

Effects of Experimentally-Altered Hydrology on Ecosystem Function in
Headwater Streams

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ABSTRACT

Forested headwater stream ecosystems are important integrators of terrestrial and aquatic systems and their function depends greatly on water availability. In the southern Appalachians, models of future climate change predict alterations to the timing and intensity of storms such that most precipitation may be relegated to winter and spring. During the summer and fall, relatively less precipitation will translate to lower stream flows in systems that rarely experience such a lack of water. Given these predicted changes to the hydrologic cycle, I experimentally reduced flow to downstream sections of three streams at the Coweeta Hydrologic Laboratory in NC to assess changes to function in perennial ecosystems. The questions that I addressed included: 1) How is organic matter decomposition regulated by changes to the availability of water? and 2) How does the relationship between nutrient uptake and metabolism change under conditions of varying water availability? The availability of water (as discharge) was shown to be a major control of ecosystem function throughout these studies. Rates of leaf decomposition varied between red maple (*Acer rubrum* L.) and white oak (*Quercus alba* L.) with lower discharge in the early autumn regulating the breakdown trajectories of leaves through facilitation of colonization by microbes and macroinvertebrates. The return of water during the winter accelerated decomposition rates in the diverted sites such that mass of leaves remaining were similar to those in upstream sections. Colonization of decomposing organic matter by heterotrophic microbes (especially fungi) increased N immobilization leading to an increase in respiration per unit leaf standing

stocks during the fall. Nitrification was detectable during summer low flows when leaf standing stocks were low. Changes in the timing and intensity of precipitation and thus discharge may in turn alter the temporal dynamics of ecosystem function. Leaves may remain in the stream unprocessed which will change the availability of food for macroinvertebrates, the production of which provides nutrition to higher trophic levels. Local-scale differences in organic matter processing and nutrient immobilization may translate to regional differences in food availability over both time and space. Hydrology not only acts as a local control of endogenous processes but acts also regionally through the transport of resources and nutrients to downstream reaches.

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Chapter 1: General Introduction

Forested headwater stream ecosystems function as an important integrator of terrestrial and aquatic systems, while also providing resources to downstream reaches (Vannote et al. 1980). Processing and movement of organic matter provides a nutritional resource to a variety of invertebrate (Wallace et al. 1997) and ultimately vertebrate consumers (Cloe and Garman 1996). Additionally, immobilization and mineralization of inorganic nitrogen in headwater reaches can regulate transport to downstream rivers and estuaries, influencing water quality at those sites (Hall 2003). Inherent to all of these processes is the presence of water and significant flow to assist in the movement of particulates and nutrients to subsidize downstream reaches. Climate change predictions for the future indicate an alteration in the timing and intensity of precipitation, which may lead to wetter winters and longer, drier summers (Bates et al. 2008, Wu et al. 2012a,b). Given the importance of flow to ecosystem function in streams, a greater understanding of this factor in the context of future climate change is needed.

A variety of consumers rely on detrital organic matter inputs to headwater streams. Shredders utilize the biofilms accumulating on wet, conditioned leaves (Petersen and Cummins 1974), generating particulate organic matter (POM) used to drive production of collector guilds of invertebrates. Leaf breakdown has been shown to be much slower in the absence of water (Hutchens and Wallace 2002). Even with significant accumulation of coarse organic matter during dry periods (e.g. Lugthart and Wallace 1992, Larned 2000), the ability for microbes to colonize and initiate the process of litter breakdown is limited by water (Kaushik and Hynes 1971). In many cases, leaf packs will remain unprocessed on the dry streambed, but with some internal moisture, leaf packs may provide refuge for biofilm taxa (Robson et al. 2008) or invertebrates (Hutchens and Wallace 2002). When leaves are rewet and microbial activity is

stimulated again (Romani et al. 2006), shredders and detritivores were able to recolonize and capitalize on the abundant food source (Lugthart and Wallace 1992, Larned 2000).

Streams may respond to drought by contracting into spatially segregated reaches or isolated pools (Stanley et al. 1997), which may potentially become small areas of productivity (Lake 2003). Even so, accumulation of detrital matter may stimulate increases in respiration, offsetting the effects of increased GPP and driving streams to greater heterotrophy (Acuña et al. 2004). Additionally, stream ecosystem metabolism may be altered by changes in microbial activity (i.e. increases in respiratory demand) as a result of drying and rewetting of benthic sediments (Harms et al. 2009). Streams are important bioprocessors of nutrients and reactions within low order reaches can have strong effects on downstream water bodies (Hall 2003, Alexander et al. 2007, Young and Collier 2009). Traditional models of nutrient uptake demonstrate the importance of both biota and hydrology to biogeochemical cycling in ecosystems (Wollheim et al. 2001, Doyle 2005, Poole et al. 2008). In streams, discharge has been shown to be a major factor driving uptake of nitrogen and phosphorous (Webster et al. 2001).

As droughts are unplanned events, a continual compilation of environmental data will help us understand the true nature of change; comparisons of pre-, during, and post-drought data sets will provide robust assessments of change (e.g. Rees et al. 2006, Harms et al. 2009). In the studies presented here, I investigated how predicted changes in future precipitation patterns would translate into discharge-regulated alterations to ecosystem function. The questions that I address with this research included: 1) How is organic matter decomposition regulated by changes to the availability of water? And 2) How does the relationship between nutrient uptake and metabolism change under conditions of varying water availability?

In Chapter 2, I present the background for the experimental manipulations necessary for determining changes to ecosystem function in subsequent chapters. By using stream diversions, I was able to create a series of sites to control for stream discharge as the factor of interest in alterations of ecosystem function. Unlike past studies which have been interrupted by droughts or unplanned changes to stream flow, this experimental design allowed me an opportunity to test predictions related to climate change in a relatively controlled manor. In Chapter 3, I set up a gradient of water availability to investigate changes in organic matter decomposition in leaves of varying quality. Changes in decomposition were assessed over a six-month period. I assessed finer scale changes in leaf mass loss due to hydrologic controls of colonization and functional dynamics. Finally in Chapter 4, I assessed how nutrient dynamics and metabolism changed over a year between diverted and upstream sites. At the end of the year, I removed the diversions and investigated changes in nutrient dynamics in the same streams as a result of a storm. This research contributes to the literature on climate change effects on ecosystems but through controlling only one aspect of that change. I further developed a conceptual model for headwater streams, demonstrating how hydrologic controls regulate multiple components of these ecosystems, including inputs, outputs, and endogenous processes.

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Chapter 2: An Experimental Reduction of Baseflow in Southern Appalachian Perennial Streams

Introduction

Headwater reaches comprise a major amount of stream miles in the world (Meyer and Wallace 2001). Alterations in precipitation regime or land cover may alter the hydrologic pathways important for the maintenance of stream flow (Naiman and Turner 2000, Jackson et al. 2001, Barnett et al. 2008). Changes directly related to streams include alteration of precipitation and temperature regimes (Mulholland et al. 1997, IPCC 2007, Bates et al. 2008), which may have multiple effects on ecosystem function.

The ability of streams to sustain baseflow depends a great deal on groundwater inputs in the absence of precipitation; with less precipitation, groundwater is less likely to be recharged (Dahm et al. 2003). Predominance of drought conditions in the southern Appalachians would be regulated to some extent by forest cover, with streams draining oak-hickory systems less prone to massive water loss than those dominated by *Liriodendron tulipifera* and *Pinus strobus* (Ford et al. 2011a). Forest cover dominated by coniferous species and others with high levels of evapotranspiration may increase soil water retention during times of increased precipitation thus regulating high flows, but lead to extreme losses of stream flow during drier periods (Ford et al. 2011b).

Climate predictions for the southern Appalachians are less certain than other parts of the world, but models indicate a shift in the timing and intensity of precipitation (IPCC 2007, Bates et al. 2008, Wu et al. 2012a,b). Annual rainfall in this region will not be altered, but instead, more intense winter storms will occur, with longer periods without significant precipitation (IPCC 2007, Bates et al. 2008). This suggests that extended low-discharge conditions may prevail in the future, especially during the summer (Wu et al. 2012a,b). Stream structural aspects,

such as longitudinal linkage, wetted width, and stream-hyporheic connectivity may become altered in response to changes in precipitation (Stanley et al. 1997, Dahm et al. 2003). Although many regions of the world experience consistent wet-dry cycles (e.g. Oki and Kanae 2006), losing stream connectivity in the typically water-rich southern Appalachians will have implications across all ecological hierarchies (Larned et al. 2010, Rolls et al. 2012).

Stream ecosystems are important integrators of biotic, climatic, and landscape factors, and as such may be prone to future changes in climate. Changes to the frequency and intensity of precipitation in the southern Appalachians may lead to periods of significantly decreased surface flow, especially during summer months. In order to assess the magnitude of possible changes to surface flow, experimental weir diversions were constructed to remove water from three replicate reaches in Coweeta Hydrologic Laboratory from summer 2010 to autumn 2012. The objective was to assess the extent to which surface water diversion would affect annual discharge patterns in perennial headwater stream ecosystems. Discharge was expected to decrease in manipulated reaches as compared to control sites. While within-site discharge was expected to be different, the overall annual patterns should track seasonal differences in water availability typical of headwater streams within a mixed-deciduous forested landscape.

Methods

Site Description

Three streams within the Coweeta Hydrologic Lab basin in North Carolina were selected for use in this study (Fig. 1). The streams were specifically chosen for their similarities, including disturbance history, topography, and drainage area (Table 1, Swank and Waide 1988). Additionally, the streams used here were similar in terms of physical and chemical characteristics (Table 2). As with other streams in the Coweeta basin, these were perennial, with

substantial groundwater input sustaining baseflow even during low precipitation years (Swank and Waide 1988). Additionally, these three streams had structurally-sound weirs, which were used in the diversion experiments.

Stream Diversions

I diverted water away from the main channels of streams in order to experimentally address changes to ecosystem function as a result of decreased annual baseflow (e.g. Dewson et al. 2007a,b, Fig. 2). Overgrown and sediment-filled weir ponds were cleared out prior to diversion. A large piece of plywood was inserted behind the weir blade with a piece of landscape piping inserted through the board to drain water away from the main channel. This resulted in an approximately 30-m reach of diverted flow below the weir before the piped water was returned to the main channel.

Approximately 50-m reaches were measured upstream of the weir for use as un-manipulated comparison sites. I replicated this design across the three streams (WS 22, WS 40, and WS 41) for total of six stream sections (n=3 for both upstream and diverted experimental units). Diversion of WS 40 occurred in September 2010, while WS 41 and WS 22 were completed in July and August 2011, respectively. The manipulation remained in place for approximately 16 (WS 41, 22) and 27 (WS 40) months, throughout all four seasons. Diversions were removed from all three streams on 18 November 2012.

Stream Measures

Physical stream measures, including temperature, wetted cross-sectional area, and discharge were measured at least monthly from summer 2011 to autumn 2012. Stream discharge ($L s^{-1}$) was estimated using the salt-slug technique (Gordon et al. 2004) and normalized to watershed area ($L s^{-1} ha^{-1}$; Table 1). HOBO water-level pressure and temperature probes (Onset

Computer Corp., Bourne, ME, USA) were suspended in PVC wells inserted into the stream bottom in order to measure changes in temperature and stream level. Rating curves were developed for each of the six stream reaches in order to relate water level (as pressure) to discharge (Holmes et al. 2001). The resulting curves were applied to each stream's daily pressure values to create annual hydrographs to monitor the extent of the downstream diversions as compared to upstream reaches.

Results

Average stream temperatures were similar across all six reaches, regardless of treatment (Table 3). While minimum temperatures were essentially the same at all six sites, the temperature maxima depended on the stream (WS 22 > WS 41 > WS 40). Temperatures did not differ between upstream and diverted reaches of the same stream (Table 3).

Rating curves were unable to be calculated for five of the six stream sections, with the exception of upper WS 22 (Fig. 3). Patterns of discharge in WS 22 reflected changes to precipitation throughout the year of the diversions, with more frequent high flows occurring in winter (Fig. 3). Discharge was much lower during the summer months, with a small increase during the beginning of November 2012 (Fig. 3). Other experimental watersheds (WS 40, 41) experienced similar precipitation patterns annually, although the magnitude of discharge depended on the watershed area (e.g. Fig. 4).

The diversions reduced baseflow throughout the time of the manipulations in all three experimental reaches (Fig. 4). Mean discharge for all upstream sites was similar ($0.24 - 0.26 \text{ L s}^{-1} \text{ ha}^{-1}$), while diverted sites varied between $0.10 - 0.16 \text{ L s}^{-1} \text{ ha}^{-1}$ over the course of the manipulation. Actual reduction in baseflow (in diverted compared to upstream sites) ranged from a low of 6% in WS40 and WS41 in the winter of 2011-2012 to a high of nearly 90-95% in all

three diverted reaches during the autumn of 2011. Baseflow differences between upstream and diverted sites gradually increased as late spring progressed into summer 2012 (Fig. 4).

While stream depths varied somewhat across sites, the greatest differences existed for wetted widths (Table 3) resulting in greater differences in wetted cross-sectional area (Fig. 5). Stream wetted cross-sectional area roughly tracked increases in discharge over time, with higher values for both measures during the winter and spring (Figs. 4 and 5). Even so, as discharge decreased through the summer and into autumn 2012, wetted cross-sectional area in all three watersheds increased until the end of the study (Figs. 4 and 5). Diverted reaches in each watershed showed an obvious spike in both discharge (Fig. 4) and wetted cross-sectional area (Fig. 5) after the manipulations were removed on 18 November 2012, nearly matching measures taken at upstream sections.

Discussion

Stream manipulations at WS 22, WS 40, and WS 41 resulted in consistent decreases in the presence of water in all downstream sites. Stream diversions from the weirs not only decreased baseflow discharge relative to upstream reaches but contracted the wetted area of the stream sections similar to changes hypothesized by Stanley et al. (1997), Boulton (2003), and Lake (2003). All sites demonstrated annual highs and lows of discharge, tracking seasonal changes due to evapotranspiration and the development of deciduous terrestrial vegetation in the surrounding watershed (Lutz et al. 2012).

While the diversions experimentally altered baseflow and wetted area as predicted, temperatures at both upstream and downstream sites within a stream were unaltered (Tables 2 and 3). As such, further measures of ecosystem processes and rates should only be affected by the physical presence (or absence) of water and not by confounding changes in reaction rates due

to temperature variations (e.g. Curie et al. 2009). These data indicated that the diversions managed to reduce flow in downstream sites, with overall patterns in discharge tracking what would be predicted in the future (Wu et al. 2012 a,b). Therefore, this design provided an opportunity to measure changes in ecosystem function experimentally, while accounting for potential future changes to streams at Coweeta.

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Table 1. Descriptions of experimental watersheds used in this study at Coweeta Hydrologic Laboratory in Otto, NC, USA.

| Watershed | Stream | Area (ha) | Elevation Range (m) | Historical Watershed Treatment |
|-----------|------------------|-----------|---------------------|--|
| WS 22 | Lick Branch | 34 | 847-1246 | 1955-1960: Chemical killing of woody vegetation, 50% basal area lost |
| WS 40 | Wolf Rock Branch | 20 | 872-1219 | 1955: Selection cut, 22% basal area lost |
| WS 41 | Bates Branch | 29 | 893-1298 | 1955: Selection cut, 35% basal area lost |

Table 2. Pre-diversion physical and chemical characteristics of the three streams used in this study. Monitoring data from 2009 – 2011 were used for WS 40 and 41, while only data from summer 2011 were available for WS 22. BD = below detection limits ($5 \mu\text{g L}^{-1}$).

| Measure | WS 22 | | WS 40 | | WS 41 | |
|--|-------|--------------|-------------------|----------------|-------------------|----------------|
| | Value | Range | Mean \pm SE | Range | Mean \pm SE | Range |
| Discharge (L s^{-1}) | 6.2 | 2.0 – 12.0 | 7.7 ± 1.2 | 1.0 – 25.0 | 11.3 ± 2.9 | 1.0 – 25.0 |
| Width (cm) | 168.6 | 100 – 160 | 129.5 ± 8.8 | 59.5 – 162.4 | 111.9 ± 11.2 | 59.5 – 162.4 |
| Depth (cm) | 4.8 | 2.4 – 7.8 | 4.5 ± 0.8 | 1.3 – 11.5 | 5.6 ± 1.1 | 1.3 – 11.5 |
| Wetted cross-sectional stream area (cm^2) | 809.3 | 250 – 1117.7 | 592.9 ± 123.3 | 163.0 – 1687.1 | 653.1 ± 164.5 | 163.0 – 1687.1 |
| Specific Conductance ($\mu\text{S cm}^{-1}$) | 13.4 | 16.6 – 19.6 | 17.9 ± 0.4 | 15.1 – 18.7 | 16.7 ± 0.4 | 15.1 – 18.7 |
| Temperature ($^{\circ}\text{C}$) | 15.8 | 9.5 – 17.8 | 13.6 ± 1.7 | 8.9 – 17.3 | 14.5 ± 1.0 | 8.9 – 17.3 |
| Dissolved Oxygen (mg L^{-1}) | 8.9 | 8.3 – 11.1 | 9.2 ± 0.7 | BD | BD | BD |
| $\text{NH}_4\text{-N}$ ($\mu\text{g L}^{-1}$) | 7.2 | BD | BD | BD | BD | BD |
| $\text{NO}_3\text{-N}$ ($\mu\text{g L}^{-1}$) | 47.7 | 11.9 – 47.5 | 28.3 ± 2.2 | 5.6 – 28.7 | 14.9 ± 1.8 | 5.6 – 28.7 |

Table 3. Physical characteristics of the six stream reaches used in this study from July 2011 to November 2012.

| Stream/Reach | Slope (%) | Temperature (°C) | | Depth (cm) | | Width (cm) | |
|--------------|-----------|------------------|-------------|------------|-----------|---------------|--------------|
| | | Range | Mean ± SE | Range | Mean ± SE | Range | Mean ± SE |
| WS 22 | Upstream | 16.0 | 12.3 ± 0.03 | 3.3 - 7.3 | 4.8 ± 0.4 | 122.6 - 285.7 | 187.4 ± 12.0 |
| | Diverted | 7.9 | 12.2 ± 0.03 | 2.2 - 6.0 | 3.7 ± 0.4 | 67.7 - 259.3 | 175.0 ± 17.4 |
| WS 40 | Upstream | 10.8 | 12.5 ± 0.02 | 1.4 - 4.2 | 2.9 ± 0.3 | 118.0 - 197.7 | 165.3 ± 8.4 |
| | Diverted | 12.2 | 12.4 ± 0.02 | 1.3 - 3.6 | 2.5 ± 0.3 | 76.4 - 148.4 | 109.3 ± 7.8 |
| WS 41 | Upstream | 18.8 | 12.4 ± 0.02 | 2.3 - 7.1 | 4.6 ± 0.6 | 128.9 - 200.0 | 159.1 ± 9.5 |
| | Diverted | 12.2 | 12.3 ± 0.02 | 1.9 - 6.6 | 4.0 ± 0.6 | 86.9 - 170.0 | 113.4 ± 7.8 |

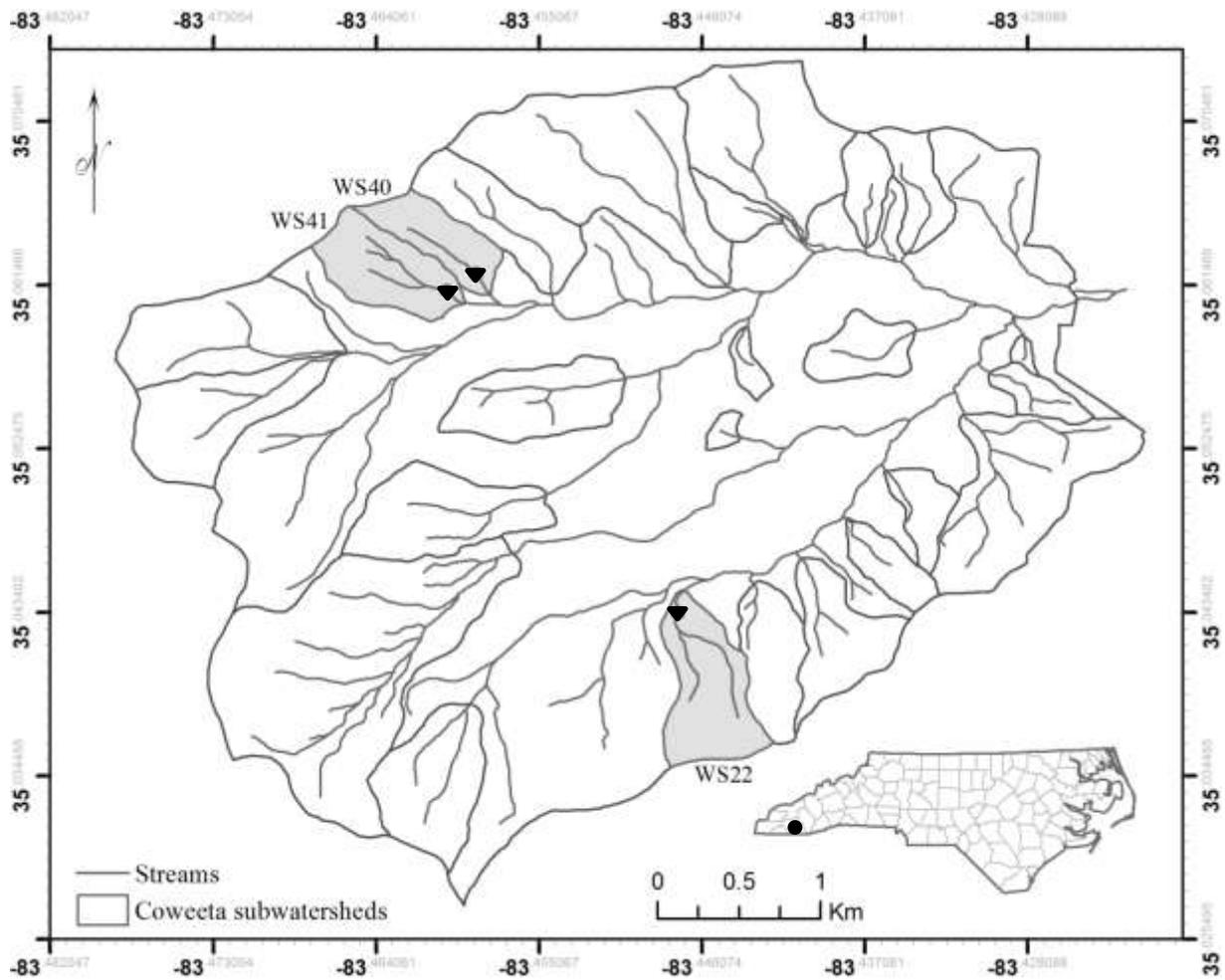


Figure 1. A map of the Coweeta Creek watershed in Macon County, NC (indicated by the dark circle on the North Carolina state map). Sub-watersheds used for this study are highlighted in gray, with the location of weirs at the inverted triangles (▼) on each of the three streams. Map courtesy of M. Hall-Brown, UNC-Greensboro Department of Geography.



