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Stream discharge and floodplain connections affect seston quality and stable isotopic signatures in a coastal plain stream

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Abstract. Connections of a stream to its floodplain are important ecological linkages that affect spatial and temporal dynamics of the basal resources available to primary consumers in streams. Suspended organic material and associated microorganisms (seston) vary in quality seasonally and interannually within streams because of changing inputs from riparian and floodplain sources. Researchers have investigated the quality of different size fractions of material, but these differences have not been assessed with respect to the hydrology and the geomorphic structure of streams. We investigated how quality, represented by the stoichiometric ratio C:N, and stable isotopic signature ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of 3 seston size classes varied in Ichawaynochaway Creek, a 5th-order tributary of the lower Flint River in the Coastal Plain of southwestern Georgia, USA. Samples were collected throughout the basin during varying flow regimes to estimate the quality and source of materials available over different temporal and spatial scales. Our results indicate significant differences in quality and stable isotopic signature based on particle size, discharge, and geomorphic structure of the stream and floodplain (constrained vs unconstrained reaches). The constrained portions of this stream occur in the lower portions of the basin. During low flow conditions, seston had higher quality with less depleted $\delta^{13}\text{C}$ and more enriched $\delta^{15}\text{N}$ signatures in the constrained than in the unconstrained portions of the stream. However, during high flow conditions, higher quality seston entered the stream from the adjacent floodplain in all portions of the basin. Insights gained from our study indicate how terrestrial and aquatic linkages and the natural flow regime affect the dynamics of basal resources and their availability to primary consumers in streams.

Key words: seston, floodplain, flood pulse, discharge, drainage-network position, stoichiometry, stable isotope, C:N, particle size, lateral connectivity.

Seasonal flooding is a dynamic process that drives essential ecological interactions between a river channel and its floodplain (Junk et al. 1989, Ward 1989, Martin and Paller 2008). Frequently flooded low-gradient streams with extensive riparian forests are a common feature of the Coastal Plain of the southeastern US, and these forests contribute large quantities of

organic material to streams (Cuffney 1988, Meyer and Edwards 1990, Benke et al. 2000). These seasonally pulsed floods create spatial and temporal variation in basal resources used by a range of detritivores and filter-feeders.

The flood pulse concept describes inputs to low-gradient streams with a broad floodplain (Junk et al. 1989) and is applicable to many southeastern streams (Benke et al. 2000). In the flood pulse concept, high flows typically are regarded as predictable events that fuel seasonal productivity in streams. Organic matter originating in floodplain forests tends to accumulate

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and is partially processed while on the forest soils. During flood pulses, substantial quantities and different qualities of organic materials are transported to stream channels (Meyer and Edwards 1990, Golladay et al. 2000). Understanding variability in food resources is necessary for recognizing patterns of community composition and life-history strategies. However, few studies have addressed how the quality of material entering the stream varies with cycles of flooding. This seasonal variability is especially important to study because extremes in rainfall (floods and droughts) are predicted to increase (IPCC 2007).

Understanding how food quality, expressed as the stoichiometric ratio C:N in available food sources, and sources of detrital resources vary in response to seasonal flooding is important for determining the basis of instream productivity. Ecological stoichiometry focuses on the balance between the elemental requirements of organisms and the composition of their food sources. This approach has been used to integrate energy, available food materials, and trophic linkages in many types of ecosystems (Sturner and Elser 2002, Elser et al. 2007). Stable isotope analysis has been used to study aquatic food webs and trophic structure (Vander Zanden and Rasmussen 1999, Post 2002, Zueg and Winemiller 2008). Carbon isotopic signatures vary with source material, and C_3 plants typically have a $\delta^{13}C$ signature of -28‰ (Fry 2006). Biogeochemical transformations by microbes can cause systematic variation in $\delta^{15}N$ (Macko and Estep 1984, Robinson 2001). Systematic differences in food quality and in the isotopic signature of food resources, which indicates the source of material, can be caused by differences in particle size, stream discharge, and hydrological connectivity. Lateral exchange processes have been measured in large rivers and coastal plain streams (Jones and Smock 1991, Golladay et al. 2000), but rarely has the quality or source of transported materials been assessed.

Our study focused on the lateral and temporal dimensions of hydrological connectivity, defined herein as the permanent or episodic links between the main channel of a river and the various water bodies of its alluvial floodplain (e.g., Ward 1989). We hypothesized that episodic flooding would entrain high-quality materials of floodplain origin. Variation in quality and isotopic signature was determined across a range of 3 suspended particle sizes that included materials in different states of biogeochemical breakdown. Differences in food quality and isotopic signature were investigated in areas with varying connectivity to the floodplain (constrained and unconstrained reaches) and across a range of flow regimes in an entire basin.

Our goal was to examine temporal and spatial variation of seston quality (C:N) and stable isotopic signature ($\delta^{13}C$ and $\delta^{15}N$) in relation to particle size, hydrology, floodplain width, and drainage-network position within the basin.

Methods

Study sites

Nine sampling sites, including 2 sites on tributaries, Pachitla and Chickasawhatchee Creeks, were established in the Ichawaynochaway Creek (IC) basin (Fig. 1, Table 1). IC is a 5th-order, low-gradient tributary to the lower Flint River on the Gulf Coastal Plain of southwestern Georgia, USA (Golladay et al. 2000). The IC basin is situated in the Dougherty Plain physiogeographic district where the mantled karst physiography controls the hydrology (Hicks 1981). IC discharges into the Flint River ~10 km downstream from the confluence with Chickasawhatchee Creek (CC). CC flows through Chickasawhatchee Swamp, the 2nd-largest tract of wetlands in Georgia (Golladay and Battle 2002). Riparian areas in the region are composed of maturing secondary-growth hardwood forest (Golladay et al. 2000). These areas vary greatly in floodplain width (55–981 m).

