these areas are subject to seasonal flooding. The magnitude of each carbon pool is reflective of the species composition of the successional stage. Awareness of the processes that influence carbon allocation in riparian forests facilitates defining the trajectory of ecosystem response and provides mechanisms for riparian restoration.

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