Figure 2. Photographs of the stream diversion technique used for these studies. Photographs taken by the author.

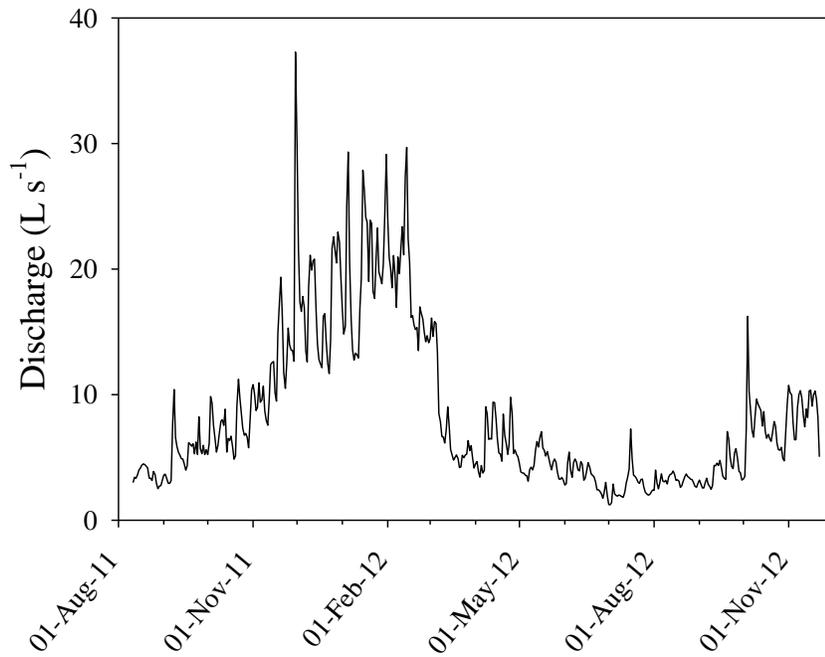


Figure 3. Changes in annual discharge patterns in upper WS 22 in Coweeta from August 2011 to November 2012. Daily discharge was calculated from a site-specific rating curve.

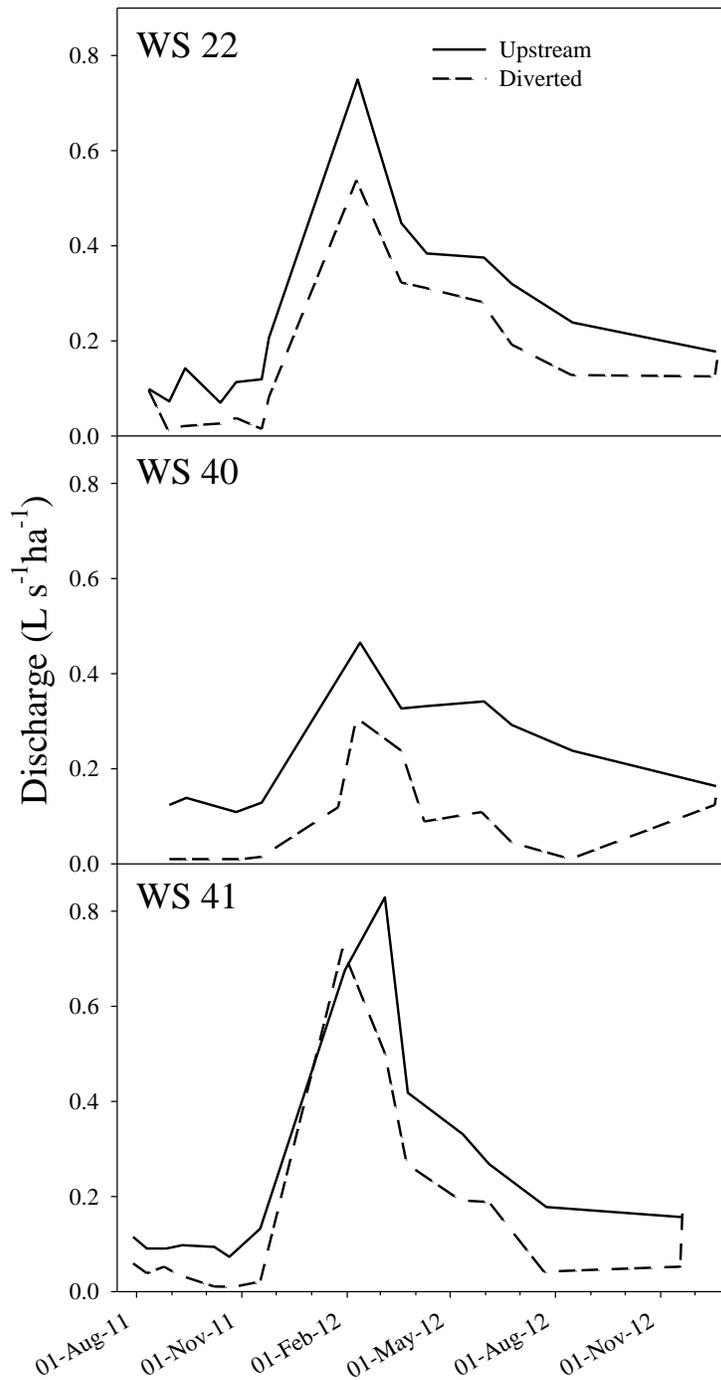


Figure 4. Annual discharge comparisons for upstream and diverted sections of the three study streams in Coweeta.

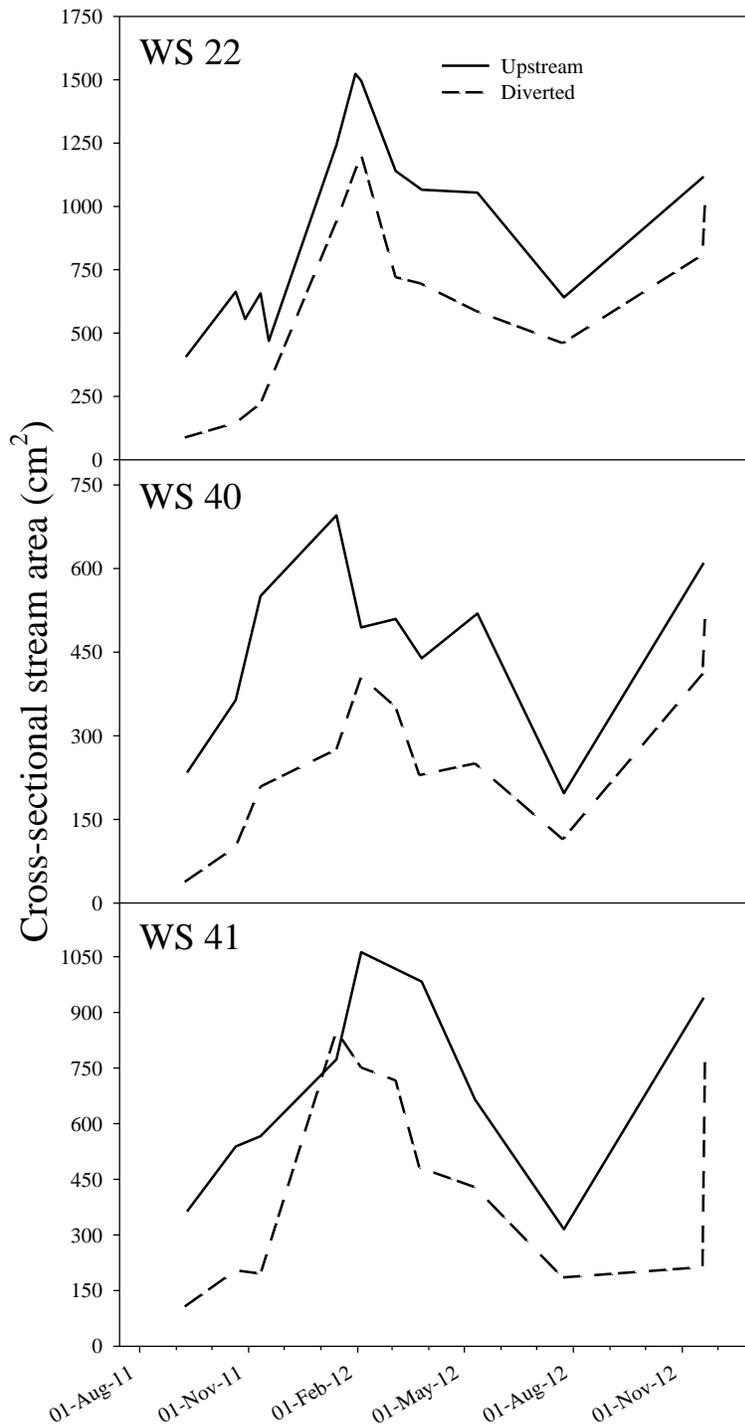


Figure 5. Wetted cross-sectional area comparisons for upstream and diverted sections of the three study streams in Coweeta

Chapter 3: Leaf Decomposition along an Inundation Gradient in Southern Appalachian Perennial Streams

Introduction

Headwater streams (orders 1-4) account for over 95% of stream length in the United States (Meyer and Wallace 2001, Poff et al. 2006). These headwater stream ecosystems, especially in forested regions, are strongly connected to their surrounding watersheds by the reliance on terrestrial subsidies (Wallace et al. 1997) and serve as sources of nutrients and energy for downstream locations (Vannote et al. 1980). In-stream organic matter processing is thus an important function in these ecosystems (Cummins 1974, Webster and Benfield 1986, Webster et al. 1999). In addition, another major function in streams is material transport. With a loss of flow, a concomitant decrease in velocity and material transport will occur. In Hawaiian streams, Larned (2000) found that significant amounts of detritus (mostly leaves) were retained during drought conditions. Similar results were noted in southern Appalachian streams during an extreme drought, where leaves were highly retained on bedrock outcrops, thus altering habitat availability for biota (Lugthart and Wallace 1992, Whiles and Wallace 1995). In both cases, the accumulated leaves were mostly exported downstream with the arrival of storm flows (Lugthart and Wallace 1992, Larned 2000), suggesting that streams become more depositional during periods of decreased flow.

Leaf breakdown has been shown to be much slower in the absence of water (Hutchens and Wallace 2002). Even with significant accumulation of coarse organic matter during dry periods (e.g. Lugthart and Wallace 1992, Larned 2000), the ability for microbes to colonize and initiate the process of litter breakdown is limited by water availability (Kaushik and Hynes 1971). In many cases, leaf packs will remain unprocessed on the dry streambed but with some internal moisture providing refuge for biofilm taxa (Robson et al. 2008) or invertebrates

(Hutchens and Wallace 2002). When leaves are rewet and microbial activity is stimulated again (Romani et al. 2006b), shredders and detritivores were able to recolonize and capitalize on the abundant food source (Lugthart and Wallace 1992, Larned 2000).

In many areas of the world, the frequency of dry periods may increase in the future due to changes in precipitation patterns (IPCC 2007, Bates et al. 2008). Empirical studies of drought in stream ecosystems do exist, but most are opportunistic and fail to account for pre-drought conditions (Lake 2003). Much of the current knowledge on the effects of drought in streams focuses on macroinvertebrate (e.g. Lugthart and Wallace 1992, Whiles and Wallace 1995), with less attention paid to functional ecosystem components. While most studies of the relationship between variable precipitation patterns and ecosystem function have been performed in arid (i.e. Dahm et al. 2003) or Mediterranean regions more prone to drought conditions (i.e. Acuña et al. 2005), data for temperate regions are lacking (but see Lugthart and Wallace 1992, Whiles and Wallace 1995).

In a region where water has characteristically been abundant (Sun et al. 2005), relatively little work has addressed the possibility of future decreases in stream flow on ecosystem function. The objective of this study was to better understand how organic matter processing would be affected by the presence of water. Using a system of retired weirs at the Coweeta Hydrologic Laboratory in NC, experimental diversions and a gradient of wetness from stream to upslope sites were created to evaluate organic matter breakdown. The intention was to experimentally alter the amount of water available to leaves and track changes to organic matter loss and colonization by microbes and macroinvertebrates that contribute to decomposition.

Methods

Site Description

These studies took place in three watersheds located at the Coweeta Hydrologic Laboratory in Otto, NC (Chapter 2). Surface flow from three stream reaches downstream of established, but non-functional, weirs was reduced using diversions in September 2010 (WS 40) and Summer 2011 (WS 22, 41). All downstream, diverted sections ranged from 25-30 m in length, with water being piped back into the stream below the experimental sections. Reference study reaches were also established upstream of the weir diversions in each of the three watersheds.

In order to address the influence of inundation levels on leaf breakdown, a transect was established from the stream to upslope terrestrial sites in all three watersheds. Besides the diverted sites, three sites were established along a transect away from the upstream reference site: in-stream, bank, and terrestrial. In-stream sites were located in the thalweg of non-diverted reference sites. Bank sites were established within areas of the stream that would become wetted only during storms. Finally, terrestrial sites were established on the forested hillslope, which were uninfluenced by the stream. This resulted in a balanced, replicated design ($n = 3$) for each site type.

Leaf Breakdown

Leaf breakdown was assessed at all sites using both Red Maple (*Acer rubrum* L.) and White Oak (*Quercus alba* L.). These leaf species were chosen to represent a range of decomposition based on previous studies at Coweeta (Webster et al. 1999). Five gram leaf packs were made for both species using plastic mesh bags (mesh size = 5 mm). Packs were randomly chosen and nailed into the sediment or soil at each site. One maple and one oak pack were collected from each site on six occasions from October 2011 to March 2012. Leaf material was washed gently with stream water into a pan and small subsamples were taken for microbial

analyses (see below). The rest of the leaf material was placed in paper bags for transport and drying in the laboratory. Dried leaf material was weighed, ground, and a subsample was burned in a muffle furnace at 550°C for 1 hour for calculation of ash-free dry mass (AFDM; Benfield 2006). Breakdown rates (day^{-1}) were determined from the log-transformed AFDM remaining over time (Benfield 2006).

Biotic Collections

Eight leaf subsamples (16-mm diameter) were removed from each leaf pack immediately after collection. Four of the punches were preserved in methanol for quantification of ergosterol, while the other four were preserved in 4% formalin for determination of bacterial abundance (Findlay et al. 2002). Ergosterol concentration was determined by saponification and extraction into pentane (Gulis and Suberkropp 2006). Leaf material preserved for bacterial counts was sonicated at 10W for 2 minutes (Findlay et al. 2002). Bacteria were enumerated on a Petrov-Hauser slide counter using light microscopy. Ergosterol and bacteria concentrations were converted to units of C for the development of fungal:bacterial ratios (Findlay et al. 2002).

Macroinvertebrates washed from leaf material were preserved in 95% ethanol for enumeration and identification using keys of Brigham et al. (1982) and Merritt et al. (2008). All organisms were also measured to the nearest 1 mm for conversion to biomass using length-weight equations of Benke et al. (1999) and Caballero et al. (2004). A length-weight equation for *Ephydra* was created using individuals from my collections due to lack of published data for this region, where DM= dry mass in mg and X= body length in mm:

$$\text{DM} = 0.0249e^{0.5935X}$$

Macroinvertebrate biomass and functional feeding group (FFG; e.g. Merritt et al. 2008)

Shannon-Weiner diversity was determined for each leaf pack.

Physical Stream Measures

HOBO water-level loggers were suspended inside pvc wells hammered into the stream substrate at each site prior to the beginning of this study. Salt slug discharge (Gordon et al. 2004) was measured at all stream sites throughout the sampling period for the development of discharge rating curves. Wetted stream cross-sectional area was also measured throughout the sampling period.

Nutrient Analyses

During each sampling day, water was collected and filtered through 0.7- μm GFF filters and frozen for analysis of background nutrient levels in each site. In the laboratory, ammonium concentrations were determined using the phenate method (APHA et al. 2005) with a flow-injection analyzer (Lachat Quickchem 8500, Lachat Corporation, Loveland, CO). Nitrate and phosphate concentrations were determined using ion chromatography (Dionex DX500 ion chromatograph, Thermo Fisher Scientific, Inc., Waltham, MA, USA). Specific conductance and stream temperature was measured using a YSI 30 probe (Yellow Springs, OH). Total carbon and nitrogen content of leaf material was measured using a FlashEA 1112 Elemental Analyzer (CE Elantech, Lakewood, NJ). Stream pH was measured using a YSI 556MPS multi-parameter handheld probe (Yellow Spring, OH).

Organic Matter Standing Stocks

Course particulate organic matter, including leaves, twigs, and bark, was sampled from a known area (0.25 m^2) of each stream reach on each sampling date. Material was placed in paper bags and allowed to dry in an oven at 60°C for at least three days. Mass was measured for each sample and corrected for sampling area. A total of six samples were taken from each stream during each collection ($n = 3$, for both upstream and diverted reaches).

Statistical Analyses

Two-way ANOVA was used to determine differences in background measures (Q, wetted cross-sectional stream area, conductivity, temperature, DO, pH, nutrients, and organic matter standing stocks) for both upstream and diverted sites over time. Differences in leaf breakdown rates among sites were assessed using a one-way ANOVA to assess differences between leaf pack locations for each species, with watersheds as replicates. A mixed-model ANOVA with repeated measures, blocking by watershed, was used to determine significant differences in leaves, locations, and days for a series of response variables: %AFDM remaining, microbial biomass, macroinvertebrate biomass, and C:N ratios. Non-significant factors and interactions were removed from the mixed model and it was re-analyzed with Tukey-Kramer corrections for all pairwise comparisons of significant factors and interactions ($\alpha=0.05$). Diversity of macroinvertebrate taxa on leaves was assessed for date, FFG, and site using a three-way ANOVA for each leaf species. A three-way ANOVA was also used to determine differences in leaf, date and location for fungal:bacterial biomass ratios and FFG biomass (Zar 1999).

Stepwise regression (addition threshold of $\alpha = 0.05$) was used to determine the best set of predictors for % leaf AFDM remaining, microbial biomass, and macroinvertebrate biomass on leaf packs. In assessing % AFDM remaining for each species of leaf, the set of predictors used for the model included fungal biomass, bacterial biomass, macroinvertebrate biomass, wetted stream cross-sectional area, and discharge. The macroinvertebrate biomass predictor set included fungal biomass, bacterial biomass, total microbial biomass, discharge, leaf C, leaf N, and leaf C:N. The total microbial biomass predictor set included discharge, leaf C, leaf N, and leaf C:N. Predictor sets for fungal and bacterial biomass was the same as for total microbial biomass. All analyses were run with either JMP 9.0 or SAS 9.3 (SAS Institute, Inc., Cary, NC USA).

Results

Hydrologic Changes

Weir diversions on each of the three watersheds used for this study successfully removed surface flow from downstream reaches when compared to upstream reference sites (Chapter 2). Upstream sites had significantly higher discharge compared to diverted sites ($p = 0.04$), with maxima occurring in February and March ($p < 0.0001$; Fig. 1A). Differences in wetted cross-sectional area generally followed patterns in discharge, with greater wetted areas in upstream sites ($p = 0.02$), with February and March also showing the widest stream areas ($p = 0.01$; Fig. 1B). Leaves in bank sites were wet when cross-sectional areas of the study streams were the widest (Fig. 1B) and were noticeably moist (but not inundated) when sampled (personal observation).

Background measures

Temperature changed significantly as the seasons progressed during the experiment (Table 1). In contrast, both conductivity and pH remained relatively similar across all stream reaches over time. Dissolved oxygen also varied significantly over time, generally responding to changes in temperature ($r = -0.93$, $p < 0.001$; Tables 1 and 2). Background levels of nutrients remained low over the course of the experiment. There were no detectable levels of ammonium during the study (MDL = $5.0 \mu\text{g L}^{-1}$). Measurable levels of nitrate were seen, but without a clear, significant pattern (Table 2).

Organic matter standing stocks significantly differed over time ($p = 0.001$), but not between reaches (Fig. 2). There was a trend of greater standing stocks in diverted sites during the fall (Fig. 2). The accumulation of organic matter coincided with changes to discharge at each of the sites (Figs. 1A and 2).

Leaf breakdown rates

Overall breakdown rates were not significantly different ($p = 0.9$) between leaf species (0.0049 vs. 0.0050 d^{-1} for red maple and white oak, respectively), but site differences did exist. Leaves in sites with some water present at all times (upstream and diverted sites) showed a trend of faster breakdown rates than those on bank or terrestrial sites, although only red maple demonstrated significant differences ($F_{3,8}=9.52$, $p=0.005$, Fig. 3). While breakdown rates of red maple and white oak leaves in diverted and upstream sites varied between 0.0056 and 0.0070 d^{-1} , both leaf species decomposed at essentially the same rates at all terrestrial and bank sites (range: 0.0033 - 0.0035 d^{-1}).