In the southeastern US, streamflow, evapotranspiration, and temperature variations are strongly seasonal (Benke 2000). Periods of low flow occur during summer and autumn, and periods of higher flow and flooding occur during winter and spring. Inundation of floodplains tends to occur between October and April, and the greatest extent of flooding occurs in Chickasawhatchee Swamp. Swampy wetlands in the midreaches of the basin cause the channel to be very wide and unconfined with a broad floodplain (Fig. 1). Bottomland hardwood forests adjacent to the stream serve as storage areas for detritus in low flow conditions and are sources of exported detritus during high flow conditions. Downstream reaches of the stream are more confined and have smaller floodplains and greater flow than do the midreaches.

Field collection and sample analysis

Seston samples were collected at the study sites 6 times between June 1994 and October 1996. Material was fractionated into 3 size categories at the time of collection with different sized plankton nets and sieves: large ($>250\text{ }\mu\text{m}$), medium ($45\text{--}250\text{ }\mu\text{m}$), and small ($10\text{--}44\text{ }\mu\text{m}$). Samples were dried, ground, and archived as part of a long-term study to determine effects of agricultural development on seston availability and water quality. Samples were collected

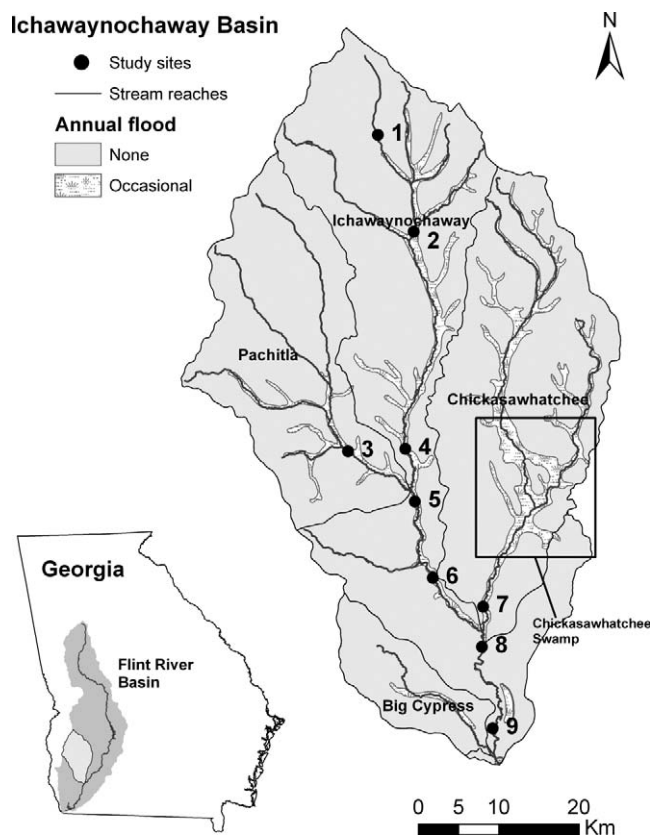


FIG. 1. Study sites in Ichawaynochaway Creek basin, which flows into the Flint River, in southwest Georgia, USA. Gauge station data were available at sites 3, 6, and 7. Shaded areas around the stream channel represent an estimate of the area of land that is flooded in a typical year (USDA 1994).

seasonally during a variety of flow regimes. Total C and total N composition and N and C stable isotopic signatures were determined using a Finnigan Delta Plus mass spectrometer in the University of Georgia's Ecology Analytical Laboratory. Isotope ratios were expressed as

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N}(\text{per mil}) = ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1000$$

where R is the $^{13}\text{C}:^{12}\text{C}$ ratio or $^{15}\text{N}:^{14}\text{N}$ ratio. A bovine protein (peptone) laboratory standard was referenced against an international standard, and precision averaged ≤ 0.1 per mil.

Historical discharge data for 3 sampling sites (sites 3, 6, and 7; US Geological Survey [USGS] gauges 02353500, 02354500, and 02353400, respectively) were obtained from the USGS Water Watch website (<http://water.usgs.gov/waterwatch/?m=real&r=ga>). Floodplain width and wetted channel width were determined with use of the methods of Golladay et al. (2000) for the IC basin and were used as a measure of floodplain connectivity (floodplain width/channel

TABLE 1. Summary of physical characteristics of the 9 sampling sites in the Ichawaynochaway Creek basin, Georgia. Floodplain connectivity was estimated as floodplain width/channel width.

| Site | Distance from headwaters (km) | Floodplain width (m) | Channel width (m) | Floodplain connectivity (m/m) |
|------|-------------------------------|----------------------|-------------------|-------------------------------|
| 1 | 10.00 | 328 | 6.3 | 51.7 |
| 2 | 22.50 | 609 | 15.0 | 40.6 |
| 3 | 39.86 | 476 | 21.3 | 22.3 |
| 4 | 51.25 | 869 | 22.6 | 38.6 |
| 5 | 57.50 | 981 | 30.0 | 32.7 |
| 6 | 68.75 | 281 | 13.5 | 20.8 |
| 7 | 71.86 | 314 | 17.8 | 17.6 |
| 8 | 81.25 | 74 | 29.5 | 2.5 |
| 9 | 96.25 | 57 | 35 | 1.6 |

width) and channel constraint (constrained and unconstrained). The 1-y flood-recurrence interval discharge was calculated from the annual maximum data series, which uses the single largest discharge for each year of record, from USGS 02353500 (site 6; Fig. 1). The recurrence interval (T in y) was calculated as

$$T = (n + 1)/N$$

where n is the number of years of record, and N is the rank of the particular event (Knighton 1998). If the average discharge during the sampling date was greater than the 1-y flood-recurrence interval discharge, the date was considered as being in high flow condition. If the average discharge during a sampling date was less than the 1-y flood-recurrence interval discharge, the date was considered as being in low flow condition.