When examining breakdown rates at the beginning of the experiment prior to the influence of heavy winter storms (Fig. 1), greater differences existed in breakdown rates than at the conclusion of the experiment. Decomposition in general was faster until the end of 2011 compared to overall rates (Fig. 3 vs. 4). Red maple decomposition was significantly higher overall ($p = 0.001$) than white oak (0.010 vs. 0.007 d^{-1} , respectively) over the first 36 days of the study (Fig. 4). Within leaf species, there were also significant differences in rates based on deployment location. Red maple decomposition rates in stream sites were significantly greater than those at bank and terrestrial sites (Fig. 4). In contrast, white oak leaves had faster breakdown in upstream sites only, while diverted, bank, and terrestrial sites had similar rates (Fig. 4). Rates of decomposition across sites after January 2012 were not different.

Mass loss of leaves over time

At the conclusion of the experiment, there was a greater mass ($F_{1,128} = 41.22$, $p < 0.0001$) of white oak ($73.6\% \pm 2.4\%$) than red maple ($66.1\% \pm 2.4\%$). With the exception of leaves on the bank, red maple mass decreased significantly over the first day of the experiment in all other

sites ($p < 0.02$; Fig. 5). After 8 October 2011, leaves in the upstream sites had significantly less mass than in all other sites ($p < 0.02$), which were not significantly different than one another until January 2012. From January until March 2012, terrestrial and bank sites clustered together and had consistent mass over that time span (~ 55-60%; Fig. 5). Diverted and upstream sites clustered together in January and February 2012, but with significantly less mass remaining than the other sites (~35-40%; $p < 0.01$). On the last day of the experiment, the mass in upstream packs was not different than in bank and terrestrial sites (Fig. 5) but was significantly greater than in diverted sites ($p < 0.05$).

The trajectory of decomposition for white oak leaves was different than that of red maple (Fig. 5). White oak leaf mass declined from the beginning of the experiment until 12 November 2011, where leaf packs in upstream sites had significantly less mass remaining as compared all others ($p = 0.004$). Leaf mass significantly declined in all sites (except terrestrial) from the November until January 2012 ($p = 0.009$). The mass of white oak remaining in diverted sites began to overlap with those of leaves in upstream sites from January until the conclusion of the experiment in March 2012 (Fig. 5). After January 2012, the mass of white oak remaining in diverted and upstream sites were significantly lower than those of terrestrial and bank sites ($p < 0.007$). Additionally, there was little change in white oak mass for the remainder of the experiment (~ 70% in bank and terrestrial sites and ~ 40% in diverted and upstream sites; Fig. 5).

Microbial Biomass

There was no differential colonization of leaves by microbes based on location ($F_{3,87} = 0.58$, $p = 0.63$). Total microbial biomass increased from the beginning of the experiment until January ($F_{5,87} = 8.02$, $p < 0.0001$), after which biomass remained constant. By the end of the

experiment, a greater accumulation of microbial biomass had occurred on white oak than red maple ($F_{1,87} = 4.30$, $p = 0.04$).

Microbial biomass on white oak showed an increasing trend over the first three months of the experiment, after which accumulation was significantly greater than found initially ($p < 0.05$). In contrast, microbial accumulation on red maple only increased slightly by the end of the experiment, but this pattern was not significant. The greatest difference in microbial biomass accumulation between leaves was seen in January on white oak ($p = 0.0001$), after which biomass on both leaf types became similar.

The greatest microbial changes on leaves were driven by the accumulation of fungal biomass during this study (Fig. 6). Fungal biomass accumulated significantly on leaves from October until November before reaching a peak in January ($p < 0.001$, Fig. 6). White oak leaves were colonized by a greater proportion of fungi than red maple ($p = 0.02$) especially at non-stream sites. Fungal colonization on leaves in upstream sites increased initially, but remained fairly constant through March (Fig. 6). Red maple leaves in diverted sites steadily increased in fungal biomass over time, while a distinct peak of fungi on white oak was seen in January (Fig. 6). Although there were no site differences in fungal biomass, there was a trend for higher biomass at bank and terrestrial sites (Fig. 6).

Bacterial biomass on leaves was several orders of magnitude lower than that of fungi (Fig. 6) but demonstrated patterns different from that of fungi. Red maple leaves accumulated significantly more bacterial biomass than white oak ($p = 0.04$). Bacterial biomass also increased over the course of the experiment ($p < 0.0001$) but more so in the two stream sites compared to bank and terrestrial locations ($p < 0.0001$). Peaks of bacterial biomass generally occurred during

or on dates subsequent to highs of fungal biomass (Fig. 6), usually during the three sampling periods in 2012.

Macroinvertebrate Colonization

Macroinvertebrate biomass was not different between leaf species ($F_{1,88} = 0.02$, $p = 0.90$). In contrast, biomass on leaves did change significantly over time ($F_{5,88} = 5.06$, $p = 0.0004$) and differed across some sites ($F_{5,88} = 6.72$, $p = 0.0004$). Leaves in downstream and upstream sites had similar macroinvertebrate biomass but significantly more ($p > 0.05$) than terrestrial and bank leaves, which were also similar. Maximum macroinvertebrate biomass on leaves occurred in January and March 2012, which were both significantly greater than on all other days ($p > 0.04$).

Although the diversity of FFG did not differ among leaves and sites over time ($F_{24,35} = 1.09$, $p = 0.40$), the relative abundances of FFG showed distinct differences (red maple: $F_{72,109} = 4.99$, $p < 0.0001$; white oak: $F_{83,96} = 3.10$, $p < 0.0001$). Collector-gatherer and shredding macroinvertebrates were the most commonly found FFG colonizing leaf packs in this study, comprising nearly 80% of the total samples (Appendix A1). Shredders had significantly greater biomass compared to any other group colonizing red maple leaves ($p < 0.01$), while no differences in FFG biomass existed on white oak leaves over time (Figs. 7 and 8).

Shredders began to appear in November, but their greatest increases in biomass occurred with greater discharge in January. In upstream sites, shredder biomass on red maple leaves appeared to be high and far greater than any other FFG but was relatively stable from January through March (Fig. 7). On the other hand, there was a steady increase in shredders and predators on red maple in diverted sites, both reaching a peak in biomass during March (Fig. 7). Red maple leaves in bank sites were not colonized by any FFG until February, and collector-gatherers appeared to be dominant based on biomass (Fig. 7).

Biomass of FFG colonizing white oak leaves was more variable over time and among sites. Shredders were again dominant in the two stream sites but with nearly 2.5x greater peak biomass occurring in the diverted sites (Fig. 8). Predators appeared co-dominant with shredders in the upstream sites, with collector-gatherers appearing towards the end of the experiment (Fig. 8). White oak leaves on bank sites were also not colonized by macroinvertebrates until the latter part of the experiment, with collector-gatherers biomass dominating in February (Fig. 8). Terrestrial invertebrates, especially Collembola (Appendix A1), appeared mostly on leaves in bank sites (Figs. 7 and 8).

Leaf nutrients

The initial C:N of maple and oak leaves were significantly different, with red maple having higher ratios than white oak (red maple: 59.2 ± 3.9 , white oak: 23.7 ± 0.3 ; $p = 0.01$). Differences in initial C:N for each species was driven solely by N content of leaves ($p = 0.005$), with red maple having much less compared to white oak. Significant differences in leaf C:N were also found between species over time (interaction $F_{6,106} = 4.63$, $p = 0.003$). A significant spike ($p > 0.02$) in white oak C:N occurred in January 2012 ($p > 0.001$), mostly due to smaller concentrations of leaf N on that sampling day ($p < 0.05$). Species-specific C:N on all other days were similar, although a pattern of lower C:N was evident for white oak relative to red maple (Fig. 9).

Relationships between variables

Discharge was the most frequently-chosen predictor for determining changes to leaf packs during this study (Table 3). Approximately 30% of the changes to red maple leaf mass and microbial colonization of those leaves were explained by discharge. Macroinvertebrates found on red maple depended exclusively on the fungal biomass on leaf matter (Table 3). While the mass

of white oak leaves remaining was dependent partially on discharge, a much greater proportion of the change could be explained by including macroinvertebrate biomass. In contrast to red maple, macroinvertebrate biomass was explained in white oak by bacteria (Table 3). Leaf C was more important to both total microbial and fungal biomass colonizing white oak ($r^2 = 0.35 - 0.36$).

Discussion

Role of water permanence

Standing stocks of organic matter responded to changes in discharge throughout the study. Although there were no site differences in organic matter standing stocks, there was a clear pattern of accumulation in diverted sites (Fig. 2). Significant decreases in organic matter in the late winter was likely due to flushing by storms. This is consistent with previous studies in Coweeta during an extreme drought in the late 1980's, where streams demonstrated a clear retentiveness during low flows followed by organic matter flushing with the return of storms (Lugthart and Wallace 1992, Whiles and Wallace 1995).

The leaf species used in this study were meant to represent end-members of decomposition, where obvious differences could be seen between a fast and slower-decomposing species (Table 4). While the low-end of the range of breakdown for red maple was much less than previously reported, the mean aligns well with previous data from Coweeta streams (Gulis and Suberkropp 2003). White oak breakdown rates in this study match most others found in this region of the United States (Table 4).

In a similar study to this one in Coweeta, Hutchens and Wallace (2002) demonstrated a clear pattern of faster breakdown in in-stream sites compared to bank and upland sites. Results from my study generally agree with theirs but with diverted sites pairing consistently with

upstream sites here. Hutchens and Wallace (2002) concluded that the abundance of *Tallaperla* (a shredding stonefly) drove many of the differences between stream and less-wet sites. Clearly invertebrates play a role in decomposition in streams (e.g. Wallace et al. 1982, citations in Table 4), but, recently water permanence has been shown to be a stronger control over decomposition of leaves (Leberfinger et al. 2010, Treplin and Zimmer 2012). Similarly, results here demonstrated that water permanence (as discharge) was the strongest control over breakdown in both leaf species. Indirectly, discharge appeared to control longer-lasting white oak leaves by stimulating colonization of microbes, which then attracted shredding invertebrates (Figs. 6-8, Table 3).

Decomposition during the initial two months of the experiment was much faster than overall rates. These changes to the trajectory of decomposition were mostly related to discharge, where % AFDM remaining reached a plateau from January until March 2012. The influence of water after January 2012 slowed decomposition to levels indistinguishable across sites and leaves (Figs. 1 and 5). The initially-faster loss of red maple did in fact translate to significantly lower mass by the end of the experiment than white oak, generally in agreement with past studies (Table 4). Thus, the initial stages of breakdown were driven more by the differential presence of water, which set the trajectory for mass loss in both species (Figs. 4 and 5).

Aquatic hyphomycetes, the dominant fungal colonizers of leaves in streams (Baldy and Gessner 1998), have been shown to perform much better in the presence of water (Nikolcheva et al. 2005, Gonçalves et al. 2006), which may explain the pattern of lower fungal biomass on red maple in bank sites and in leaves during the fall in diverted sites. In contrast, the appearance of fungal biomass in both bank and terrestrial sites, and generally lower biomass of bacteria, may

suggest a potentially greater importance of terrestrially-derived fungi (Bärlocher and Kendrick 1974, Das et al. 2008; Fig. 6).

Organismal changes and trophic relations on detritus

Fungi are important initiators of microbial colonization in leaves (Romani et al. 2006a), further demonstrated by the data in this study (Fig. 6). Infiltration of leaves by fungal hyphae allows for the mechanical disturbance of the leaf structure and allows for subsequent colonization by bacteria (Suberkropp and Klug 1980), which together form biofilms on the leaf surface (Romani et al. 2006a). Bacterial biomass on leaves was estimated to be from ~1-5% of overall microbial biomass, similar to levels seen by others (Baldy and Gessner 1997, Hieber and Gessner 2002). Such low levels of bacteria on decomposing leaves has been a common finding (Findlay et al. 2002, Gulis and Suberkropp 2003), mostly due to the areal extent of fungal biomass and high rates of bacterial turnover in the leaves. Typically, these surficial biofilms are thought to be responsible for instigating the next wave of detrital colonization by macroinvertebrates (Cummins et al. 1989).

While the presence of macroinvertebrates on leaf packs was not as clearly related to discharge, their reliance on microbial food sources (Table 3) indicated an indirect role of water. In spite of differences in timing of colonization at different sites, at least some shredders and collector-gatherers were the first FFG to appear (Figs. 7-8). Even the later colonization of bank sites was initiated by shredders and collectors-gatherers. These findings agree well with classic studies of the timing of invertebrate colonization of leaves in headwater streams (Kaushik and Hynes 1971, Cummins et al. 1989), where shredding macroinvertebrates take advantage of the microbial biofilms forming on the detrital matter (Cummins 1974, Bärlocher 1985; Table 3).

The appearance of macroinvertebrate FFG coincided well with microbial biomass on leaves, as mitigated through site-specific flow permanence. Even so, the identity of macroinvertebrates varied only slightly from site to site. As seen in a river in France, the specific composition of an invertebrate assemblage (although not FFG) varied based on the presence of water, with more drought-tolerant organisms appearing in stream beds with reduced surface flow (Datry 2012, Datry et al. 2012). Leaves in intermediate sites were colonized by similar macroinvertebrates as those in stream sites, but terrestrial invertebrates (especially Collembola; Appendix A1) became an important component of the assemblages (Figs. 7-8). Collembolans can be considered analogous to aquatic collector-gatherers as they tend to forage on detrital matter, especially for fungi (Briones et al. 1999). The appearance of collembolans coincided well with increases in relative abundances of fungal biomass on leaf packs in intermediate sites (Fig. 6).

The appearance of *Ephydra* was also a unique finding, as these species are typical of highly arid, saline systems (Herbst 1999) or other stressful environments (Foote 1995). Given this, and the fact that they appeared in diverted reaches, indicated that the assemblage of invertebrates may have been somewhat altered (albeit temporarily) by removing surface flow. Steward et al. (2011) described this as a common phenomenon in dry river systems, where the lack of water may provide a unique habitat for colonization by invertebrates less common to in-stream and riparian zones. These dipterans may be analogous to traditional collector-gatherers and detritivores due to their reliance on organic matter and the microbes that colonize a variety of habitats (Foote 1995).

Leaf chemistry changes

Chemical composition of detritus is a major influence on decomposition rates in both terrestrial and aquatic ecosystems (Webster and Benfield 1986, Hättenschwiler et al. 2005). In a meta-analysis of decomposition and leaf chemistry data, Enriquez et al. (1993) demonstrated that nearly 89% of the variation in plant breakdown rates could be explained by foliar chemistry, including C:N. As red maple have generally been shown to have faster rates of decomposition compared to oak species (Webster et al. 1999), it follows that these leaves should be relatively more labile (i.e. lower C:N, sensu Enriquez et al. 1993). Even so, Nagel et al. (2002) and Kominoski et al. (2007) demonstrated that red maple leaves commonly have higher C:N relative to oak leaves growing in the same area of forest, a pattern also seen in this study (Fig. 9). In spite of these initial differences in leaf C:N, the significant initial breakdown rates (Figs. 3 and 5) followed a more typical pattern of faster mass loss by maple leaves (Webster et al. 1999).

Significant mass loss over the first day of the experiment (Fig. 5), combined with increases in leaf C:N (Fig. 9) suggest the importance of rapid leaching of DOM (Gessner 1991, Yoshimura et al. 2010, Treplin and Zimmer 2012), especially in red maple. After this initial stage of leaching leaf C:N decreased similarly to patterns seen by Cheever et al. (in press), although the magnitude of C:N was different between these two studies. Microbes have been shown to be important immobilizers of nutrients in later stages of decomposition, especially N (Suberkropp 1995, Cheever et al. in press). My data suggest that increases in microbial biomass (Fig. 6) was a driver of the significant spike in white oak C:N in January.

Fungi are clearly the most important component of microbial biomass and reached their peak biomass in November and January in most sites, with significant declines after these times (Fig. 6). It follows then, that some living components of the fungal community were turning over (e.g. Gessner et al. 1993), thus translocating nitrogen to conidial production (Gulis et al. 2006).

Decreases in C:N in both leaf species by the end of the experiment most likely was due to a combination of lower microbial biomass and sloughing of the dead biofilm components (Gulis et al. 2006). Therefore, the relatively greater biomass of microbes (especially fungi) per unit mass of white oak made these losses of N significantly more drastic.

Ecosystem Consequences

Decomposition of organic matter, and especially leaf breakdown, has long been characterized as an important ecosystem-level function in streams (Cummins 1974, Webster and Benfield 1986, Webster et al. 1999). While there was variation in actual rates of breakdown between species and among sites, decomposition remained resilient against diversion and species replacement in this study (e.g. Lake 2003, Dodds et al. 2004). Rates of decomposition were slower in terrestrial and bank sites and earlier in the experiment in diverted sites (Fig. 4). While overall decomposition rates in upstream and diverted sites were not different, the initial differences in water initiated different breakdown trajectories for leaves in these sites (Fig. 5). Only after water returned did breakdown trajectories become similar in stream sites, thus creating similar breakdown rates.

The decomposition of organic matter in the future will be tied to the alterations in the timing and frequency of precipitation suggested by climate change models (IPCC 2007, Bates et al. 2008). While low stream flows will accumulate organic matter and higher ones will remove it (e.g. Lugthart and Wallace 1992, Whiles and Wallace 1995), the ability of streams to decompose organic matter will depend on how often the detritus is submerged. There was obvious functional redundancy in the varied taxa that colonized the leaves (e.g. Rosenfeld 2002, Appendix A1), so shredding and collecting invertebrates will be available to take advantage of detrital resources at the return of flow.

If future precipitation patterns follow predictions, then heavy spates will not allow for enough contact time between water and organic matter for appropriate processing. In the past, consistent patterns of rainfall have regulated the timing of detrital processing across microbial and animal domains, leading to a predictable pattern of decomposition in headwater streams (Petersen et al. 1989). Not only could changes in the frequency and intensity of rain displace decomposition processes, as seen in bank sites, but also increase the buildup of organic matter in the stream channel. Clearly, the accumulation of CPOM in the diverted sites was due to less water and limited decomposition. When the winter storms came, CPOM was washed away to levels below that of control sites (Fig. 2). Consequently, decomposition of this mostly unconditioned detritus may be shifted to far downstream reaches, where this process may be further influenced by anthropogenic and climatic factors (Hagen et al. 2006, Kominoski and Rosemond 2012).

With a potential reduction of in-stream processing in headwaters, distinct impacts on downstream organisms may occur (Vannote et al. 1980). Production and success of stream animals is tied to the availability of processed food sources transported from upstream locations (Wallace et al. 1997, England and Rosemond 2004). Studies of other aquatic ecosystems have clearly demonstrated that alterations to food availability may lead to a mismatch in consumer life history dynamics and their diets (Winder and Schindler 2004, Woodward et al. 2010), affecting success in systems to which these organisms have adapted. The energetic basis of heterotrophic headwater streams may be disrupted with a lack of in-stream processing and translocation of detrital resources, thus altering the stability of the system (Kominoski and Rosemond 2012).

This relationship would not have been apparent in simply examining rates of decomposition from the beginning to the end of the experiment. Instead, these data demonstrate

the importance of examining ecosystem processes and how they vary on both short and long time scales (Jentsch et al. 2007). The timing of water availability will be important in the future not only for stream and groundwater recharge but also in terms of the processing capabilities of streams. When leaf inputs enter a stream in the fall and no water is present to stimulate breakdown processes, then the buildup of organic matter could alter the timing of resources to downstream consumers, decoupling trophic interactions and altering the overall energy basis of headwater ecosystems (e.g. Vannote et al. 1980, Cummins et al. 1989, Woodward et al. 2010).

Conclusions

Clearly, the presence of water played both direct and indirect roles in the processing of leaf organic matter in headwater streams in Coweeta. The simple presence of water set the trajectory of decomposition of detritus by providing a means through which microbial biofilms formed and led to macroinvertebrate colonization. The return of water to reaches where it had been reduced actually slowed decomposition rates due to a flattening of decomposition trajectories. This study demonstrated that future changes to the timing of water availability may alter typical patterns of colonization and decomposition in forested headwater streams through the buildup and translocation of organic matter resources to downstream consumers.

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Table 1. Background abiotic conditions of stream reaches used in this study. Missing data (-) were due to malfunctioning equipment. Day groupings that were significantly different have different letters based on Tukey's post-hoc analysis ($\alpha = 0.05$).

| Date | Reach | Temperature (°C) | | | Specific Conductance ($\mu\text{S cm}^{-1}$) | | | pH | | |
|-----------|----------|-------------------------|------------|--|--|-------------|--|-----------|-----------|--|
| | | Mean (SE) | Range | | Mean (SE) | Range | | Mean (SE) | Range | |
| 8 Oct 11 | Diverted | 12.7 (0.5) ^a | 11.8 -13.3 | | 19.7 (4.1) | 13.2 – 27.3 | | - | - | |
| | Upstream | 12.7 (0.4) | 11.9 -13.2 | | 17.0 (2.1) | 12.8 – 19.3 | | - | - | |
| 22 Oct 11 | Diverted | 10.7 (0.4) ^b | 9.9 – 11.3 | | 20.6 (3.8) | 14.5 – 27.7 | | - | - | |
| | Upstream | 10.5 (0.3) | 10.1 -11.2 | | 17.7 (2.0) | 13.7 – 20.0 | | - | - | |
| 12 Nov 11 | Diverted | 8.7 (0.8) ^c | 7.2 – 9.8 | | 21.4 (2.5) | 16.8 – 25.6 | | 7.2 (0.5) | 6.6 – 8.1 | |
| | Upstream | 8.4 (0.5) | 7.6 – 9.3 | | 19.6 (2.0) | 15.6 – 21.9 | | 7.1 (0.5) | 6.8 – 7.6 | |
| 14 Jan 12 | Divertec | 4.9 (0.2) ^e | 4.4 – 5.1 | | 14.8 (2.5) | 10.0 – 18.3 | | 7.4 (0.2) | 7.1 – 7.7 | |
| | Upstrear | 4.8 (0.2) | 4.5 – 5.1 | | 14.8 (2.5) | 9.9 – 18.3 | | 7.4 (0.1) | 7.2 – 7.6 | |
| 4 Feb 12 | Diverted | 8.2 (0.4) ^c | 7.4 – 8.7 | | 17.0 (2.3) | 12.5 – 20.4 | | 6.9 (0.2) | 6.7 – 7.2 | |
| | Upstream | 8.3 (0.5) | 7.4 – 8.8 | | 16.9 (2.3) | 12.3 – 20.1 | | 7.0 (0.3) | 6.7 – 7.6 | |
| 5 Mar 12 | Diverted | 7.0 (0.4) ^d | 6.6 – 7.2 | | 15.1 (2.6) | 10.3 – 19.0 | | 6.9 (0.1) | 6.7 – 7.1 | |
| | Upstream | 6.9 (0.2) | 6.6 -7.1 | | 15.3 (2.6) | 10.1 – 18.1 | | 7.1 (0.2) | 6.8 – 7.4 | |

Table 2. Dissolved oxygen and nutrient concentrations in stream reaches used in this study. Missing data (-) were due to malfunctioning equipment. All ammonium values were below detection (BD; 5.0 $\mu\text{g L}^{-1}$). Day groupings that were significantly different have different letters based on Tukey's post-hoc analysis ($\alpha = 0.05$).

| Date | Reach | Dissolved Oxygen (mg L^{-1}) | | NO ₃ -N ($\mu\text{g L}^{-1}$) | |
|-----------|----------|--|-------------|--|------------|
| | | Mean (SE) | Range | Mean (SE) | Range |
| 8 Oct 11 | Diverted | 6.7 (0.5) ^a | 5.8 – 7.6 | 27.9 (13.9) | 9.5 – 55.1 |
| | Upstream | 8.5 (0.5) | 7.6 – 9.4 | 10.2 (3.2) | 7.1 – 13.4 |
| 22 Oct 11 | Diverted | 8.0 (0.5) ^a | 6.9 – 8.6 | 6.0 (0) | - |
| | Upstream | 9.5 (0.3) | 9.0 – 10.0 | BD | - |
| 12 Nov 11 | Diverted | 10.9 (0.8) ^b | 9.4 – 12.3 | 15.9 (7.7) | 6.5 – 25.4 |
| | Upstream | 11.9 (0.3) | 11.5 – 12.5 | 20.7 (0) | - |
| 14 Jan 12 | Diverted | 13.6 (0.2) ^c | 13.3 – 14.0 | 14.2 (0) | - |
| | Upstream | 13.8 (0.2) | 13.5 – 14.0 | 6.4 (2.0) | BD – 8.4 |
| 4 Feb 12 | Diverted | 10.6 (0.3) ^b | 10.2 – 11.1 | 11.2 (0) | - |
| | Upstream | 10.8 (0.3) | 10.5 – 11.3 | 8.5 (3.3) | BD – 15.0 |
| 5 Mar 12 | Diverted | 11.2 (0.5) ^b | 10.2 – 11.9 | 8.6 (0.8) | 7.7 – 9.6 |
| | Upstream | 11.2 (0.1) | 11.0 – 11.3 | 7.2 (2.1) | BD – 11.4 |

Table 3. Regression equations for predicting a variety of leaf, macroinvertebrate, and microbial responses in this study.

| Response | Equation | r ² | p-value |
|--|---|----------------|---------|
| Red maple (<i>Acer rubrum</i> L.) | | | |
| % AFDM remaining | -28.07(Q) + 55.83 | 0.32 | 0.009 |
| macroinvertebrate biomass | 0.71(fungal biomass) + 1.06 | 0.49 | 0.0006 |
| microbial biomass | 12.57(Q) + 2.73 | 0.33 | 0.009 |
| bacterial biomass | 0.75(Q) + 0.38 | 0.30 | 0.013 |
| fungal biomass | -3.63(Q) + 2.35 | 0.32 | 0.01 |
| White oak (<i>Quercus alba</i>) | | | |
| % AFDM remaining | -24.53(Q) - 1.03(macroinvertebrate biomass) + 77.24 | 0.75 | 0.0002 |
| macroinvertebrate biomass | 32.98(bacterial biomass) - 5.22 | 0.40 | 0.02 |
| microbial biomass | -3.68(leaf C) + 32.70 | 0.36 | 0.02 |
| bacterial biomass | None | - | - |
| fungal biomass | -3.63(leaf C) + 32.02 | 0.35 | 0.02 |

Table 4. Breakdown rates of leaves (d^{-1}) in a variety of streams in the United States. Numbers without ranges were reported averages from the given source.

| Red Maple | White Oak | Source | Location | Notes |
|---------------|---------------|---------------------------|------------------|---------------------------------------|
| 0.009 | 0.005 | Chaffin et al. 2005 | VA | Reference sites upstream of As inputs |
| 0.006 – 0.009 | 0.003 – 0.004 | Meegan et al. 1996 | WV | In sites with high acid deposition |
| 0.008 – 0.015 | 0.006 – 0.011 | Webster et al. 1999 | Coweeta, NC | |
| 0.004 – 0.015 | - | Entrekin et al. 2008 | MI | |
| 0.005 | - | Gulis and Suberkropp 2003 | Coweeta, NC | Control sites, no nutrient amendment |
| 0.005 – 0.018 | - | Hagen et al. 2006 | Macon County, NC | Across a variety of land use types |
| - | 0.011 | Kominoski et al. 2007 | Coweeta, NC | Single-leaf treatment |
| - | 0.006 | Fritz et al. 2011 | KY | |
| - | 0.003 – 0.026 | Simon and Benfield 2001 | WV | Habitat types including cave streams |
| - | 0.004 – 0.007 | Suberkropp 2001 | Coweeta, NC | |
| 0.002 – 0.008 | 0.002 – 0.013 | This Study | Coweeta, NC | Across a range of inundation |

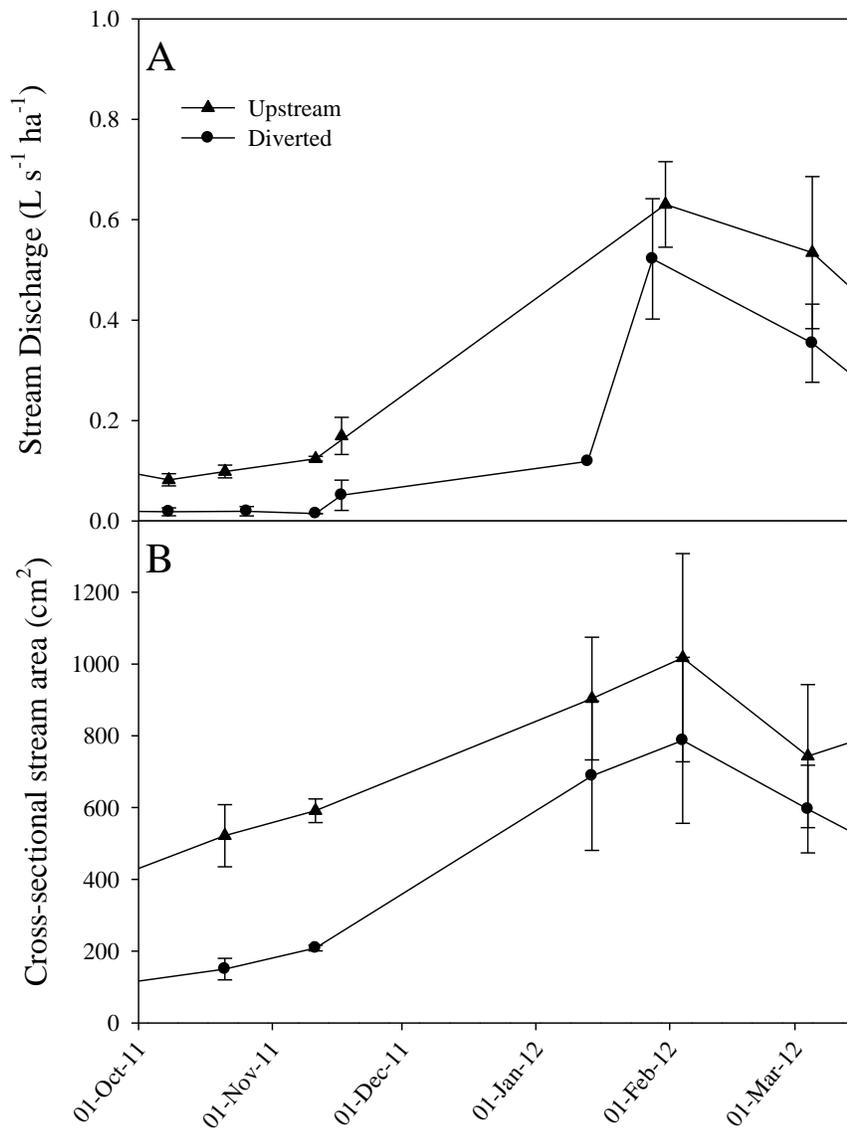


Figure 1. Stream characteristics during this study, including A) discharge and B) wetted cross-sectional area. Bars represent 1 SE of the mean.

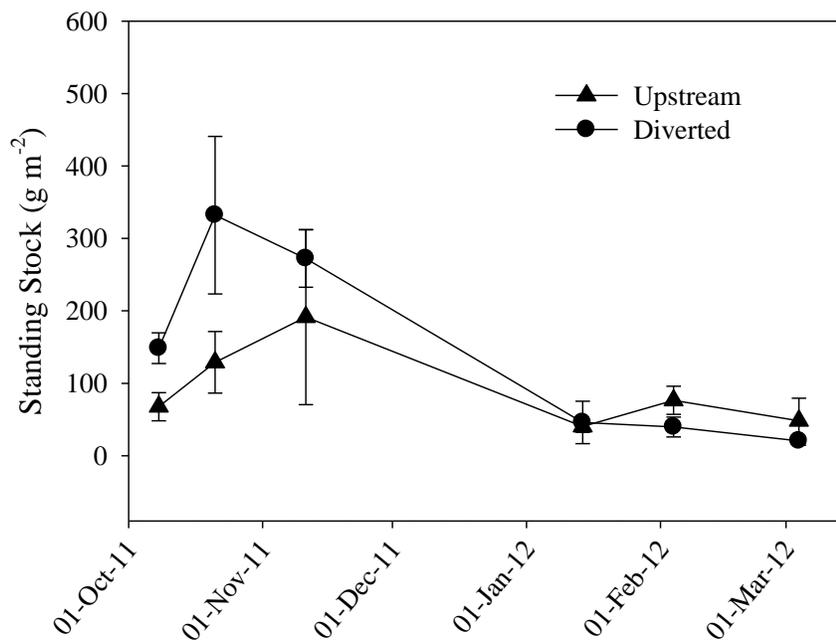


Figure 2. Coarse particulate organic matter (CPOM) standing stocks over the course of the experiment. Error bars represent 1 SE of the mean.

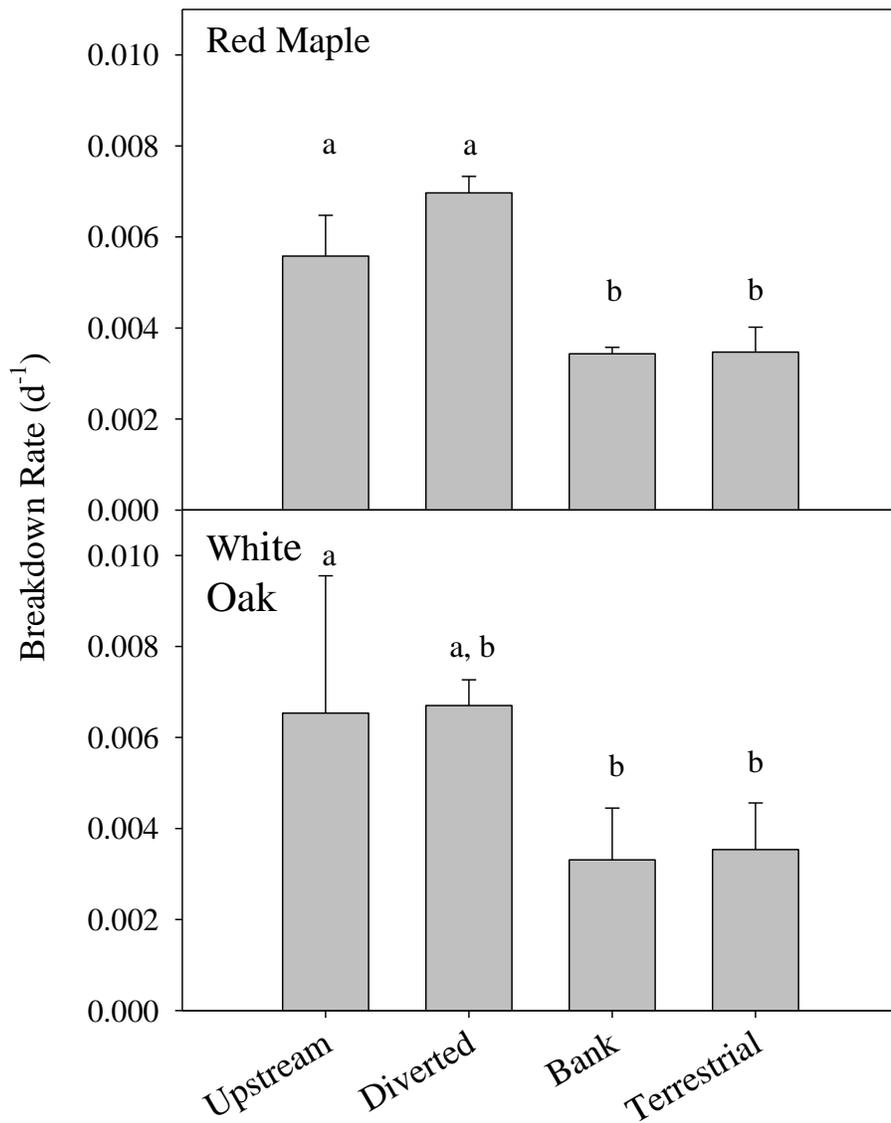


Figure 3. Breakdown rates for leaves along a gradient of inundation at streams in Coweeta Hydrologic Laboratory from October 2011 to March 2012. Error bars represent 1 SE of the mean, different letters represent significant differences among sites.

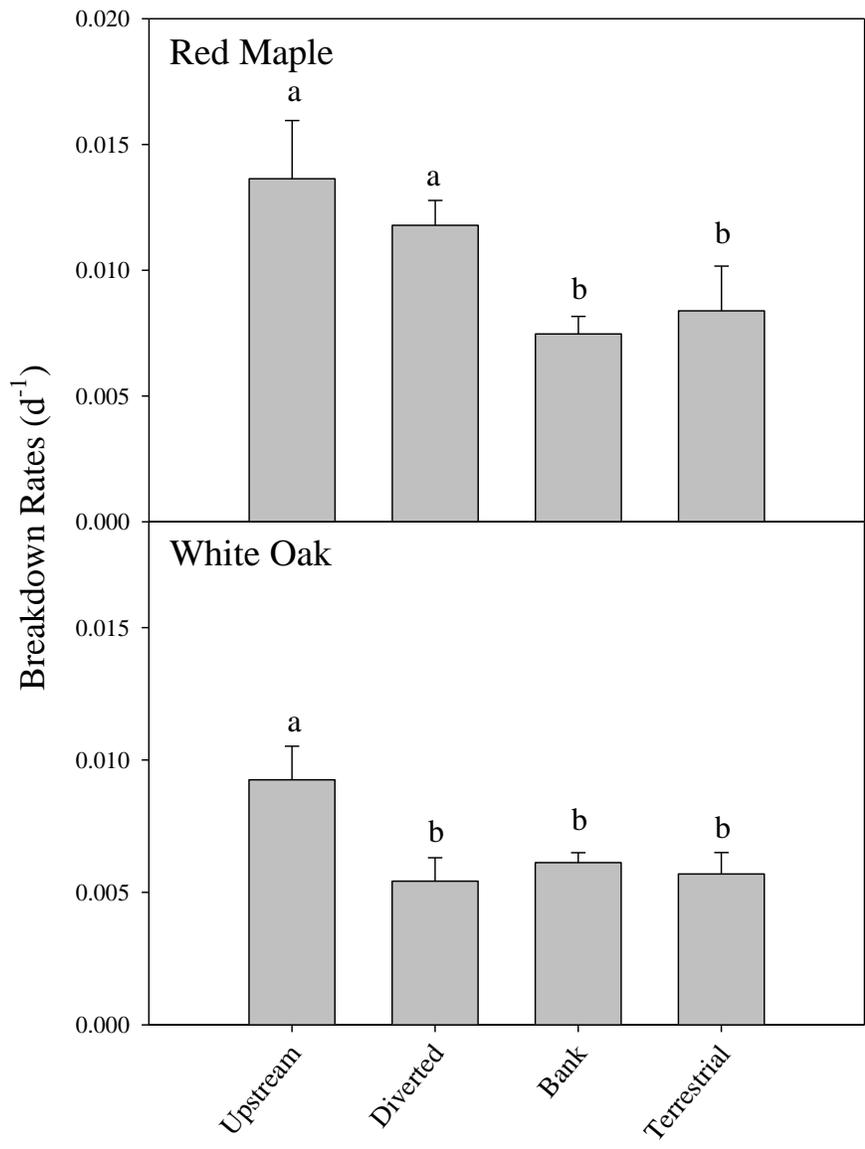


Figure 4. Initial breakdown rates for leaves along a gradient of inundation at streams in Coweeta Hydrologic Laboratory from October to December 2011. Error bars represent 1 SE of the mean, different letters represent significant differences between sites.

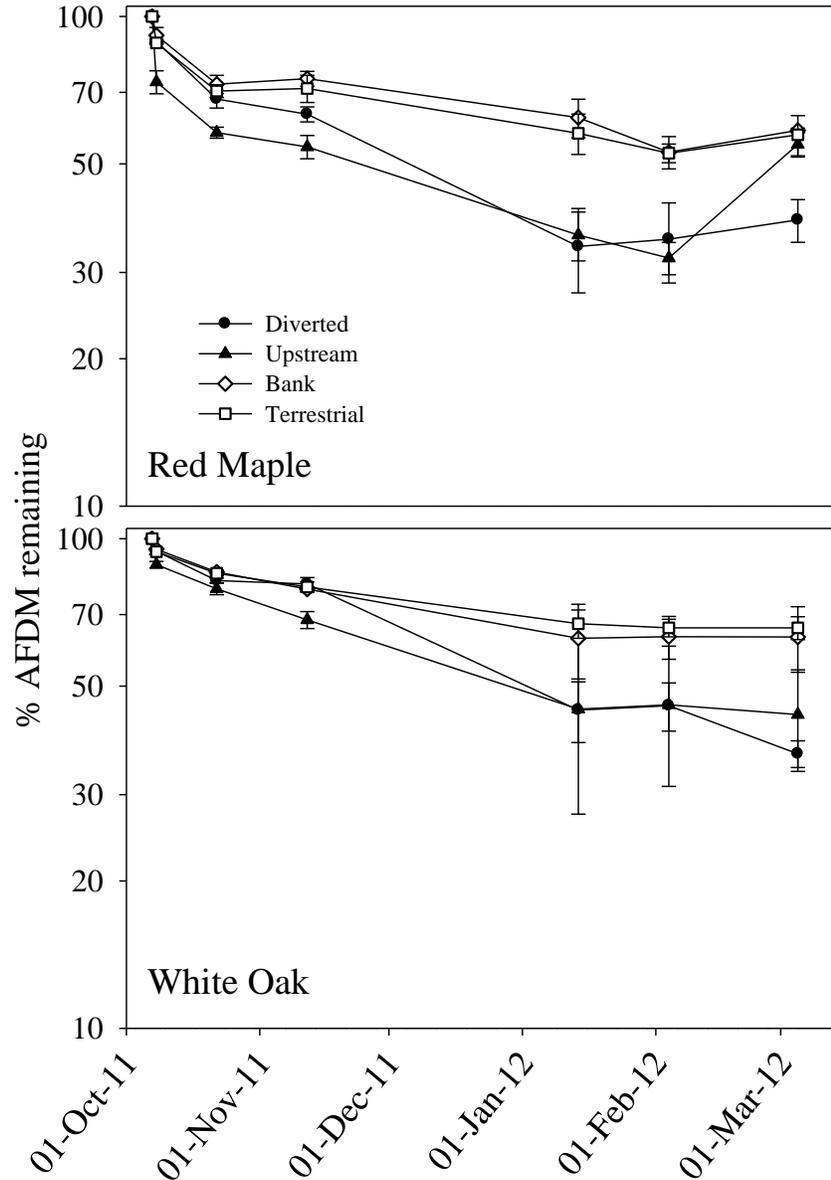


Figure 5. Patterns in breakdown leaves over time along a gradient of inundation at streams in Coweeta Hydrologic Laboratory from October 2011 to March 2012. Data are on a log scale, and error bars represent 1 SE of the mean.