Data analysis

Our goal was to determine how much seston quality and stable isotope signature were affected by particle size, hydrology, floodplain width, and drainage-network position within the basin. Seston quality was quantified as C:N, with the assumption that a lower value indicated higher quality. C:N values were $\log(x)$ -transformed to meet the assumptions of normality and homogeneity of variance implicit in parametric analyses. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values met the assumptions of normality, so those values were not transformed. All statistical analyses were done with SAS (version 9.1; SAS Institute, Cary, North Carolina).

Two-way analyses of variance (ANOVAs) (PROC GLM) were used to determine whether C:N, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ of seston differed with particle size class, flow condition (high vs low flow), or their interaction. Significant ANOVAs were followed by Tukey's Hon-

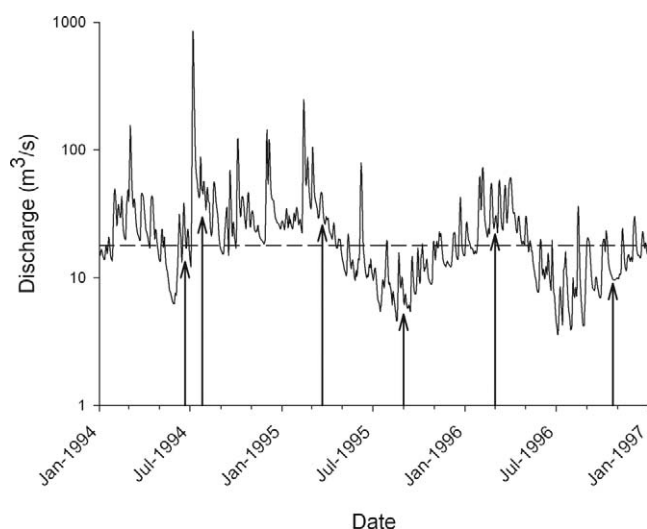


FIG. 2. Discharge at US Geological Survey gauge 02353500 (site 6) on Ichawaynochaway Creek from 1 January 1994 to 1 January 1997 is indicated by the solid line. The dashed line indicates the mean daily discharge. Arrows indicate dates when samples were collected.

estly Significant Difference (HSD) multiple comparisons to identify differences among size classes and between flow conditions ($\alpha = 0.05$; Littell et al. 2002). Linear regressions (PROC REG) were used to assess relationships between C:N, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ of seston and stream discharge. Discharge data from the 3 sites with USGS gauging stations were used in the analyses (sites 3, 6, and 7; Fig. 1). Linear regressions were used to determine if floodplain connectivity (floodplain width/channel width) affected C:N, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ of seston during high and low flow conditions. Data for high and low flow conditions (unconstrained vs constrained channel) were analyzed separately to isolate temporal variation in floodplain connectivity. Linear regression analyses were used to determine if mean C:N, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ across dates varied systematically with distance from the headwaters with high or low flow conditions. Data for high and low flow conditions (unconstrained vs constrained channel) were analyzed separately.

TABLE 3. Mean (\pm SE) values of C:N, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ during all flow conditions ($n = 150$), low flow conditions ($n = 102$), and high flow conditions ($n = 48$). Values with the same letter are not significantly different among seston size classes within flow conditions.

| Flow condition | Size class | C:N | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) |
|----------------|------------|--------------------|---------------------------|---------------------------|
| All | Small | 15.74 ± 0.34^A | -27.57 ± 0.06^A | 5.45 ± 0.15^A |
| | Medium | 17.75 ± 0.44^B | -27.53 ± 0.05^A | 5.02 ± 0.17^A |
| | Large | 27.65 ± 0.86^C | -27.87 ± 0.07^B | 3.85 ± 0.16^B |

TABLE 2. Classification of dates as high flow or low flow based on the 1-y recurrence-interval flood. The 1-y recurrence-interval flood discharge is based on a previous record of 78 y of discharge data. Discharge was measured at US Geological Survey gauge 02353500.

| Date | Discharge (m^3/s) | Hydrology |
|------------------|-------------------------------------|-------------------------------|
| 78-y record | 27.00 | 1-y recurrence-interval flood |
| 22 June 1994 | 20.78 | Low flow |
| 25 July 1994 | 48.14 | High flow |
| 22 March 1995 | 43.89 | High flow |
| 31 August 1995 | 7.48 | Low flow |
| 29 February 1996 | 25.34 | Low flow |
| 23 October 1996 | 9.63 | Low flow |

Results

Hydrology

Our study encompassed a range of streamflow variability in the IC basin (Fig. 2). Tropical Storm Alberto and other tropical storms caused near-record precipitation (192 cm total, 60 cm above average) during the summer and autumn 1994 (Golladay et al. 2000). Thus, discharges were above average in IC from summer 1994 to spring 1995 and included the greatest flow on record. Based on the annual duration series, the 1-y recurrence-interval flood discharge at the USGS gauging station at site 6 (USGS 02353500) was $27.00 \text{ m}^3/\text{s}$ (Table 2). Low flow conditions existed on 22 June 1994, 31 August 1995, 29 February 1996, and 23 October 1996, and high flow conditions existed on 25 July 1994 and 22 March 1995 (Table 2).