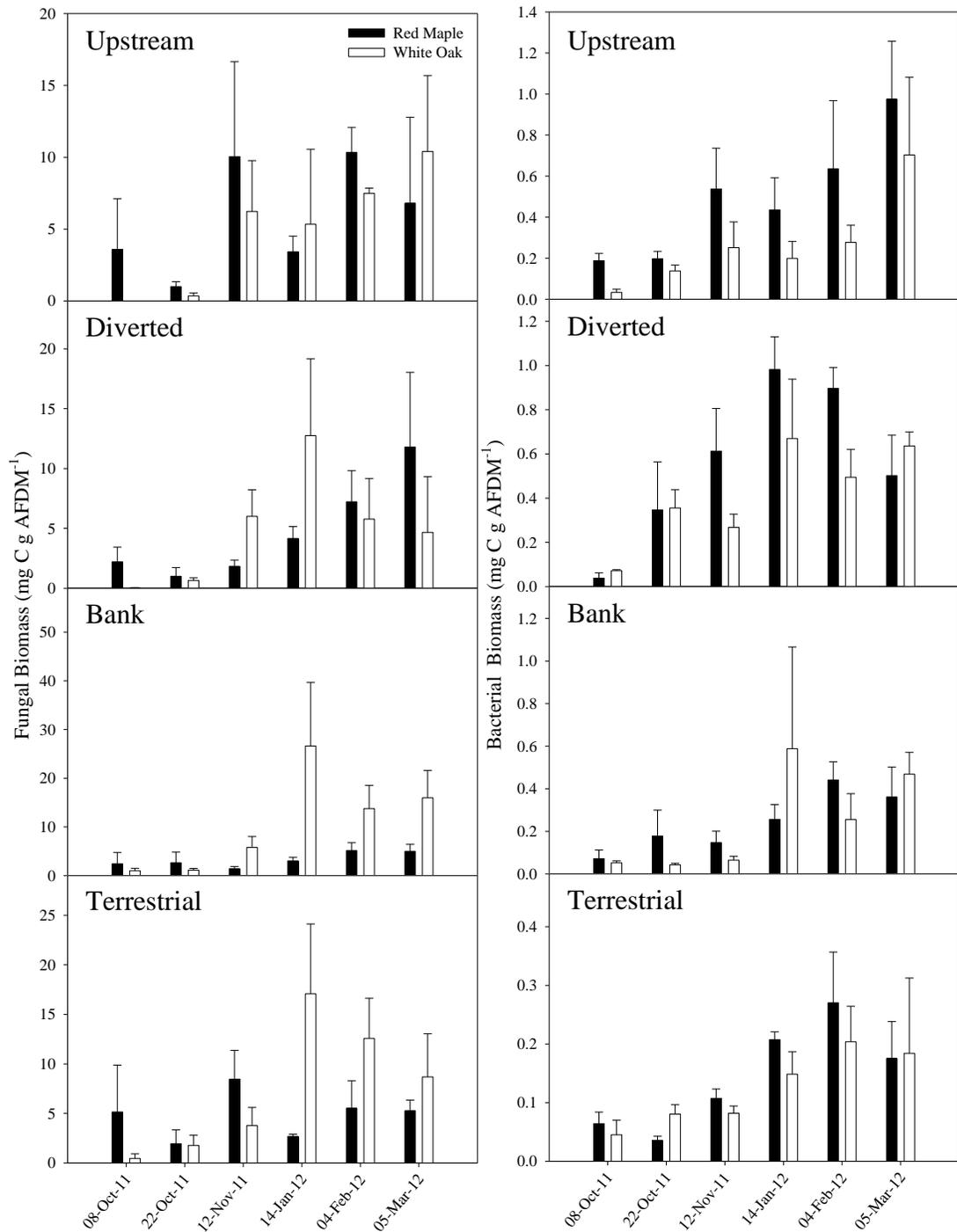


Figure 6. Patterns in fungal (left panel) and bacterial (right panel) biomass accumulation on leaves in the four sites over time at watersheds in Coweeta from October 2011 to March 2012. Error bars represent 1 SE of the mean. Note the differences in scale for each type of biomass.

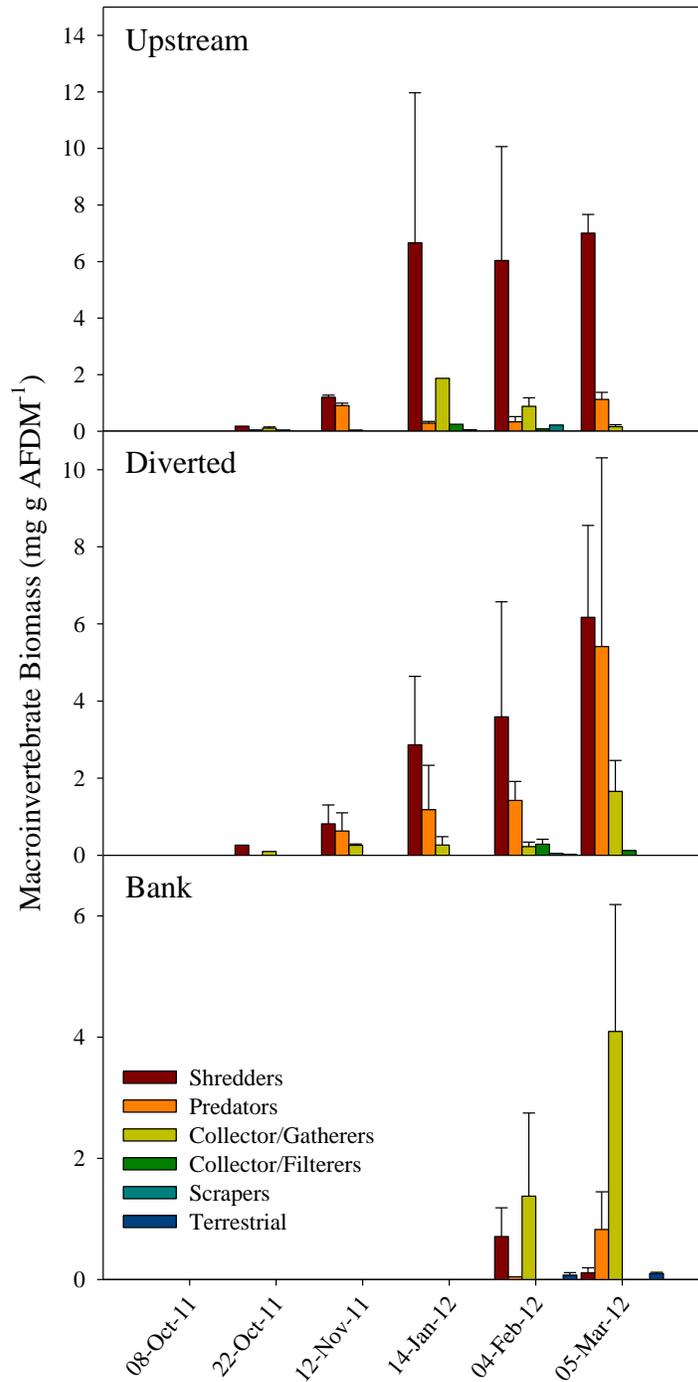


Figure 7. Changes to the biomass of macroinvertebrate functional feeding group (FFG) taxa colonizing red maple leaves over the course of the experiment across sites in stream reaches in Coweeta. Error bars represent 1 SE of the mean.

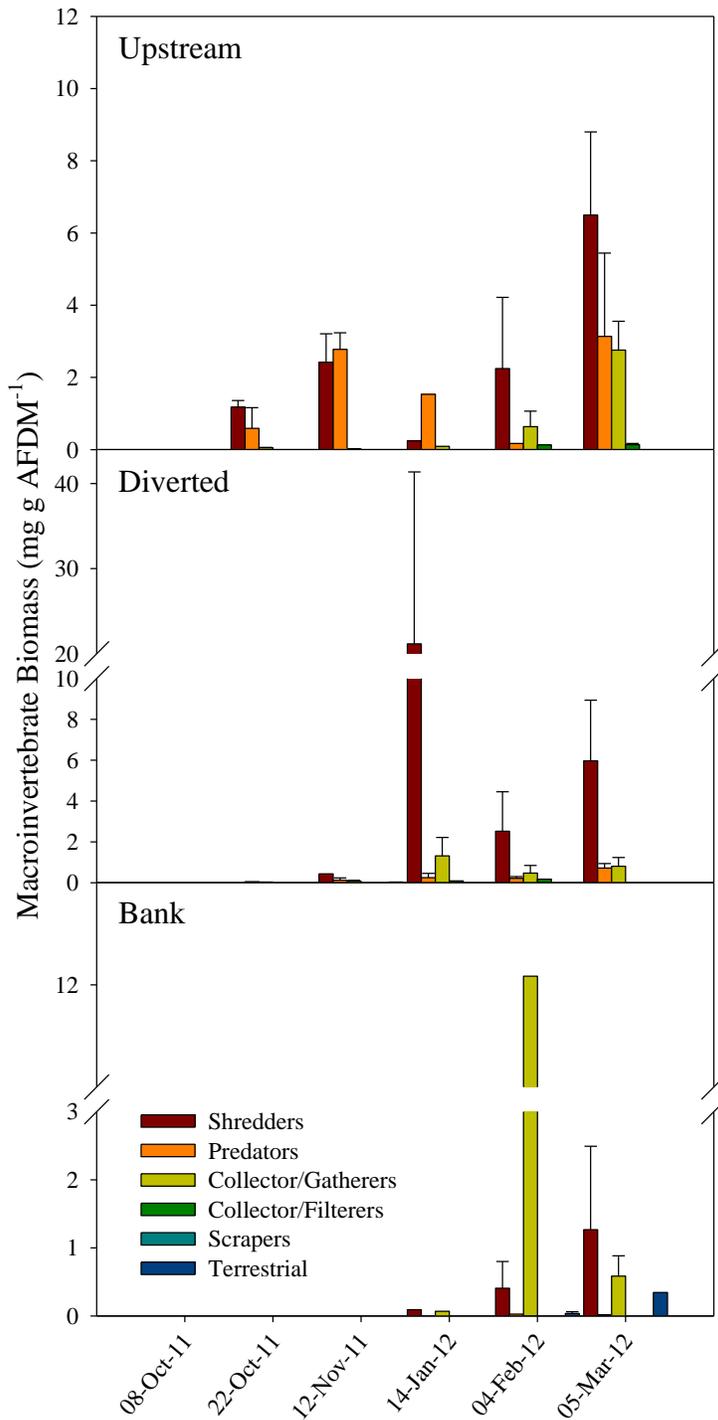


Figure 8. Changes to the biomass of macroinvertebrate functional feeding group (FFG) taxa colonizing white oak leaves over the course of the experiment across sites in stream reaches in Coweeta. Error bars represent 1 SE of the mean.

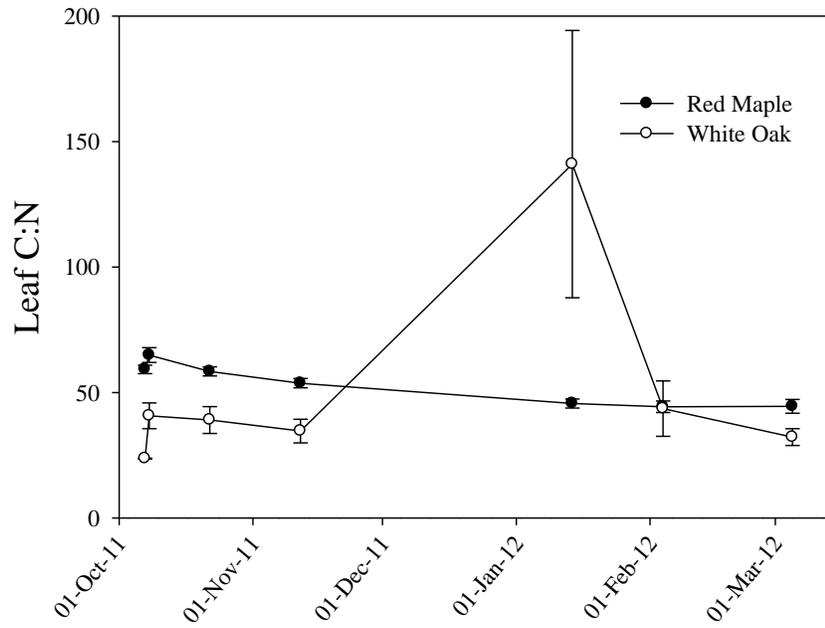


Figure 9. Changes in C:N of leaves over time at streams in Coweeta from October 2011 to March 2012. Error bars represent 1 SE of the mean.

Chapter 4: Metabolism and Ammonium Uptake in Perennial Streams under Altered Hydrology

Introduction

Interactions of biotic, hydrologic, and climatic factors can lead to changes in ecosystem function. Streams may respond to periods of drought by contracting into spatially segregated reaches or isolated pools (Stanley et al. 1997), which may become local patches of productivity (Lake 2003). The availability of nutrients can thus regulate the bioenergetics of stream ecosystems, indicating a tight relationship between uptake and metabolism (Fellows et al. 2006, Roberts and Mulholland 2007). While ammonium and nitrate are important predictors of both gross primary production and ecosystem respiration (Bernot et al. 2010), hydrology has been shown to be a more important contributor to metabolism in many stream ecosystems (Mulholland et al. 2001).

Nutrient accumulation during times of low discharge (e.g. Caruso 2002, Robson et al. 2008) may create a more heterotrophic system (Young and Huryn 1996) due to greater contact between the stream sediments and nutrient rich water (Findlay 1995). In fact, Harms et al. (2009) concluded that hydrologic characteristics of the stream landscape ultimately influence the ability of streams and riparian areas to process nutrients. Even with drought directly affecting stream flow, it is clear that functions within a stream are not independent of one another but are truly interactive; a change in one functional component (e.g. organic matter processing) can indirectly impact other processes (i.e. nutrient cycling and primary production).

Traditional models of nutrient uptake demonstrate the importance of both biota and hydrology to biogeochemical cycling in ecosystems (Wollheim et al. 2001, Doyle 2005, Poole et al. 2008). In streams, discharge has been shown to be a major factor driving uptake of nitrogen and phosphorous. Specifically, aerial uptake (U) was lower, while uptake length (S_w) was longer

in intermittent vs. perennial Mediterranean streams, indicating a less efficient system in terms of biogeochemical processing (von Schiller et al. 2008). In arid systems, the frequency and duration of floodplain inundation regulates the importance of nitrification and denitrification and thus nutrient export (Harms et al. 2009). Additionally, Romani et al. (2006) concluded that any buildup of nutrients during dry times would then be translated into a pulse of in-stream nitrate levels with the return of precipitation to the floodplain in Mediterranean streams.

Extreme variation in precipitation due to climate change may be more important than changes to mean conditions. The net effect of climate change on annual precipitation would be no change to mean rainfall, only variations in the frequency and duration. As a result, there will be potentially greater occurrences of drought-like conditions in systems unaccustomed to significant decreases in water availability (Marshall et al. 2008, Wu et al. 2012a,b). Climatic variations have the potential to alter ecosystem processes and greatly affect the resilience of those ecosystems (Scheffer et al. 2001). A greater mechanistic understanding of how ecosystems may attain multiple stable states or resilience thresholds as a result of disturbance is needed to understand how ecosystem functions may be altered in light of predicted changes to climate (Folke et al. 2004, Dodds et al. 2010).

Empirical studies of low flows in stream ecosystems do exist, but most have been opportunistic and failed to account for pre-drought conditions (Lake 2003). Much of the current knowledge on the effects of drought in streams focuses on stream structural measures, such as macroinvertebrate assemblage characteristics (i.e. Lugthart and Wallace 1992, Whiles and Wallace 1995), though a few studies have addressed functional ecosystem components (Humphries and Baldwin 2003, Dewson et al. 2007). Additionally, most studies have been done in arid (e.g. Dahm et al. 2003) or Mediterranean regions more prone to drought conditions (e.g.

Acuña et al. 2005). Future ecological studies must address both climate change and examinations of extreme events (Jentsch et al. 2007). If there is any certainty to climate predictions, it is that extreme events (e.g. droughts, floods) will predominate in the future (Marshall et al. 2008). As such, the ability of ecosystems to respond to and recover from disturbances may be affected (e.g. Uehlinger 2000).

Low-order streams are important integrators of biotic, climatic, and landscape factors, but as such, are functionally influenced by both fine and broad-scale environmental conditions (Meyer and Wallace 2001, Peterson et al. 2001). Alterations in precipitation regime or land cover may alter the hydrologic pathways important for the maintenance of stream flow (Naiman and Turner 2000, Barnett et al. 2008). Hydrologic models suggest alterations in the timing and type of precipitation, less infiltration and recharge of subsurface aquifers, and reduced summertime flows (Wu et al. 2012a,b). Stream structural aspects, such as longitudinal linkage, wetted width, and stream-hyporheic connectivity may also become altered in response to changes in precipitation (Stanley et al. 1997, Pringle 2001, Dahm et al. 2003).

The major objective of this study was to assess how changes in stream function, specifically nutrient uptake and metabolism, would be affected by altered stream flow in perennial, headwater ecosystems. My prediction was that any changes to stream flow would alter the relationship between nutrients and metabolism typically present in detrital-based ecosystems. Further, drier streams may become localized areas of biogeochemical reactions due to decreases in wetted areas, and metabolism may become more heterotrophic at these sites due to the accrual of organic matter during low flows. As such, hydrological variation between sites would greatly control biogeochemical processes and metabolism.

Methods

Site description

This study took place in three watersheds (WS 22, 40, 41) located at the Coweeta Hydrologic Laboratory in Otto, NC. All were located at similar elevations and were similar in watershed area and slope (Chapter 2). All streams were low order and heavily forested. At the current time, streams in Coweeta are considered perennial and rarely go dry (e.g. Swank and Waide 1988).

Surface flow alterations

Surface flow from three reaches downstream of established, but unmonitored, weirs was reduced using diversions beginning in September 2010 (WS 40) and summer 2011 (WS 22, 41). Boards were placed behind the weir blades to restrict water flow, with the diverted water being piped back into the stream below the experimental reaches (Fig. 1A). Reference study reaches were also established upstream of the weir diversions in each of the three watersheds. For the year of the study (September 2011 to July 2012), changes in nutrient cycling and metabolic parameters were assessed between upstream and diverted sites ($n = 3$ for both site types).

All three weir diversions were removed on 18 November 2012, allowing all water retained in the weir ponds to flow freely into the downstream, formerly-diverted sites (Fig. 1B). The removal of diversions thus allowed for the simulation of a small, but intense flood. Stable surface flow was allowed to return to all three formerly-diverted sites for two days before post-flood measures were taken.

Background stream measures

Prior to beginning the experiments, I established 50-60 m stream reaches in the upstream control sites and 25-30 m reaches in the diverted sites. On each day of nutrient uptake and

metabolism measurement, 60-mL samples of stream water were filtered through 0.7 μ m GF/F syringe-tip filters stream-side for background nutrient concentrations. Wetted cross-sectional areas (cm²) were taken along the transects at each site, in addition to measures of temperature (°C) and specific conductance (μ S cm⁻¹) using YSI handheld meters (YSI 30, Yellow Springs, OH). Discharge was measured using the slug-addition technique (Gordon et al. 2004) and normalized to watershed area in each stream (L s⁻¹ ha⁻¹). Coarse benthic organic matter (BOM) was sampled over the course of the study using a 0.25-m² benthic sampler (g m⁻²; Chapter 3).

Nutrient uptake

A co-injection of ammonium (as NH₄Cl) and NaCl was used to measure uptake in all stream reaches. In order to not over-saturate the streams (i.e. Mulholland et al. 2002), the injection solution was made to raise the background levels of ammonium as little as possible, ~ 50 μ g L⁻¹. Injections lasted for several hours, until background levels of specific conductance had increased and reached similar levels throughout the reach (Webster and Valett 2006). Triplicate samples of water were taken at seven sites along the reach in each of the six reaches, and filtered stream-side similarly to background water collections. Samples were frozen and taken back to the laboratory for further analyses.

Background and plateau ammonium concentrations were determined using the phenate method (APHA et al. 2005) with a flow-injection analyzer (Lachat Quickchem 8500, Lachat Corporation, Loveland, CO). Nitrate and chloride in all water samples were estimated using ion chromatography (Dionex DX500 ion chromatograph, Thermo Fisher Scientific, Inc., Waltham, MA, USA). The natural log of the chloride-corrected loss of ammonium over distance was used to calculate its uptake length (m , S_w ; Stream Solute Workshop 1990) in all stream reaches. Areal uptake rate (U , μ g NH₄⁺ m⁻² min⁻¹) was calculated using the equations of Webster and Valett

(2006). The proportion of ammonium that was nitrified ($k_{\text{NIT}}/k_{\text{A}}$) was calculated by dividing the absolute values of rates of nitrate gain (k_{NIT}) by rates of ammonium loss (k_{A}) throughout a study reach on each date (Bernhardt et al. 2002). Nitrate gain (k_{NIT}) was determined from the slope of the natural log of chloride-corrected nitrate concentration along the reach. Uptake measures were normalized to standing crop of BOM (U:SC) in order to determine the turnover rate of ammonium per unit leaf mass.

Ecosystem metabolism

Hydrolab minisondes (Hach Environmental, Loveland, CO) were placed at the bottom of all stream reaches during each sampling period. Dissolved oxygen (DO; mg L^{-1}) was measured during 2-minute intervals over a 36-hour period. Metabolism measures were taken simultaneously with measures of ammonium uptake, as described above. Saturation levels of DO were then corrected to atmospheric pressure for measures of both gross-primary production (GPP) and ecosystem respiration (ER; Bott 2006, Grace and Imberger 2006).

Sulfur hexafluoride (SF_6) was bubbled into the stream at the nutrient injection sites until plateau levels of specific conductance had been reached (Bott 2006, Webster and Valett 2006). Water samples were collected with air tight syringes and injected to 50% of the volume of sealed, airtight glass vials in order to later assess headspace concentrations of SF_6 at all sites. In the laboratory, headspace air was analyzed on a gas chromatograph (SRI 8610/9300 equipped with an ECD detector, SRI Instruments, Torrance, CA 90503) for relative abundance of SF_6 , and reaeration was estimated using the slope of the log-corrected loss of gas with distance downstream. Net ecosystem production (NEP) was assessed in each stream over time as the difference between GPP and ER. Respiration per unit organic matter was also determined with the ratio of ER:BOM standing stocks.