Particle size

Seston quality decreased with particle size and flow. C:N differed significantly among particle sizes (ANOVA, $p < 0.0001$; Table 3, Fig. 3). C:N was lowest for small particles and increased with increasing particle size (Tukey's HSD, $p < 0.0001$). C:N differed between flow conditions (ANOVA, $p = 0.018$). C:N of small and medium particles was lower during high than during low flow conditions (Tukey's HSD, $p = 0.0015$, $p = 0.0072$, respectively; Fig. 3). C:N of large particles did

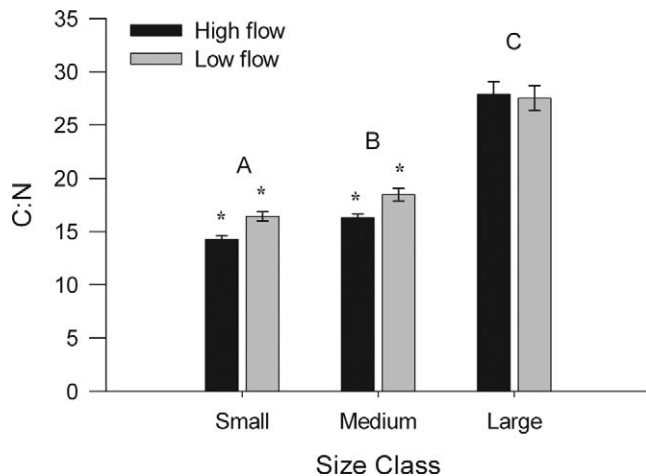


FIG. 3. Mean (± 1 SE; $n = 150$) C:N of seston in different particle size classes during high and low flow conditions in Ichawaynochaway Creek basin. Seston particle size classes were: small (S; 10–45 μm), medium (M; 45–250 μm), and large (L; >250 μm). Size classes with the same letters are not significantly different (Tukey's Honestly Significant Difference, $\alpha = 0.05$; Littell et al. 2002). Asterisks indicate significant differences between high and low flows within size classes (Tukey's Honestly Significant Difference, $\alpha = 0.05$; Littell et al. 2002).

not vary with flow condition (Tukey's HSD, $p = 0.6634$; Fig. 3). C:N was not affected by the interaction between particle size and flow condition (ANOVA, $p = 0.055$).

Isotopic signature differed with particle size and flow condition. $\delta^{13}\text{C}$ differed among the 3 particle sizes (ANOVA, $p = 0.0002$; Table 3, Fig. 4). Small and medium particles were less depleted in $\delta^{13}\text{C}$ than were large particles (Tukey's HSD, $p < 0.001$). $\delta^{13}\text{C}$ varied between flow conditions (ANOVA, $p < 0.04$). Small and medium particles were less depleted in $\delta^{13}\text{C}$ than were large particles during low flow conditions (Tukey's HSD, $p = 0.0005$), whereas $\delta^{13}\text{C}$ did not differ among particle size classes during high flow conditions (Tukey's HSD, $p = 0.1142$). $\delta^{13}\text{C}$ was not affected by the interaction between particle size and flow condition (ANOVA, $p = 0.6446$). $\delta^{15}\text{N}$ differed among particle sizes (ANOVA, $p < 0.0001$; Table 3, Fig. 4). Small and medium particles were more enriched in $\delta^{15}\text{N}$ than were large particles (Tukey's HSD, $p < 0.0001$). $\delta^{15}\text{N}$ varied between flow conditions (ANOVA, $p < 0.0001$). Small, medium, and large particles were more enriched in $\delta^{15}\text{N}$ during low than during high flow conditions (Tukey's HSD, $p = 0.0006$, $p = 0.0008$, $p = 0.0014$, respectively; Fig. 4).

Hydrological effects on nutrients

Effects of discharge on seston quality were dependent on particle size. Seston quality of small particles,

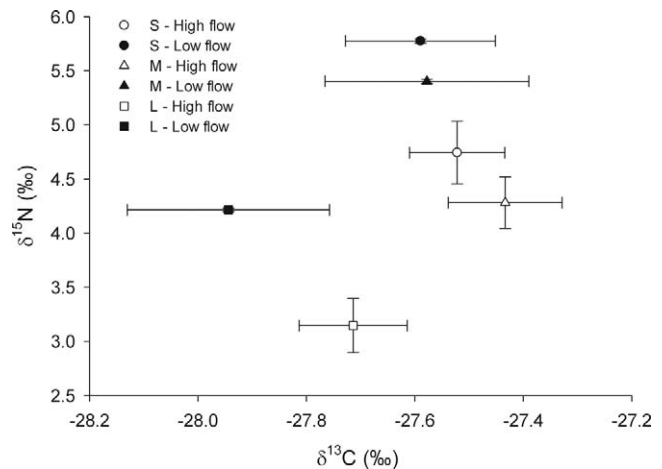


FIG. 4. Mean (± 1 SE; $n = 150$) stable isotopic signatures of seston in different particle size classes during high and low flow conditions in Ichawaynochaway Creek basin. Seston particle size classes were: small (10–44 μm), medium (45–250 μm), and large (>250 μm).

as measured by C:N, increased with increasing discharge ($y = -0.095x + 16.97$, $r^2 = 0.56$, $p = 0.001$, $n = 15$; Fig. 5A). C:N of medium and large particles did not vary with discharge ($p = 0.313$, $p = 0.334$; data not shown). $\delta^{13}\text{C}$ of small particles increased with increasing discharge ($y = 0.018x - 27.882$, $r^2 = 0.44$, $p = 0.007$, $n = 15$; Fig. 5B). $\delta^{13}\text{C}$ of medium and large particles showed similar, but nonsignificant, trends ($p = 0.16$, $p = 0.48$, respectively; data not shown). $\delta^{15}\text{N}$ of small, medium, and large particles did not vary with discharge ($p = 0.985$, $p = 0.83$, $p = 0.42$, respectively).

Floodplain geomorphology

Floodplain connectivity, measured as the floodplain/channel ratio, interacted with flow condition and particle size to determine seston quality. C:N of small particles increased with floodplain connectivity during low flow conditions ($y = 0.083x + 14.506$, $r^2 = 0.66$, $p = 0.009$, $n = 9$; Fig. 6A) but not during high flow conditions ($r^2 = 0.12$, $p = 0.353$; Fig. 6A). The range of C:N values tended to be smaller during high flow conditions (7.62–16.07) than during low flow conditions (12.50–25.34). C:N of medium particles increased nonsignificantly with floodplain connectivity during low flow conditions ($r^2 = 0.36$, $p = 0.122$; data not shown) but was unrelated to floodplain connectivity during high flow conditions ($r^2 = 0.03$; $p = 0.65$; data not shown). C:N of large particles was unrelated to floodplain connectivity during low or high flow conditions ($p = 0.82$, $p = 0.93$, respectively; data not shown).

Because floodplain connectivity varied predictably

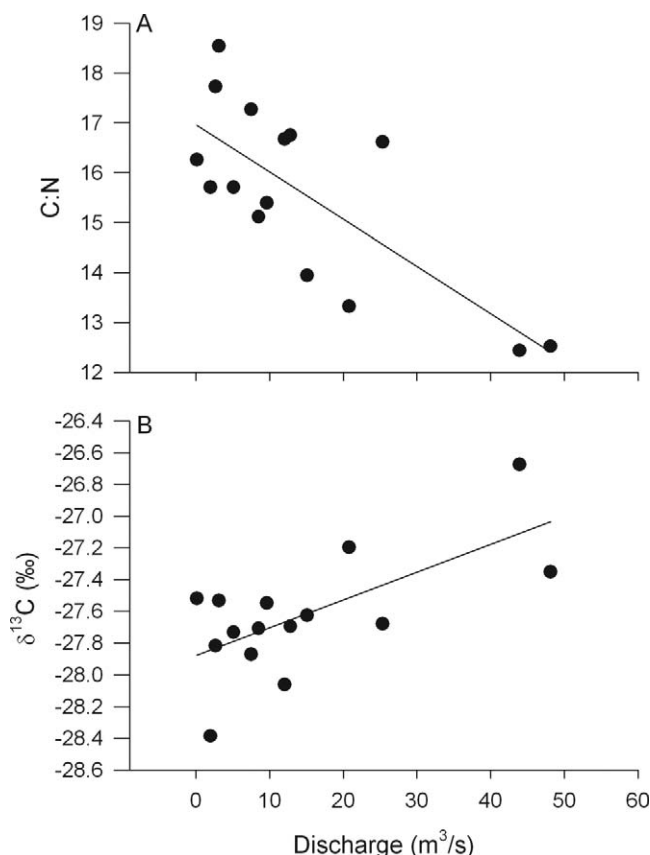


FIG. 5. Linear regression for C:N (A) and $\delta^{13}\text{C}$ (B) of the small seston particles as functions of average discharge the day the sample was taken. Discharge data were available for sites 3, 6, and 7.

(decreasing downstream), the effect of drainage-network position in the basin on seston quality varied with flow and particle size. C:N of small particles decreased with distance from the headwaters during low flow conditions ($y = -0.0578x + 19.822$, $r^2 = 0.84$, $p = 0.001$, $n = 9$; Fig. 7A) but was unrelated to distance from the headwaters during high flow conditions ($r^2 = 0.14$, $p = 0.29$; Fig. 7A). C:N of small particles was lower during high than during low flow conditions at all sampling sites (Fig. 6A). C:N of medium particles decreased nonsignificantly with distance from the headwaters during low flow conditions ($r^2 = 0.36$; $p = 0.09$; data not shown) but was unrelated to distance from the headwaters during high flow conditions ($r^2 = 0.06$; $p = 0.53$; data not shown). C:N of the large class was unrelated to distance from the headwaters during low or high flow conditions ($p = 0.33$, $p = 0.94$, respectively; data not shown).

Floodplain connectivity and distance from the headwaters affected isotopic signatures, but the effects were dependent on particle size and flow condition. $\delta^{13}\text{C}$ values of small (Fig. 6B) and large (data not