Statistical Analyses

Two-way ANOVAs, comparing stream site, date, and their interaction, were run for background measures (temperature, specific conductance, dissolved oxygen, nitrate, ammonium, percent of ammonium nitrified, and BOM). A mixed model ANOVA, blocking for sites nested within watersheds, was used to assess differences in discharge, wetted cross-sectional area, uptake parameters (U , S_w), and metabolic factors (GPP, ER, NEP). For all analyses, post-hoc multiple comparisons tests were run to determine site, date, and interactive differences (Zar 1999).

Pearson correlations (ρ) were run between all background and functional variables measured annually and for each season. Those found to have significant associations ($p < 0.05$) were included in stepwise regressions to determine predictive relationships for nutrient uptake and metabolic variables. All analyses were run on SAS v.9.3 (SAS Institute, Cary, NC).

Results

Background Measurements

Temperature varied significantly over time and between reaches coinciding with seasonal changes (interaction $p = 0.006$; Table 1). Oxygen remained fairly high over the course of the experiment, with significant increases in the winter associated with decreases in temperature (Table 1). Nitrate was undetectable in the fall and winter of both 2011 and 2012. In the months where nitrate was detectable in these streams, concentrations were fairly low, except for a significant increase during July 2012 (Table 2). Both temperature and ammonium demonstrated significant increases in diverted sites from the initial measures on 18 Nov 12 until after the diversion removals on 20 Nov 12, while no changes in any other measure existed (Tables 1 and 2).

Benthic organic matter standing stocks from October 2011 to March 2012 were found to be significantly different over time in a previous study (Chapter 3). Additional standing stocks taken for this study were not different in diverted and upstream sites prior to the diversion removal in November 2012 (mean \pm SE: 221.1 ± 59.8 and 101.4 ± 50.7 , respectively), although there was a trend for more BOM in diverted reaches. After the diversions were removed, BOM in formerly-diverted sites significantly declined (32.6 ± 4.5 , $p = 0.01$) as a result of the release of water from the weirs (Figs. 1 and 2A, Table 3).

Stream discharge and wetted cross-sectional area

Overall, there was greater discharge at upstream compared to downstream sites ($F_{17,48} = 14.65$, $p < 0.0001$), although during January there were no differences due to large storms during that time. Seasonally, discharge was significantly lower in the summer and fall months of both 2011 and 2012 compared to those measured in winter and early spring ($F_{1,48} = 25.10$, $p < 0.0001$; Fig. 2A).

Stream wetted cross-sectional area was not different during the summer and fall of 2011 but significantly increased into January 2012 ($F_{9,32} = 10.43$, $p < 0.0001$). Wetted cross-sectional area again decreased significantly from January into late summer 2012 before rebounding in November 2012 (Fig. 2B). There were no significant differences in upstream and downstream wetted cross-sectional area throughout the study. After the diversions were removed on 18 November 2012, both discharge and wetted cross-sectional area rebounded to levels measured in upstream sites (Fig. 2).

Ammonium uptake

Ammonium uptake did not differ over time, although significant patterns did exist between upstream and diverted reaches ($F_{1,32} = 6.27$, $p = 0.02$). Stream sites were not different in

the fall of each year, although diverted sites in September 2011 and November 2012 had, on average, greater uptake (Fig. 3A). Upstream sites appeared to follow seasonal changes to discharge and wetted cross-sectional area (Fig. 2), as uptake significantly increased over diverted ones in March and May 2012 ($p < 0.04$). Diverted sites remained at a fairly consistent level of uptake from September 2011 to July 2012, not following the pattern seen in upstream sites (Fig. 3A). Although average uptake in diverted sites appeared to decrease after the diversions were removed, this change was not significant.

Uptake length of ammonium changed significantly over time ($F_{9,32} = 8.91$, $p < 0.0001$), with longer S_w seen in times of greatest discharge (Fig. 2A, 3B). During fall 2011, all S_w were relatively low and similar across sites, although a pattern for longer S_w was seen in upstream reaches (Fig. 3B). Stream sites in winter and spring 2012 had significantly longer S_w than at other times of the experiment, with January S_w (58 – 185m) representing the peak of the differences ($p < 0.05$). Uptake lengths decreased in July, with a non-significant pattern of longer S_w in upstream sites. On 18 November, S_w in diverted sites was essentially the same as those seen in July, but significantly increased 4x (mean difference: 44m, $p = 0.01$) after the diversions were removed (Fig. 3B). This increase in diverted reach S_w was also 2x those in upstream sites around the same time (mean difference: 24m, $p = 0.02$), although discharge at the reaches had returned to equivalent levels after the diversions were removed (Fig. 2A).

Ammonium per unit benthic organic matter increased over time ($p = 0.05$). A much smaller turnover was seen in the fall when BOM was greatest (Fig. 4) compared to significantly larger turnover during the winter ($p < 0.05$) when discharge was higher (Fig. 2A) and BOM had been washed away (Chapter 3). Turnover again was smaller in the fall of 2012 in both site types, with the loss of BOM due to diversion removal driving the greater turnover seen in those sites on

20 November 2012 (Fig. 4A). During October, the uptake per unit fungal biomass was the same in both diverted and upstream sites (Fig. 4B) with diverted sites demonstrating a consistent declining trend ($p = 0.2$) through March. After an initial decline in November, the apparent uptake per unit fungal biomass increased again in January and March in the upstream sites (Fig. 4B).

Nitrification

Nitrification was clearly occurring in stream reaches in September 2011 (Table 2). While the proportion nitrified was not different between upstream and downstream reaches, upper WS22 had a rather large amount of ammonium (92%) nitrified compared to the other two upstream sites (11-30%). Diverted reaches on this same date were consistently nitrifying ammonium at a moderately high rate (66 -74 %).

No nitrification was seen from fall 2011 to spring 2012, indicated by the lack of any detectable nitrate in the streams over that time (Table 1). In March, nitrate was measured in the streams but was not different from background during the injection, indicating no transformation of added ammonium into nitrate. Only the upstream sites had in-stream nitrification (83% of the added ammonium) in May 2012, but July 2012 sampling indicated that the process had returned to both upstream and diverted sites (Table 2). Neither nitrification nor detectible concentrations of in-stream nitrogen could be seen during November 2012.

Ecosystem metabolism

Gross primary production declined from September 2011 throughout the winter of 2011, until increasing significantly in January and March 2012 ($F_{5,18} = 3.86$, $p = 0.01$; Fig. 5A). July 2012 GPP was equivalent to that for the previous summer. No site differences in GPP appeared over time, although there was a slight non-significant pattern of greater GPP in upstream sites.

Ecosystem respiration did not change significantly throughout the course of the experiment or between sites (Fig. 5B). In upstream sites, ER appeared to show a pattern of decrease from September 2011 to January 2012 before rebounding in March. Diverted site ER appeared to stay constant initially before increasing in January and March, a pattern opposite of that in upstream sites (Fig. 5B). Both sites showed lower ER in May compared to other times, although this difference was not significant. Consistently negative values of NEP at all sites over time indicated that these sites were heterotrophic (Fig. 5C). Patterns in NEP strongly mirrored those of ER ($\rho = -0.99$), with GPP only accounting for an average of 13% of stream metabolism. Respiration per unit benthic organic matter in diverted sites was extremely low during fall 2011 before increasing greatly in January (Fig. 6). In upstream reaches, ER:SC remained low until March 2012 (Fig. 6).

Annual relationships between variables

Background characteristics of the streams drove many significant relationships in functional variables over the course of the study. In-stream NH_4^+ concentrations increased with stream size and decreased with standing stocks of BOM (Table 3). Ammonium was also positively related to U, S_w , and GPP. Discharge was the most strongly related to wetted cross-sectional stream area, while both negatively influenced BOM standing stocks (Table 3). Both Q and wetted cross-sectional area were also positively related to U, S_w , and GPP. Benthic organic matter negatively influenced both S_w and GPP. Both S_w and U positively influenced GPP annually. The proportion of ammonium nitrified was not strongly related to any other variables measures (Table 3). When uptake was normalized to BOM, it demonstrated many significant relationships with other measured variables, especially for hydrology (discharge and wetted cross-sectional stream area) and all measures of metabolism (Table 3).

Seasonal relationships between variables

In the fall, background nutrient levels and hydrology drove many of the significant relationships seen during that season. Ammonium levels were positively related to both discharge and wetted cross-sectional stream area, while more strongly related to U and S_w (Table 4). Benthic organic matter standing stocks were negatively related to NH_4^+ , Q, and S_w , while there was a positive relationship between BOM and stream cross-sectional area (Table 4). Hydrologic variables (discharge and wetted cross-sectional area) showed positive associations with nearly all functional components, except ER, which were negatively related to hydrology (Table 4). Annual patterns in BOM-normalized uptake were driven mostly by the patterns seen during the fall, as there were strong, significant relationships with all measured variables except GPP (Table 4).

Winter measures did not demonstrate any significant relationships with one another, but this was most likely due to the single sampling event at all six reaches versus several across other seasons. In the spring, both NH_4^+ and NO_3^- were related to one another, but only NH_4^+ was related to uptake (Table 5). Discharge was again strongly related to wetted cross-sectional stream area, and positively related to both U and NEP. Ecosystem respiration and discharge had a negative relationship (Table 5). Standing stocks of BOM showed no significant relationship with any other variables in the spring (Table 5).

In the summer, fewer significant relationships existed among variables. Ammonium levels again were positively associated with U and GPP, while Q was only associated with wetted cross-sectional area and S_w (Table 6). For the first time during the study, uptake was positively associated with GPP (Table 6).

Predicting ecosystem function

Although many associations existed between measured variables in this study both annually and within seasons (Tables 3-6), only NH_4^+ concentrations and Q consistently predicted ecosystem function in this study. Discharge appeared to be the controlling factor in ecosystem function when the greatest differences between upstream and diverted sites existed (fall), with NH_4^+ concentrations becoming important during times of generally higher flow and less difference between site types (Fig. 2A, Table 7). These seasonal relationships translated into a dual importance for these factors in predicting ecosystem function annually (Table 7). Benthic organic matter was a secondary predictor of S_w annually (Table 7), but even this was regulated by discharge (Table 3).

In terms of function, ammonium uptake appeared to be the most consistently predictable function. Uptake and S_w were predicted by some combination of factors both annually and seasonally (Table 7). Gross primary production was the only component of metabolism that could be predicted annually or in the summer, with all three components (GPP, NEP, ER) having relationships driven by Q in the fall (Table 7).

Discussion

Hydrological influences on nitrogen uptake

Surface flow in streams is a significant regulator of ecosystem function, a pattern which was further demonstrated in this study. Hydrology (as discharge and wetted cross-sectional area) has been consistently shown to be an important regulator of ammonium uptake in streams (Webster et al. 2003). In a comparison of Mediterranean streams, von Schiller et al. (2008) found a 2x-shorter $S_w\text{-NH}_4^+$ in perennial streams compared to intermittent ones, a pattern opposite to that seen here. Retention of NH_4^+ was also stronger in the perennial streams, due to greater background levels of DIN in the intermittent streams (von Schiller et al. 2008). These Coweeta

streams had consistently low levels of DIN, demonstrating clear seasonal patterns consistent with other streams in this region (Mulholland and Hill 1997). Patterns of shorter $S_w\text{-NH}_4^+$ seen here are more consistent with changes to discharge (Webster et al. 2003).

In these streams, S_w consistently responded to changes in hydrology seasonally and annually, only responding to BOM when it was abundant in the fall. Butturini and Sabater (1998) propose a biological driver for S_w in Mediterranean streams, although the patterns seen here are more consistent with a hydrological basis for S_w (Webster et al. 2001, Webster et al. 2003). While significant increases in S_w have responded to landscape perturbations (Bernot et al. 2006, Northington et al. 2011) or heavy nutrient inputs (Martí et al. 2002), this does not apply here since the watersheds used here are generally protected from disturbance, thus clearly indicating a hydrological basis for S_w .

While S_w followed similar patterns between upstream and downstream sites over the course of the experiment, patterns of uptake may indicate a temporary shift of the diverted sites into a new steady state (e.g. Heffernan 2008). Upstream sites clearly showed a pattern of low uptake in the fall, followed by increases in the late winter and spring 2012, obviously driven by seasonal changes in stream discharge. After an initial spike in uptake after the flow removal, diverted sites remained in a pattern of consistent uptake throughout the duration of the experiment into July 2012, unaffected by seasonal patterns in the same way as upstream reaches were. In spite of these difference, the removal of the dams in November 2012 shifted uptake in diverted sites to levels similar to upstream reaches. Although intermittent and drying streams have been considered unstable in N-processing due to inconsistent wetting of benthic sediments (Baldwin et al. 2005, Gómez et al. 2009), uptake in these streams may actually be resilient to

changes in discharge (e.g. Valett et al. 1994) due to historically consistent flow patterns in Coweeta.

Hydrologic influences on ecosystem metabolism

Although metabolism was not responsive to changes in hydrology nor related to many other measured variables in this study, when uptake was normalized to BOM standing stocks, a significant relationship appeared (Table 3). The greatest impacts on stream metabolism appeared during the fall, most likely related to heavy inputs of allochthonous organic matter (Chapter 3). Microbial colonization of leaves increased during this time, especially for fungi (Chapter 3). Benthic organic matter was significantly higher in fall, with diverted sites having greater standing stocks than upstream sites. Patterns in ecosystem respiration (Fig. 5B) coincided with high initial rates of decomposition in upstream sites and the accumulation of microbial biomass on leaves (Chapter 3). Although breakdown rate trajectories reported in Chapter 3 flattened after the increases in discharge in January, there was a spike in microbial biomass on the leaves in diverted sites, a pattern consistent with increases in ER (Figs. 5B and 6). Frossard et al. (2012) demonstrated a similar pattern, whereby abundant fungal colonization of organic matter significantly increased in-stream respiration on benthic organic matter.

Although significant metabolic differences were not found in fall, the distinct pattern of lower flows influenced the relationships of discharge to NEP, GPP, and ER during that time. On an annual basis, the relationship between hydrology and metabolism was more clearly seen when BOM was taken into account (Table 3). Patterns of greater metabolism during low flows were consistent with studies from both regulated systems (Uehlinger et al. 2003, Marcarelli et al. 2010) and intermittent Mediterranean streams (Acuña et al. 2004).

Primary production, typically a minor component of metabolism in shaded headwater streams, appeared to be important during some times of year. The significant increase in primary production in winter (Fig. 4A) was a unique finding in Coweeta, especially since prior work has indicated a greater light penetration into the streams during April (Webster et al. 2012). On an annual basis, GPP demonstrated a significant response to endogenous stream factors (Table 3). In drier systems, GPP has been shown to be regulated by discharge (Fisher et al. 1982, Dodds et al. 1996, Stanley et al. 2004). Primary production increased mostly due to scouring of the streambed with floods or the successional changes that occurred post-flood in these streams.

In the current study, the effects of discharge to GPP appeared to be more linked to the delivery of limiting nutrients to enhance growth. In-stream concentrations of nutrients were generally low throughout the year, but the absence of in-stream leaves in the summer reduced the demand for DIN (Cheever et al. 2012), making it available for autotrophic use (Dodds 2006). Additionally, increases in stream temperature and discharge have together been shown to significantly regulate rates of GPP (Marcarelli et al. 2010). These patterns were indicated by the positive relationship between GPP and uptake flux per organic matter annually (Table 3).

Patterns in metabolism and uptake

Although there was a clear pattern in higher uptake in upstream sites in the winter and spring (Fig. 5), the turnover of ammonium occurred in the diverted sites in the winter coinciding with a spike in ER:SC (Fig. 6). Uptake has been shown to be greater in systems with continuous inputs of organic matter, where inorganic nutrients from the water column fuel the metabolism of heterotrophs colonizing debris (Valett et al. 2002, Cheever et al. 2012). Not only do microbes and macroinvertebrates rely on leaves as a nutritional resource (Wallace et al. 1997, Cheever et al. 2012, Chapter 3), but organic matter appears to regulate other functions in low-order systems

(Valett et al. 2002). Heavy allochthonous inputs of leaves, coinciding with the negative values of NEP indicate continual heterotrophic conditions in these streams throughout the year (Chapter 3). Additionally, low values of DIN seen here can be explained by the high levels of leaves in the streams (Webster et al. 2001, Chapter 3) and usage of those nutrients by surficial heterotrophic biofilms (Cheever et al. 2012), driving shorter S_w during and after leaf fall.

Depending on the time of year, either discharge or background ammonium concentrations drove patterns in ecosystem function. On an annual basis BOM was an important predictor of S_w , but did not appear to be important seasonally (Table 7). In streams heavily influenced by allochthonous organic matter, the presence of BOM has traditionally driven uptake especially in the fall (Mulholland et al. 2000). This was clearly not the case here, as only discharge predicted any stream function during the fall (Table 7). Surprisingly, GPP appeared to be more related to measures of nutrient uptake in these streams possibly due to a more open canopy during the winter. Although autotrophic demand for N is typically higher in open systems such as Sycamore Creek, AZ, and heterotrophic demand high for N high in forested streams like in Coweeta (Webster et al. 2003), NH_4^+ uptake and S_w were more strongly related to GPP than respiration here, when not normalized to standing stocks of organic matter.

While measures of uptake and metabolism were related in this study, they were not strong predictors of one another. Measures of NEP and ER appeared unresponsive to any factors that would normally be characteristic of strongly heterotrophic streams (BOM, nutrients; Dodds 2006). However, when uptake was normalized to standing stocks in the stream, all measures of metabolism demonstrated a significant relationship with ammonium turnover (Tables 3 and 4). When taken together, the influence of hydrology on leaf inputs and microbial colonization strongly link ecosystem functions in headwater streams. Discharge regulated the standing stocks

of organic matter, on which microbial demand for DIN increased immobilization from stream water. This enhanced activity of microbes thus increased ER when the influence of leaves was greatest in the fall, although this relationship could be seen annually.

Nitrification

Although studies in similar systems have found significant levels of in-stream nitrification (e.g. Mulholland et al. 2000, Bernhardt et al. 2002), in Coweeta the results have been more variable (Starry et al. 2005). In fact, Webster et al. (2003) suggested that nitrification is a very small component of N-cycling in forested, low-order systems such as Coweeta. In the present study, the lack of nitrification in streams and general lack of any background nitrogen from October 2011 to March 2012 initially verified this finding. The scarcity in N over this period coincided with increases in allochthonous inputs and subsequent peaks in decomposition (Webster et al. 2001, Chapter 3) suggesting use of DIN by heterotrophic biofilms (Cheever et al. 2012).

In spite of this, nitrification appeared to be temporarily stimulated by the drawdown of water in summer 2011 and 2012. During this time, there had been relatively little rainfall, translating to lower discharge in both upstream and diverted sites. The combination of lower discharge, narrower stream wetted cross-sections, and relatively small amounts of BOM (Chapter 3) most likely allowed for temporary oxygen exchange within the formerly saturated benthic sediments, thus stimulating nitrification (e.g. Williard et al. 2001). This pattern is common in the desert Southwest, where the drying-down of streams after heavy rains was shown to both stimulate nitrification and create a significant source of nitrate to downstream reaches (Jones et al. 1995, Dent et al. 2001). Additionally, the lower heterotrophic demand for N during

the summer vs. fall in Coweeta streams (e.g. Tank et al. 2000) translated into more DIN available to nitrifiers (Table 2).

Given future predictions of extended low-flow periods in Coweeta (Wu et al. 2012a, b), more in-stream nitrification may occur, leading to greater export of nitrate downstream. The cumulative effect of increasing nitrate transport from headwater catchments (e.g. Peterson et al. 2001, Worrall et al. 2003) may override the efficiency of in-stream removal processes, such as uptake (Hall et al. 2009) or denitrification (Mulholland et al. 2008, 2009). This situation may exacerbate eutrophication and exceed the abilities of estuaries to store excess nitrate (Tobias et al. 2003, Paerl 2006).

Conclusions

In this short-term study, the reduction of stream flow altered ecosystem function. Hydrology (primarily discharge) regulated the streams here in two ways. First, nutrient delivery in periods of higher discharge appeared to stimulate GPP in these heavily heterotrophic systems, albeit temporarily. Secondly, the movement of water (or lack thereof) affected standing stocks of BOM, which further linked stream function to its surrounding watershed. Leaves in upstream sites were quickly colonized by microbes, which immobilized nutrients and increased respiration on those leaves initially. This pattern was delayed in diverted sites, which demonstrated increased immobilization and heterotrophic respiration after the return of water in the winter.

Relative changes in ecosystem metabolism, uptake, and nutrient levels may also indicate competition between different microbial groups for nitrogen in these streams. Undetectable levels of background N in these streams during the fall and winter suggest heavy usage by microbes over the course of this study. While some nitrification was detected in the streams, heterotrophic demand for N exceeds nitrifier demand during most times of the year in Coweeta

(Tank et al. 2000, Webster et al. 2003). In this study during the fall, there were clear patterns in both leaf- and fungal-specific uptake, suggesting heterotrophic microbes as an important immobilizer of stream N during this time. In January and March, the relatively higher uptake relative to fungal biomass most likely demonstrated that other groups were immobilizing available N. Autotrophic usage of N may be one fate of N during the winter, which coincides with increases in GPP seen during January and March in these streams.