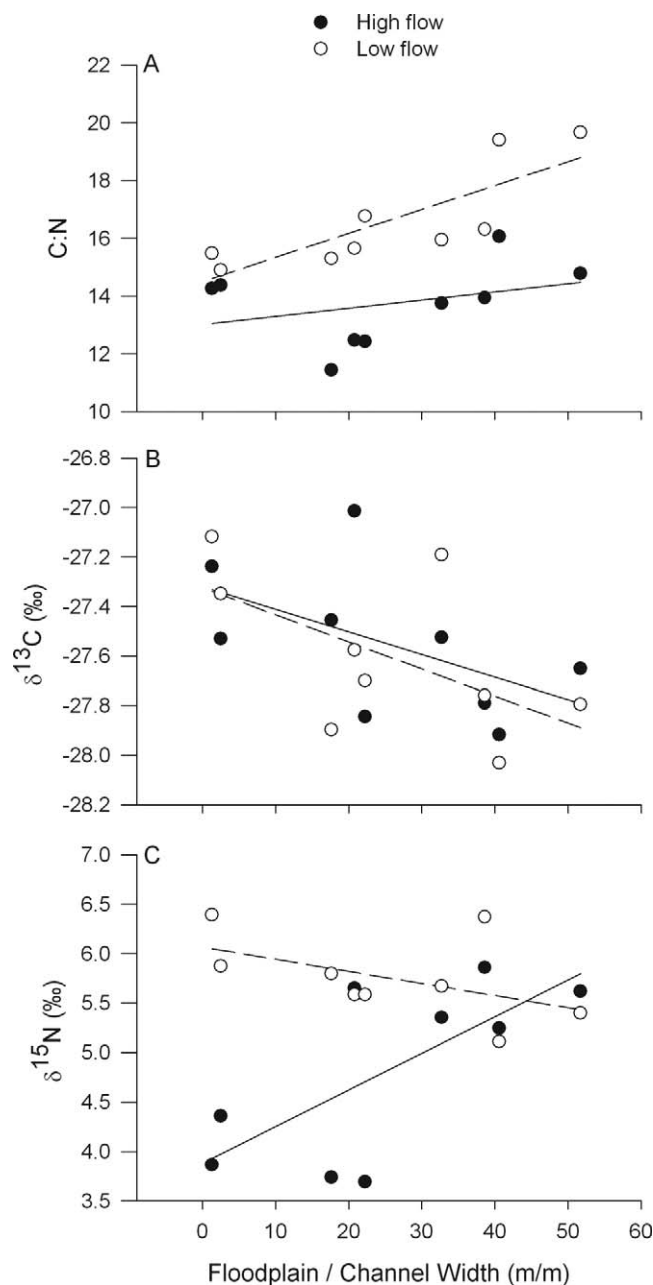


FIG. 6. Linear regression for C:N (A), $\delta^{13}\text{C}$ (B), and $\delta^{15}\text{N}$ (C) of the small seston particles as functions of floodplain connectivity (floodplain width/channel width) during periods of low and high flow.

shown) particles were not related to floodplain connectivity during low ($p = 0.09$, $p = 0.34$, respectively) or high ($p = 0.13$, $p = 0.06$, respectively) flow conditions. $\delta^{13}\text{C}$ of medium particles decreased with increasing floodplain connectivity during both low ($y = -0.0081x - 27.374$, $r^2 = 0.61$, $p = 0.013$) and high ($y = -0.016x - 27.059$, $r^2 = 0.72$, $p = 0.004$) flow conditions (data not shown). $\delta^{13}\text{C}$ of small and medium particles

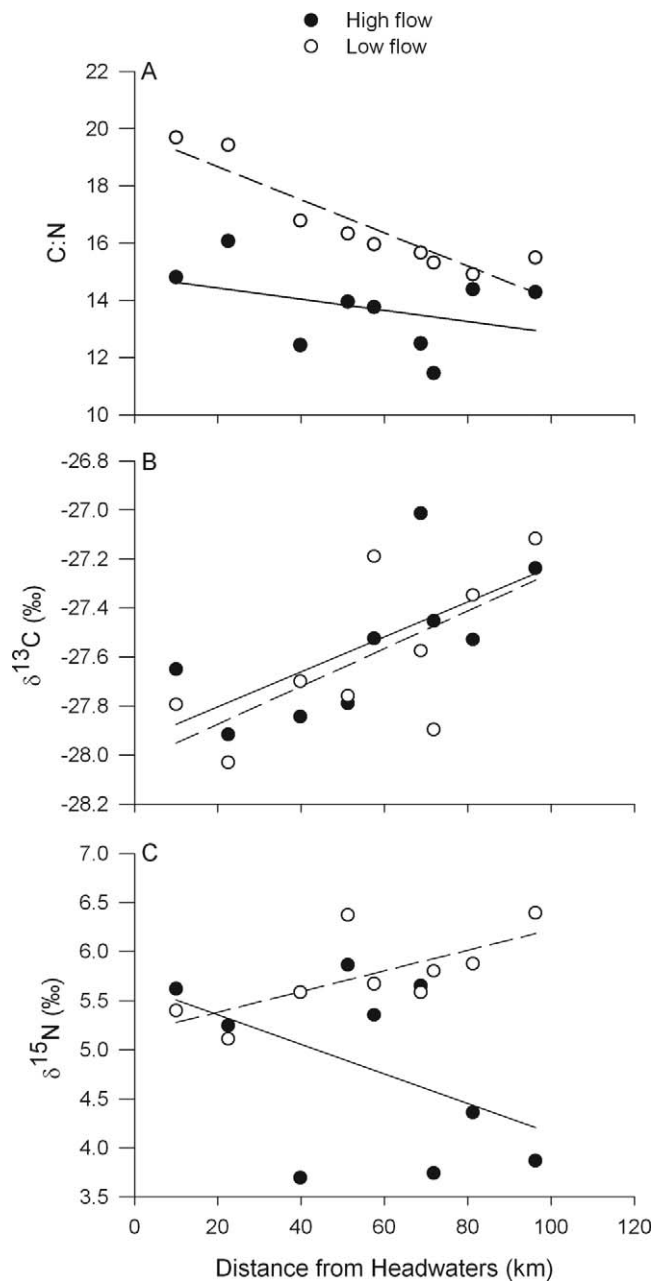


FIG. 7. Linear regression for C:N (A), $\delta^{13}\text{C}$ (B), and $\delta^{15}\text{N}$ (C) of the small seston particles as functions of distance from the headwaters during periods of high and low flow.

increased with distance from the headwaters during low flow conditions (small: $y = 0.008x - 28.029$, $r^2 = 0.45$, $p = 0.049$, $n = 9$; Fig. 7B) (medium: $y = 0.0048x - 27.844$, $r^2 = 0.56$, $p = 0.02$; data not shown) and high flow conditions (small: $y = 0.007x - 27.948$; $r^2 = 0.46$, $p = 0.04$, $n = 9$; Fig. 7B) (medium: $y = 0.0086x - 27.938$, $r^2 = 0.55$, $p = 0.02$; data not shown). $\delta^{13}\text{C}$ of large particles increased with distance from the headwaters during high flow conditions ($y = 0.0072x - 28.109$, $r^2 = 0.49$, $p =$

0.04; data not shown) but not during low flow conditions ($r^2 = 0.07$, $p = 0.51$; data not shown).

$\delta^{15}\text{N}$ of small particles increased with increasing floodplain connectivity during high ($y = 0.037x + 3.884$, $r^2 = 0.50$, $p = 0.03$, $n = 9$) but not during low ($r^2 = 0.25$, $p = 0.17$) flow conditions (Fig. 6C). $\delta^{15}\text{N}$ values of small particles were similar between low and high flow conditions for high values of floodplain connectivity (Fig. 6C). Relationships between $\delta^{15}\text{N}$ of medium and large particles and floodplain connectivity were similar to those observed for small particles, but were not statistically significant during low ($p = 0.81$, $p = 0.54$, respectively; data not shown) or high ($p = 0.06$, $p = 0.07$, respectively; data not shown) flow conditions. $\delta^{15}\text{N}$ of small particles increased with increasing distance from the headwaters during low ($y = 0.011x + 5.175$, $r^2 = 0.48$, $p = 0.04$, $n = 9$; Fig. 7C) but not during high ($r^2 = 0.22$, $p = 0.20$; Fig. 7C) flow conditions. $\delta^{15}\text{N}$ values of small particles were similar between low- and high-flow conditions in the headwaters (Fig. 7C). Relationships between $\delta^{15}\text{N}$ of medium and large particles and distance from the headwaters were similar to those observed for small particles but were not statistically significant during low ($p = 0.38$, $p = 0.89$, respectively; data not shown) or high flow conditions ($p = 0.84$, $p = 0.11$, respectively; data not shown).

Discussion

Particle size

In the IC basin, as in other streams, seston consists mostly of small particles (Wallace et al. 1982, Golladay et al. 2000, Colón-Gaud et al. 2008). Overall, the quality of small and medium particles was greater than that of large particles in the seston in the IC basin. Smaller particles generally have higher nutrient content and lower C:nutrient ratios than do large particles (Sinsabaugh and Linkins 1990, Bonin et al. 2000, Cross et al. 2003). The tendency of smaller particles to have higher C:N has been attributed to a relatively greater proportion of nutrient-rich bacterial biomass and different origin (amorphous detritus vs fragmented plant material) in smaller particles compared to large particles (Kondratieff and Simmons 1985, Edwards 1987, Kamauchi 2005). Consumption of nutrient-rich bacteria on sestonic particles by filter feeders and other consumers is an important link in stream food webs (Meyer 1994, Sterner and Elser 2002, Makino et al. 2003).

Differences in isotopic signatures among particle sizes probably reflected a combination of particle origin, state of decomposition, and microbial conditioning. Large particles had a more depleted $\delta^{13}\text{C}$ signature than did small or medium particles. This

depleted $\delta^{13}\text{C}$ signature probably reflects the origin of these particles from C_3 riparian vegetation. Smaller particles had less depleted $\delta^{13}\text{C}$ signatures that indicate possible modification of riparian particles by microbial degradation and contribution of particles from other instream sources, such as detached algae or fecal pellets. Smaller particles also had more enriched $\delta^{15}\text{N}$ signatures than did large particles, and this pattern might be linked to the pattern of higher quality of small particles. Some bacteria have enriched $\delta^{15}\text{N}$ signatures (Macko and Estep 1984), and higher microbial biomass might enrich $\delta^{15}\text{N}$ signatures in small seston particles. $\delta^{15}\text{N}$ signatures of smaller seston particles tended to be enriched in the Colorado River, and Angradi (1994) hypothesized that microbes were dominant contributors of greater ^{15}N .

The quality and isotopic signatures of particles differed between high and low flow conditions. $\delta^{15}\text{N}$ signatures of particles in all size classes were less enriched in high flow conditions than in low flow conditions. The lower $\delta^{15}\text{N}$ enrichment values indicate that particles transported during high flow conditions might have had lower bacterial biomass and might have been less decomposed (fresher) than those transported during low flow conditions. Moreover, the $\delta^{13}\text{C}$ of all particle sizes was more depleted during low flow conditions than during high flow conditions, a result that indicates a higher proportion of particles of all sizes with terrestrial origin during low flow conditions. This interpretation is supported by the observation that the quality (C:N) of large particles did not change with flow condition, but the quality of smaller particles increased during high flow conditions, a result that suggests that small particles were fresher and less decomposed during high than during low flow conditions.

Seasonal flooding

Much of the energy that drives stream food webs is derived from particulate and dissolved organic matter of riparian origin (e.g., Cuffney 1988, Wallace et al. 1997). Thus, understanding how riparian resources vary in quality over space and time is essential to understanding stream food webs. Larger quantities of seston are transported into the channel during high than during low flow conditions (Golladay et al. 2000). Particles transported during high flow conditions are of higher quality than those transported during low flow conditions. These high-quality particles probably originate from the floodplain and the benthic zone.