Ammonium uptake appeared to be resilient to changes in flow, even though flow diversions initiated a change in function for the year of the experiment. While systems that typically go through wet-dry phases vary in the spatial heterogeneity of biogeochemical processes (“biogeochemical hotspots”, Baldwin et al. 2005, Gómez et al. 2009), perennial systems such as Coweeta appear to have a greater ability to recover function lost during times of temporary flow reductions. In a future scenario of longer, dryer summer periods, nitrification may temporarily dominate, but the return of water in winter storms will initiate metabolic and biogeochemical processes that typify headwater ecosystems.

Given the possibility that the frequency and intensity of precipitation may alter stream flows in the future (Wu et al. 2012a,b), it is clear that ecosystem function may be affected. A temporal shift in function may occur in streams to better coincide with higher discharge and nutrient concentrations. Additionally, the presence of BOM (as regulated by flow) will itself regulate nutrient immobilization and ecosystem respiration. Open canopies in the winter, along with increased nutrient delivery in higher flows may even stimulate GPP in heavily shaded heterotrophic systems such as Coweeta altering the overall energy balance within forested ecosystems.

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Table 1. Background chemical parameters of the reaches used in this study. Missing data are indicated by (-). Superscripts with different letters are significantly different ($\alpha = 0.05$), and (+) indicates that all combinations of date and reach were different.

| Date | Reach | Temperature ⁺ (°C) | | | Specific Conductance ($\mu\text{S cm}^{-1}$) | | | Dissolved Oxygen (mg L^{-1}) | | |
|--------------|----------|----------------------------------|-------------|------------|---|--------------------------|-------------|--|-------|--|
| | | Mean (SE) | Range | Mean (SE) | Range | Mean (SE) | Range | Mean (SE) | Range | |
| 8-10 Sept 11 | Diverted | 15.6 (0.3) | 15.0 – 16.1 | 20.9 (3.4) | 15.9 -27.3 | 8.1 (0) ^a | - | | | |
| | Upstream | 14.8 (0.2) | 14.4 – 15.1 | 18.1 (2.1) | 13.8 – 20.2 | 8.4 (0.2) | 8.0 – 8.7 | | | |
| 26-29 Oct 11 | Diverted | 11.7 (0.6) | 10.6 – 12.7 | 20.3 (3.9) | 13.9 – 20.7 | 8.0 (0.7) ^a | 7.3 – 8.7 | | | |
| | Upstream | 10.3 (0.3) | 9.9 – 10.9 | 18.3 (2.5) | 13.4 – 21.0 | 8.6 (0.1) | 8.5 – 8.7 | | | |
| 17-19 Nov 11 | Diverted | 10.6 (0.5) | 9.8 – 11.5 | 18.2 (3.8) | 12.0 -25.1 | 9.6 (0.2) ^{b,c} | 9.4 – 9.8 | | | |
| | Upstream | 8.2 (0.3) | 7.6 – 8.7 | 16.1 (2.3) | 11.6 – 18.4 | 10.0 (0.4) | 9.3 – 10.8 | | | |
| 28-31 Jan 12 | Diverted | 6.6 (0.3) | 6.0 – 7.0 | 14.9 (2.1) | 10.9 – 18.1 | 10.7 (0.2) ^c | 10.4 – 11.1 | | | |
| | Upstream | 7.3 (0.5) | 6.2 – 8.0 | 13.7 (3.5) | 9.8 – 20.6 | 10.4 (0.5) | 9.5 – 11.2 | | | |
| 24-26 Mar 12 | Diverted | 11.8 (0.3) | 11.4 – 12.4 | 16.0 (2.6) | 10.9 – 19.8 | 9.2 (0.3) ^{a,b} | 8.6 – 9.5 | | | |
| | Upstream | 11.6 (0.2) | 11.2 – 11.8 | 15.3 (2.4) | 10.7 – 18.4 | 9.1 (0.6) | 7.9 – 9.8 | | | |
| 10-12 May 12 | Diverted | 12.5 (0.2) | 12.3 – 12.8 | 15.7 (2.5) | 10.9 – 19.1 | 9.4 (0.5) ^b | 8.5 – 10.2 | | | |
| | Upstream | 12.8 (0.1) | 12.6 – 12.9 | 15.8 (2.4) | 11.0 – 18.9 | 9.4 (0.1) | 9.3 – 9.5 | | | |

| | | | | | | | |
|---------------|----------|------------|-------------|------------|-------------|---|---|
| 23-24 July 12 | Diverted | 17.2 (0.5) | 16.7 – 18.2 | 18.8 (3.9) | 12.1 – 25.7 | - | - |
| | Upstream | 17.9 (0.4) | 16.7 – 18.2 | 16.5 (2.5) | 11.6 – 19.1 | - | - |
| 18 Nov 12 | Diverted | 7.8 (0.5) | 6.9 – 8.5 | 15.7 (2.3) | 11.2 – 18.5 | - | - |
| 19 Nov 12 | Upstream | 8.7 (0.6) | 7.5 – 9.5 | 15.5 (2.3) | 10.9 – 18.0 | - | - |
| 20 Nov 12 | Diverted | 9.4 (0.6) | 8.2 – 10.3 | 16.3 (2.5) | 11.4 – 19.3 | - | - |

Table 2. Background dissolved inorganic nitrogen (DIN) concentrations and proportions of ammonium nitrified (k_{NIT}/k_A ; Bernhardt et al. 2002) in the reaches over the course of this study. Missing data are indicated by (-), while measures below machine detection limits are denoted as (BD ; concentrations $< 5 \mu\text{g L}^{-1}$).

| Date | Reach | NH ₄ -N ($\mu\text{g L}^{-1}$) | | | NO ₃ -N ($\mu\text{g L}^{-1}$) | | | k _{NIT} /k _A | |
|--------------|----------|--|-------------|--|--|-------------|--|----------------------------------|-------------|
| | | Mean (SE) | Range | | Mean (SE) | Range | | Mean (SE) | Range |
| 8-10 Sept 11 | Diverted | BD | BD – 7.8 | | 22.7 (6.7) ^a | 15.8 – 36.1 | | 0.71 (0.03) | 0.66 – 0.71 |
| | Upstream | BD | - | | 14.4 (4.3) | 7.3 – 22.2 | | 0.47 (0.24) | 0.11 – 0.92 |
| 26-29 Oct 11 | Diverted | BD | - | | BD | - | | - | - |
| | Upstream | BD | - | | BD | - | | - | - |
| 17-19 Nov 11 | Diverted | BD | - | | BD | - | | - | - |
| | Upstream | BD | - | | BD | - | | - | - |
| 28-31 Jan 12 | Diverted | BD | - | | BD | - | | - | - |
| | Upstream | BD | - | | BD | - | | - | - |
| 24-26 Mar 12 | Diverted | 5.6 (1.7) | BD – 8.4 | | 10.3 (3.7) ^a | 6.3 – 17.7 | | 0 | - |
| | Upstream | 12.3 (0.7) | 11.4 – 13.7 | | 18.3 (4.5) | 13.8 – 22.8 | | 0.83 (0.14) | 0.69 – 0.97 |
| 10-12 May 12 | Diverted | 7.1 (2.3) | BD – 10.0 | | 17.9 (2.5) ^a | 15.3 – 22.9 | | - | - |
| | Upstream | 17.1 (0.3) | 16.6 – 17.5 | | 23.9 (3.1) | 18.5 – 29.2 | | - | - |

| | | | | | | | |
|---------------|----------|------------|------------|-------------------------|-------------|-------------|------------|
| 23-24 July 12 | Diverted | 6.4 (0.6) | 5.3 – 7.1 | 30.0 (3.6) ^b | 23.5 – 36.1 | 0.40 | - |
| | Upstream | 7.5 (2.4) | 5.0 – 12.2 | 36.3 (3.6) | 29.1 – 40.2 | 0.65 (0.25) | 0.20 – 1.0 |
| 18 Nov 12 | Diverted | 9.8 (3.9) | 5.1 – 17.5 | BD | - | - | - |
| 19 Nov 12 | Upstream | 8.2 (2.8) | BD – 13.2 | BD | - | - | - |
| 20 Nov 12 | Diverted | 15.2 (3.0) | 9.6 – 19.5 | BD | - | - | - |

Table 3. Pearson correlation coefficients (ρ) between measured variables in this study. All bolded coefficients were significant ($p < 0.05$).

| NO_3^- | NH_4^+ | Q | Wetted cross-sectional area | BOM | U | S_w | NEP | ER | GPP | k_{NIT}/k_A | U:SC | ER:SC |
|-----------------|-----------------|------|-----------------------------|--------------|-------------|--------------|-------|--------------|--------------|----------------------|--------------|--------------|
| NO_3^- | 0.17 | 0.06 | 0.05 | 0.73 | 0.31 | -0.27 | 0.36 | -0.37 | -0.14 | -0.19 | -0.29 | -0.76 |
| | NH_4^+ | 0.22 | 0.44 | -0.37 | 0.65 | 0.32 | 0.03 | -0.01 | 0.48 | 0.13 | 0.24 | 0.14 |
| | | Q | 0.82 | -0.53 | 0.33 | 0.68 | -0.18 | 0.21 | 0.67 | 0.29 | 0.68 | 0.49 |
| | | | Wetted cross-sectional area | -0.55 | 0.40 | 0.56 | -0.01 | 0.05 | 0.65 | 0.22 | 0.45 | 0.21 |
| | | | | BOM | -0.20 | -0.63 | 0.34 | -0.36 | -0.53 | -0.09 | -0.55 | -0.39 |
| | | | | | U | -0.03 | -0.03 | 0.05 | 0.45 | -0.07 | 0.42 | 0.16 |
| | | | | | S_w | | -0.04 | 0.07 | 0.57 | 0.42 | 0.37 | 0.22 |
| | | | | | | | NEP | -0.99 | -0.12 | 0.02 | -0.82 | -0.94 |
| | | | | | | | ER | 0.17 | | -0.03 | 0.84 | 0.95 |
| | | | | | | | GPP | | GPP | -0.19 | 0.63 | 0.36 |
| | | | | | | | | | | k_{NIT}/k_A | -0.22 | 0.89 |
| | | | | | | | | | | | U:SC | 0.89 |

Table 4. Pearson correlation coefficients (ρ) between measured variables in this study during the fall. All bolded coefficients were significant ($p < 0.05$).

| NH_4^+ | Q | Wetted cross-sectional stream area | BOM | U | S_w | NEP | ER | GPP | U:SC | ER:SC |
|-----------------|-------------|------------------------------------|--------------|-------------|--------------|--------------|--------------|--------------|--------------|--------------|
| NH_4^+ | 0.55 | 0.64 | -0.46 | 0.59 | 0.70 | 0.06 | -0.07 | -0.14 | 0.81 | -0.04 |
| Q | | 0.94 | -0.62 | 0.39 | 0.47 | -0.84 | 0.85 | 0.74 | 0.70 | 0.70 |
| | | Wetted cross-sectional stream area | 0.59 | 0.46 | 0.44 | -0.82 | 0.82 | 0.64 | 0.78 | 0.76 |
| | | | BOM | -0.20 | -0.50 | 0.24 | -0.22 | 0.20 | -0.65 | -0.60 |
| | | | | U | -0.05 | -0.41 | -0.40 | 0.20 | 0.63 | 0.38 |
| | | | | | S_w | -0.40 | 0.41 | 0.55 | 0.49 | 0.23 |
| | | | | | | NEP | -0.99 | -0.81 | 0.62 | -0.85 |
| | | | | | | | ER | 0.83 | 0.60 | 0.83 |
| | | | | | | | | GPP | 0.16 | 0.39 |
| | | | | | | | | | U:SC | 0.80 |

Table 5. Pearson correlation coefficients (ρ) between measured variables in this study during the spring. All bolded coefficients were significant ($p < 0.05$).

| NO_3^- | NH_4^+ | Q | Wetted cross-sectional stream area | BOM | U | S_w | NEP | ER | GPP | k_{NIT}/k_A | U:SC | ER:SC |
|-----------------|-----------------|------|------------------------------------|------|-------------|-------|-------------|--------------|-------|----------------------|-------|--------------|
| NO_3^- | 0.68 | 0.55 | 0.58 | 0.73 | 0.55 | 0.16 | 0.39 | -0.39 | 0.22 | -0.02 | -0.29 | -0.76 |
| | NH_4^+ | 0.35 | 0.45 | 0.33 | 0.77 | -0.26 | 0.25 | -0.25 | 0.10 | -0.20 | -0.03 | -0.91 |
| | | Q | 0.95 | 0.29 | 0.56 | 0.42 | 0.72 | -0.70 | 0.53 | -0.04 | -0.22 | -0.29 |
| | | | Wetted cross-sectional stream area | 0.39 | 0.71 | 0.19 | 0.58 | -0.57 | 0.49 | -0.19 | -0.42 | -0.42 |
| | | | | BOM | 0.63 | -0.53 | 0.22 | -0.29 | -0.33 | -0.09 | -0.50 | -0.64 |
| | | | | | U | -0.42 | 0.23 | -0.23 | 0.02 | -0.19 | -0.29 | -0.72 |
| | | | | | | S_w | 0.53 | -0.50 | 0.58 | 0.08 | 0.26 | 0.29 |
| | | | | | | | NEP | -0.99 | 0.32 | 0.13 | 0.36 | -0.63 |
| | | | | | | | ER | ER | -0.28 | -0.16 | -0.38 | 0.64 |
| | | | | | | | | GPP | GPP | -0.51 | 0.08 | -0.35 |
| | | | | | | | | | | k_{NIT}/k_A | -0.22 | -0.89 |
| | | | | | | | | | | | U:SC | 0.10 |

Table 6. Pearson correlation coefficients (ρ) between measured variables in this study during the summer.

All bolded coefficients were significant ($p < 0.05$).

| NO_3^- | NH_4^+ | Q | Wetted cross-sectional stream area | U | S_w | NEP | ER | GPP | k_{NIT}/k_A |
|-----------------|-----------------|------|------------------------------------|-------------|-------------|-------|--------------|-------------|----------------------|
| NO_3^- | 0.47 | 0.43 | 0.33 | 0.36 | < 0.01 | 0.37 | -0.41 | -0.44 | 0.23 |
| | NH_4^+ | 0.17 | 0.11 | 0.85 | -0.10 | 0.07 | -0.01 | 0.90 | < 0.01 |
| | | Q | 0.89 | 0.27 | 0.64 | -0.13 | 0.13 | < 0.01 | 0.08 |
| | | | Wetted cross-sectional stream area | 0.16 | 0.46 | -0.10 | 0.10 | 0.15 | 0.25 |
| | | | | U | -0.15 | 0.22 | -0.16 | 0.84 | -0.18 |
| | | | | | S_w | -0.67 | 0.68 | 0.06 | 0.04 |
| | | | | | | NEP | -0.99 | 0.16 | 0.79 |
| | | | | | | | ER | 0.09 | -0.79 |
| | | | | | | | | GPP | 0.08 |

Table 7. Regression equations for predicting functional attributes of streams used in this study. NSP = no significant predictors.

| Part of Year | Response | Equation | r ² | p-value |
|--------------|----------------------|---|----------------|---------|
| Total | Ammonium uptake | | | |
| | U | $2.21(\text{NH}_4^+) + 0.09(\text{Q}) + 7.76$ | 0.46 | 0.0001 |
| | S _w | $3.75(\text{Q}) - 0.16(\text{BOM}) + 53.86$ | 0.56 | <0.0001 |
| | Ecosystem metabolism | | | |
| | GPP | $0.02(\text{NH}_4^+) + 0.02(\text{Q}) - 0.02$ | 0.70 | <0.0001 |
| Spring | Ammonium uptake | | | |
| | U | $3.08(\text{NH}_4^+) - 0.71$ | 0.94 | 0.03 |
| | S _w | $11.64(\text{Q}) + 11.01$ | 0.97 | 0.02 |
| | Ecosystem metabolism | NSP | | |
| Summer | Ammonium uptake | | | |
| | U | $10.05(\text{NH}_4^+) - 11.50$ | 0.94 | 0.001 |
| | Ecosystem metabolism | | | |
| | GPP | $0.08(\text{NH}_4^+) - 0.11$ | 0.81 | 0.014 |

| | | | | |
|--------|----------------------|-------------------|------|-------|
| Fall | Ammonium uptake | | | |
| | S_w | $4.40(Q) + 6.77$ | 0.42 | 0.05 |
| | Ecosystem metabolism | | | |
| | NEP | $-0.85(Q) - 0.51$ | 0.71 | 0.001 |
| | GPP | $6.03(Q) + 0.01$ | 0.55 | 0.009 |
| | ER | $0.88(Q) + 0.52$ | 0.71 | 0.001 |
| Winter | NSP | | | |



Figure 1. An experimental weir in Coweeta A) before and B) during removal of diversion structures on 18 November 2012. Photographs taken by the author.

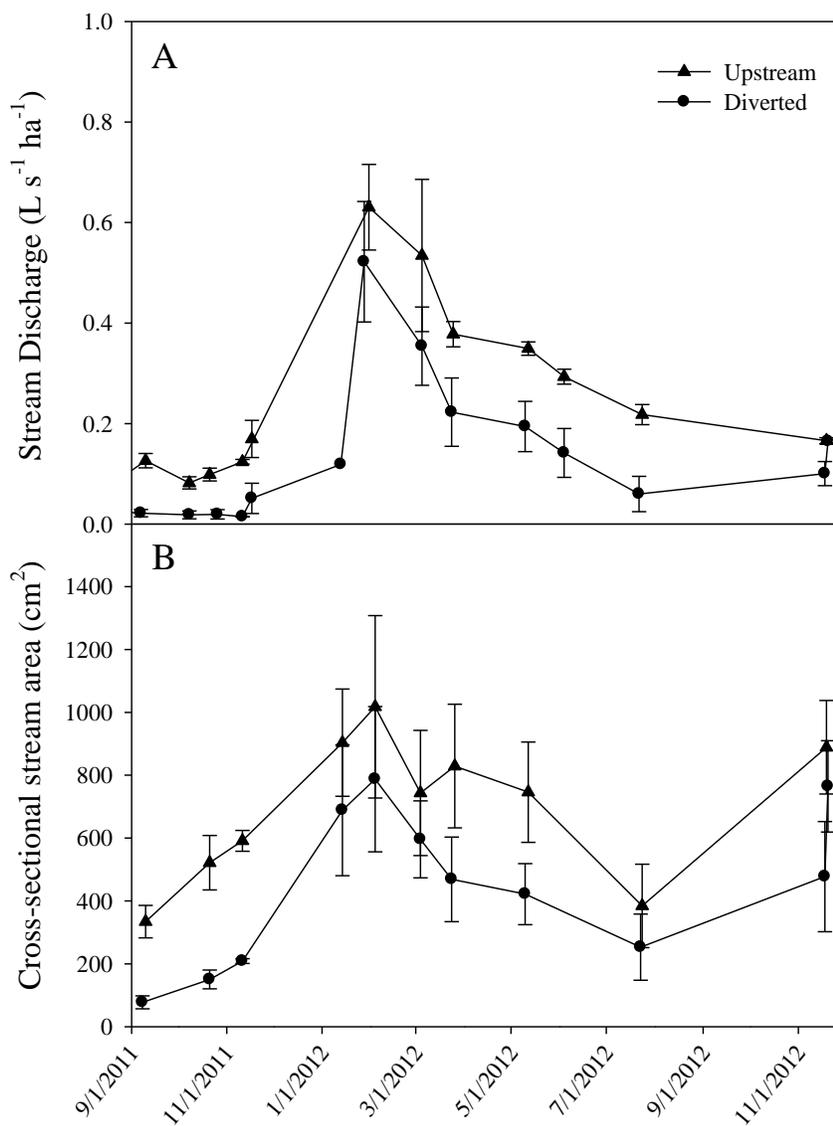


Figure 2. Stream characteristics during this study, including A) discharge and B) wetted cross-sectional area. Bars represent 1 SE of the mean.

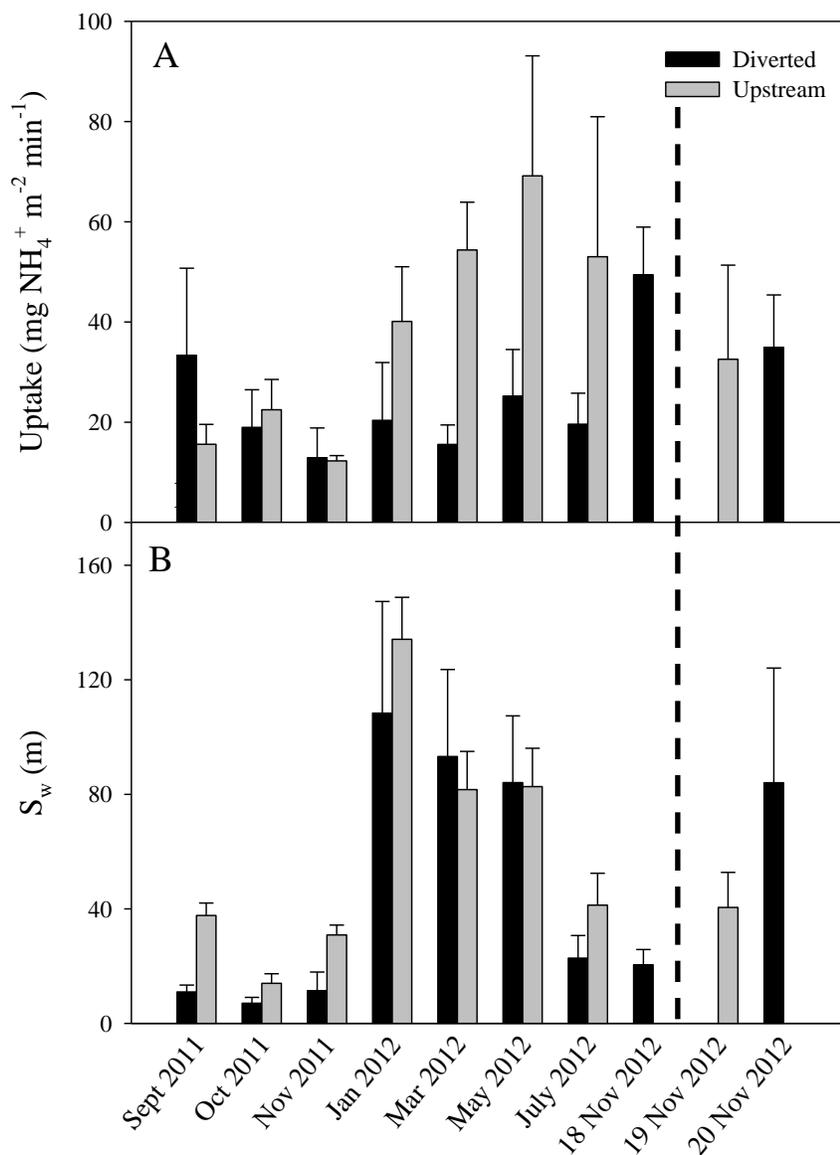


Figure 3. Differences in A) areal uptake rates (U), and B) uptake lengths (S_w) in upstream and diverted sites over the course of this experiment. Error bars represent 1 SE of the mean. The dotted line indicates the removal date of stream diversions on 18 Nov 2012.