Inadequate supplies of nutrients can slow the growth of animals and alter their life histories and behavior (Sterner and Elser 2002). High biomass and

production of aquatic insects are supported by abundant microbially enriched detritus from floodplains in other Coastal Plain streams (Edwards and Meyer 1990). Particle quality can affect the distribution and production of filter-feeding insects (Wallace and Merritt 1980). *Tipula* larvae had lower growth and consumption rates when fed conditioned leaves with high C:N than when fed leaves with low C:N (Tuchman et al. 2002). *Daphnia* had higher growth and reproductive rates in clear lakes (mean C:N = 8) than in humic lakes (mean C:N = 10.5) where materials with lower C:N also had higher fatty acid quality (Gutseit et al. 2007). Greater abundance, biomass, and secondary production of aquatic insects have been attributed to low C:nutrient consequent to nutrient enrichment in streams (Cross et al. 2006, Greenwood et al. 2007). Thus, the low C:N of the seston in the IC basin during high flow conditions might reduce elemental imbalances of food resources and promote growth of consumers, such as filter-feeding bivalves (native unionids and introduced *Corbicula fluminea*) and net-spinning caddisflies (e.g., Hydropsychidae), at the base of IC food webs (Frost et al. 2002).

In the IC and similar streams, unconstrained reaches with broad floodplains act as important source areas that export high-quality material into the stream during high flows. Riparian forests are a substantial source of suspended material in streams at all times, but our data show that high flow periods are important because they bring fresh materials into streams. A decrease in frequency and duration of flooding could reduce the availability of abundant high-quality food materials, potentially altering energy flow to consumers. Moreover, the timing of floods is important because floods transport high-quality resources needed for growth and reproduction of consumers. For example, growth and development of mayflies are sensitive to C:N in detrital food (Söderström 1988). Streams have stronger connections to riparian forests during high than during low flow conditions, especially in areas where the floodplain is broad. Seasonally flooded forests contribute significant quantities of organic material to streams (Meyer and Edwards 1990, Golladay et al. 2000), and our results show that high-quality material is transported into the stream channel during periods of inundation.

Floodplain geomorphology

Connectivity of the stream (constrained vs unconstrained) to the floodplain influenced food quality and isotopic signatures in the IC basin. During low flows, seston quality decreased as floodplain connectivity decreased. The lower quality of seston in unconfined

reaches of IC during low flow conditions probably was a result of the physical characteristics of this stream. Many of the unconfined reaches of the stream are in the upper part of the basin, and during low flow conditions, transport of material from upstream and from the floodplain is reduced. Seston quality decreases with the residence time of material in a stream (Hoffman 2005). Moreover, during summer low flow conditions, the upper portion of the IC basin is shaded and primary production is low. The combination of low autochthonous input and reduced input of fresh material from the floodplain in the upper portions of the basin probably caused seston quality to decrease and to have a more depleted $\delta^{13}\text{C}$ signature indicative of terrestrial C_3 sources (Fry 2006).

The $\delta^{13}\text{C}$ signature of biofilm typically has a pattern of downstream enrichment that is related to downstream reduction in dissolved CO_2 concentration and photosynthetic fractionation rates (Finlay 2001, 2004), and seston in IC has a similar pattern. The lower reaches of the basin, which are more confined, have more flow and less shading than do the upstream reaches. Thus, downstream reaches have higher rates of primary production than do upstream reaches. The effects of this primary production are evident because the quality of seston is greater, $\delta^{13}\text{C}$ is less depleted, and $\delta^{15}\text{N}$ is more enriched in a downstream direction during periods of low flow.

During high flow conditions, seston quality was not related to floodplain connectivity, possibly because of mixing and longitudinal homogenization of seston. However, seston quality was of higher quality in all reaches during high flow conditions when the stream was connected to the floodplain and materials were in transport. $\delta^{15}\text{N}$ increased as floodplain connectivity increased, a result that might indicate an increase in the seston of microbially enriched particles (Macko and Estep 1984, Angradi 1994, Goedkoop et al. 2006) from the floodplain.

During high flow conditions, neither C:N nor $\delta^{15}\text{N}$ varied with distance from the headwaters. Greater water velocity and stream flow increase transport distance of particles, which in turn, influences the turnover length of the seston (Meyer and Edwards 1990, Paul and Hall 2002). In IC, greater transport length during high flow conditions appeared to cause a greater degree of seston homogenization throughout the basin.

The combination of greater connectivity and longitudinal homogenization led to the presence of higher-quality materials in the seston in all reaches during high flow conditions. During low flow conditions, higher-quality materials were present in the downstream confined reaches because greater flow in those reaches enabled the export of particles from the

floodplain and a lack of shading in those reaches allowed benthic primary production. Factors at multiple scales, including spatial and temporal variability, influenced material transport and productivity in the IC basin.

Altered floodplains and potential effects on food quality

Floodplain inundation supports productivity and maintains biological diversity in large rivers and low-gradient streams (Junk et al. 1989, Amoros and Bornette 2002). Our results indicate that floods might be particularly important for supplying high-quality food resources to the stream. Reductions in the surface area of active (natural) floodplains and wetlands could have significant implications for floodplain–river food webs (Edwards 1987, Zueg and Winemiller 2008). Inundated floodplains are important habitat for young fish, and they export organic material and organisms returning to the main channel during high flow conditions (Junk et al. 1989, Poff et al. 1997). In addition, unconstrained stream reaches appear to be important source areas for material scavenged during floods (Golladay et al. 2000). Riparian forests, particularly those on reaches with broad floodplains, should be preserved or restored to support instream food webs. Our results indicate that the spatial and temporal complexity of stream ecosystems, including flooding regimes and distribution of floodplain forests, interact to determine the input and quality of basal food resources to stream consumers.

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