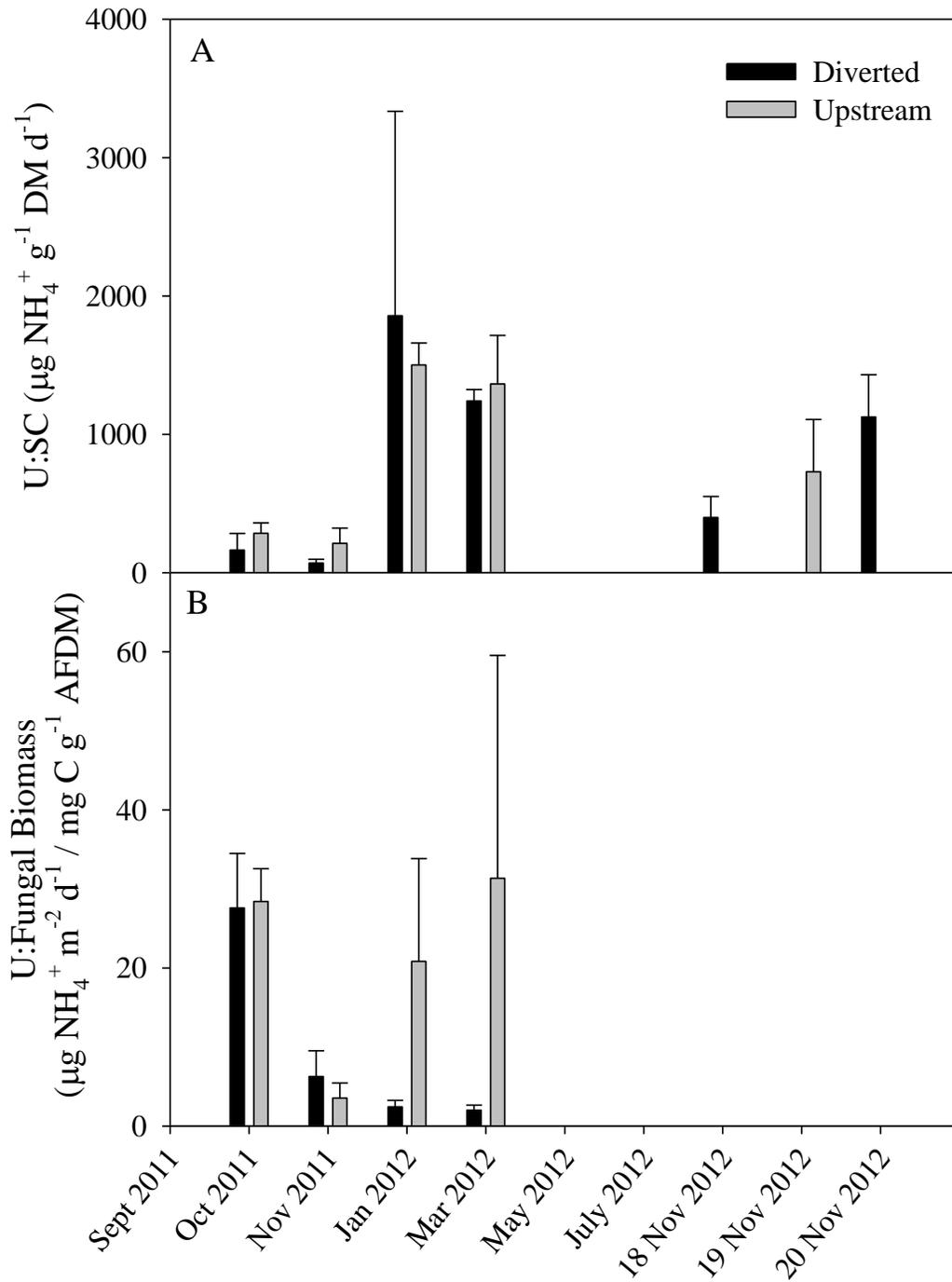


Figure 4. Changes in uptake of ammonium (U) per mass of A) benthic organic matter and B) fungal biomass over time in diverted and upstream sites. Standing stocks of organic matter (SC) were expressed in units of dry mass (DM).

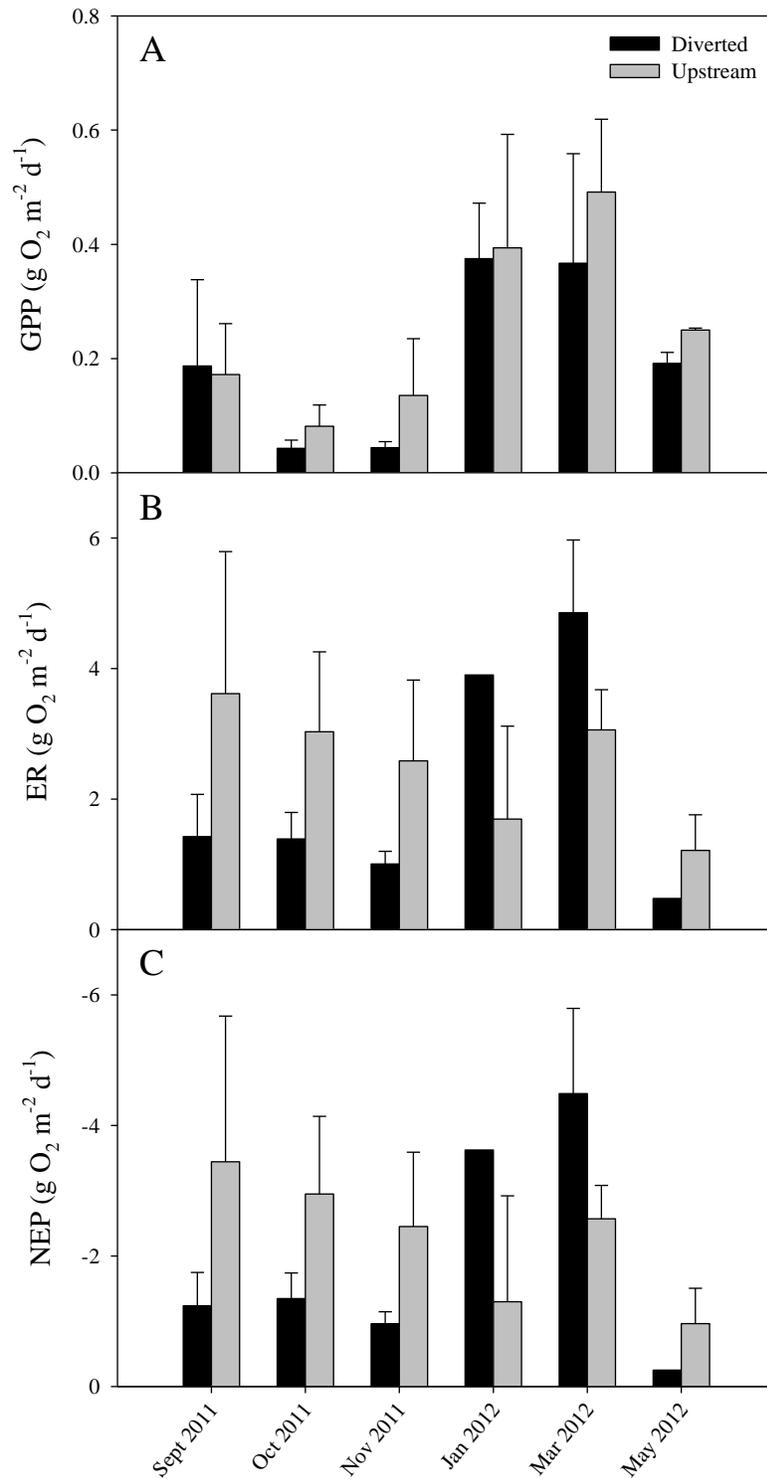


Figure 5. Differences in A) gross primary production (GPP), B) ecosystem respiration (ER), and C) net ecosystem production (NEP) in upstream and diverted sites over the course of this experiment. Error bars represent 1 SE of the mean. Note the inverted axis scale for NEP.

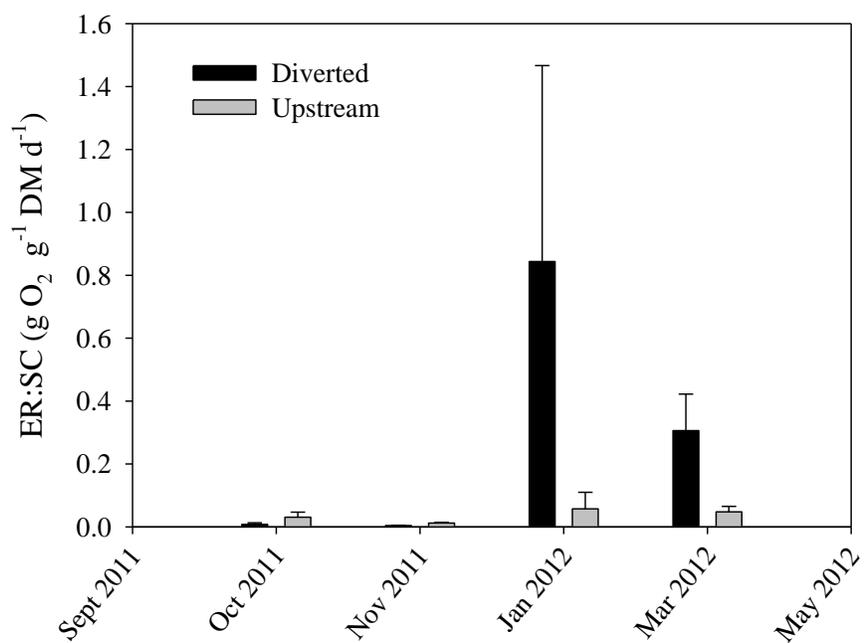


Figure 6. Changes in ecosystem respiration (ER) per mass of benthic organic matter over time in diverted and upstream sites. Standing stocks of organic matter (SC) were expressed in units of dry mass (DM).

Chapter 5: Synthesis

Stream ecosystems are variable over both time and space, but their function is dependent upon the presence of water. In a future where water is predicted to be limiting due to alterations in the pattern and intensity of precipitation, there is need to better understand the basic functions of streams to put them in a context for the future. In this research I attempted to experimentally assess changes to one component of climate change, water availability due to changes to precipitation patterns. The results of this study were successful in that it further clarified the role of water as a strong control of ecosystem processes in streams, a fact that is usually taken for granted in perennial systems.

A conceptual model for climate change impacts on perennial stream ecosystems

Annual distribution patterns of precipitation will influence the presence of surface freshwaters. In the southern Appalachians, Wu et al. (2012a,b) predict that annual precipitation levels will not change, but more intense autumn and winter storms will contribute the most to surface waters. This translates into an uneven availability of water, with long periods of the summer without rain (Bates et al. 2008). When surface levels of flow are not sufficiently recharged by alterations in precipitation patterns, groundwater inputs of freshwater may become a relatively more important component of baseflow (Oki and Kenae 2006). Interactions between climate, precipitation patterns, and water availability will greatly influence how headwater stream ecosystems function in the future (Fig. 1).

Changes in connectivity and water availability in ecosystems alter how organic matter is processed in streams. Less-frequent storms create a more retentive system, where both coarse particulate organic matter (CPOM) and nutrients accumulate (Romani et al. 2006, Steward et al. 2012). This was a pattern clearly demonstrated in diverted sites here; greater standing stocks of

organic matter were retained over the course of the experiment in Chapter 3. Corti et al. (2011) suggested that the removal of water from the system will potentially decrease microbial processes on leaves. Similarly, my data indicated a strong hydrologic control of both microbial colonization of leaves (Ch. 3) and heterotrophic immobilization annually (Ch.4). Although mineralization was not directly addressed in this study, the control of decomposition by water availability most likely exerts a similar control of movement from the organic to the inorganic pools within a stream (Fig. 1). Surprisingly, decreases in water availability over the summer stimulated nitrification in streams, which will add to a DIN pool that will likely be retained (e.g. von Schiller et al. 2008) until increased flows export these nutrients downstream (Steward et al. 2012).

While heterotrophy remained dominant in these forested, headwater systems, GPP appeared to be more responsive than respiration to changes in streams brought about by hydrologic alterations. Increased availability of DIN likely drives increases in GPP (Fellows et al. 2006), a connection made clearer in this system in Chapter 4. The effect of GPP was less obvious in the fall due to greater organic matter standing stocks and potential for interactions between the nutrients, water availability, and microbial processes on leaves (Cheever et al. 2012).

The connections seen in Figure 1 relate to the annual patterns that can be determined from these data. Clearly, there will be seasonal differences that will alter the size and shape of boxes and arrows. In the fall, the organic matter standing stocks will be greater, GPP will be even lower, and immobilization, mineralization, and export of particulates and nutrients will depend on the frequency of storms (Fig. 1). In the summer, with greater potentials for low flows, standing stocks of DIN may stimulate a slight increase in GPP but no significant change in R.

This model demonstrates the complexity and integrative nature of stream ecosystems, but clearly the role of precipitation frequency and intensity (and thus discharge) was a measurable control on these ecosystem processes.

Perspectives and scope

Recent evidence from Coweeta indicated that lack of water, as mimicked by diverted sites, may negatively affect salamander consumers. Occupancy was much lower and the body condition of blackbelly salamanders (*Desmognathus quadramaculatus*) was much poorer in diverted than upstream sites (K. Cecala, unpublished data). Habitat disturbance, in this case a decrease of water, was the most likely driver of occupancy differences (e.g. Price et al. 2012). Poor body condition in *D. quadramaculatus* was likely due to limited aquatic food resources (Davic 1991), which were driven by changes to stream flow and the availability of macroinvertebrate prey on less processed leaf material in drier sites demonstrated in earlier chapters here.

Changes to salamander dynamics, in conjunction with the results of this work, clearly indicate a role of ecosystem functions in affecting multiple levels of ecological organization. These local-scale differences suggest a disruption of trophic dynamics, which may translate to regional differences in food availability over both time and space in a variety of taxa (e.g. Winder and Schindler 2004, Woodward et al. 2010). Hydrology not only acts as a local control of endogenous processes but acts also regionally through the transport of resources and nutrients to downstream reaches (Vannote et al. 1980, Wallace et al. 1997, Hall 2003). Given that headwater streams can provide important functions across the many stream miles that they encompass, it is clear that a bottom-up perspective is necessary to address issues related to conservation of aquatic resources at larger scales (Kominoski and Rosemond 2012).

This work has demonstrated the importance of experimental approaches to climate change and how the results of those experiments can inform ecological linkages. Already, altered patterns in precipitation can be seen in this region (e.g. Wu et al. 2012a,b). Moving forward, there needs to be a more regional assessment of changes in organic matter and nutrient dynamics and their effects across multiple levels of organization. Only then will we begin to have any understanding of the interactive nature of aquatic ecosystems within their landscape.

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APPENDIX A. MACROINVERTEBRATES ON LEAF PACKS

Appendix A1. List of macroinvertebrate taxa colonizing leaves along a gradient of inundation at streams in Coweeta

Hydrologic Laboratory from October 2011 to March 2012. Sites within each stream were diverted (D), upstream (U), bank (B), and terrestrial (T). Functional feeding groups (FFG) included collector/gatherers (C/G), collector/filterers (C/F), fungus-eater (F), predators (P), shredders (Sh), and scrapers (Sc), all based on Merritt et al. 2008.

| Order | Family | Subfamily | Tribe | Genus | FFG | WS 22 | | | WS 40 | | | WS 41 | | |
|-----------|-----------------|--------------|-----------------|--------------------|-----|-------|---|---|-------|---|---|-------|---|---|
| | | | | | | D | U | B | D | U | B | D | U | B |
| Diptera | Ceratopogonidae | | | <i>Palpomyia</i> | P | * | * | * | * | * | * | * | * | * |
| | Chironomidae | Chironominae | Chironomini | | C/G | * | | * | * | * | * | * | * | * |
| | | | | | C/G | * | * | * | * | * | * | * | * | * |
| | | | Orthocladinae | | C/G | * | * | * | * | * | * | * | * | * |
| | | | Tanytopodinae | | P | * | * | * | * | * | * | * | * | * |
| | Dixidae | | | <i>Dixa</i> | C/F | | | * | | | | | | |
| | Empididae | | | <i>n/a</i> | P | | | | * | | | * | | |
| | Ephydriidae | | | <i>Ephydra</i> | C/G | * | | * | * | * | * | * | * | * |
| | Psychodidae | | | <i>Pericoma</i> | C/G | * | | | | | | | | |
| | Simuliidae | | | <i>Prosimulium</i> | C/F | * | | | | | | * | | |
| | | | | <i>Simulium</i> | C/F | * | | | * | | | | | |
| Tabanidae | | | <i>Chrysops</i> | P | | | * | | * | | | | | |
| Tipulidae | | | | <i>Dicronata</i> | P | | * | | * | | * | | | |
| | | | | <i>Hexatoma</i> | P | * | * | * | * | * | * | * | * | |
| | | | | <i>Molophilus</i> | Sh | * | | * | * | * | * | * | * | |
| | | | | <i>Pilaria</i> | P | | | * | * | * | * | * | * | |
| | | | <i>Tipula</i> | Sh | | | * | * | * | * | * | * | * | |

| | | | | | | | |
|---------------|-------------------|-------------------------|------|---|---|---|---|
| Ephemeroptera | Baetidae | <i>Baetis</i> | C/G | | | | * |
| | Ephemereliidae | <i>Serratella</i> | C/G | | * | | * |
| | Heptageniidae | <i>Stenonema</i> | Sc | * | * | * | * |
| | Leptophlebiidae | <i>Leptophlebia</i> | C/G | * | * | * | * |
| | | <i>Paraleptophlebia</i> | C/G | * | | * | * |
| Odonata | Gomphidae | <i>Gomphus</i> | P | | * | * | * |
| Plecoptera | Capniidae | <i>Capnura</i> | Sh | * | * | * | * |
| | Chloroperlidae | <i>Sweltsa</i> | P | | | | * |
| | Leuctridae | <i>Leuctra</i> | Sh | * | | | * |
| | Nemouridae | <i>Amphinemoura</i> | Sh | * | * | * | * |
| | Peltoperlidae | <i>Tallaperla</i> | Sh | * | * | * | * |
| | Perlidae | <i>Agnatina</i> | P | * | | | * |
| | | <i>Beloneuria</i> | P | * | | | * |
| | | <i>Perlinella</i> | P | | * | | * |
| | | <i>Isoperla</i> | P | * | * | * | * |
| Trichoptera | Hydropsychidae | <i>Ceratopsyche</i> | C/F | | * | | * |
| | | <i>Cheumatopsyche</i> | C/F | | | | * |
| | | <i>Hydropsyche</i> | C/F | | * | * | * |
| | Limnephilidae | <i>Ironoquia</i> | Sh | * | | | * |
| | | <i>Pycnopsyche</i> | Sh | * | * | * | * |
| | Philopotamidae | <i>Chimarra</i> | C/F | * | | | * |
| | Polycentropodidae | <i>Neureclipsis</i> | C/F | * | * | * | * |
| | | <i>Polycentropus</i> | P/Sh | * | * | * | * |
| | | <i>Rhyacophila</i> | P | * | | | * |
| Collembola | | | F | * | * | * | * |
| Amphipoda | | | Sh | | | | * |
| Oligochaeta | | | C/G | * | * | * | * |

Appendix A2. Shannon-Weiner Diversity of macroinvertebrate functional feeding groups colonizing leaves in study streams in Coweeta over the course of this study.

| Date | Red Maple | | | White Oak | | |
|-----------|-------------|-------------|-------------|-------------|-------------|-------------|
| | Diverted | Upstream | Bank | Diverted | Upstream | Bank |
| 8 Oct 11 | - | - | - | 1.30 (0) | - | - |
| 22 Oct 11 | 0.72 (0) | 0.86 (0.31) | - | 0.50 (0) | 1.09 (0.21) | - |
| 12 Nov 11 | 1.03 (0.19) | 1.52 (0.06) | - | 1.60 (0) | 0.83 (0.46) | - |
| 14 Jan 12 | 1.22 (0.26) | 1.35 (0.27) | - | 1.80 (0.07) | 1.31 (0.19) | 0.72 (0) |
| 4 Feb 12 | 1.56 (0.15) | 1.22 (0.14) | 0.72 (0.37) | 1.19 (0.36) | 0.86 (0.43) | 1.42 (0.04) |
| 5 Mar 12 | 1.06 (0.14) | 1.24 (0.27) | 1.17 (0.36) | 0.94 (0.09) | 1.52 (0.03) | 1.35 (0.11) |