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Temporal Patterns of Aquatic Macroinvertebrate Communities and Organic Matter Standing Stock Availability in a Coastal Floodplain (Altamaha River, Georgia)

Erica L. Johnson

TEMPORAL PATTERNS OF AQUATIC MACROINVERTEBRATE COMMUNITIES AND ORGANIC MATTER STANDING STOCK AVAILABILITY IN A COASTAL FLOODPLAIN (ALTAMAHA RIVER, GEORGIA)

by

ERICA L. JOHNSON

(Under the direction Checo Colon-Gaud)

ABSTRACT

River floodplain habitats of the Southeastern United States are sites of high biological productivity that rely on a predictable flooding event as a keystone process. This study took place in a river-floodplain area of the Altamaha River, an unimpounded large-order river in the Coastal Plains region of the US. This study aims to investigate how aquatic macroinvertebrate communities changed over the course of the annual flood pulse. I predicted that the communities would be different and that the differences would be driven by hydrology at the main stem and organic matter standing stock availability. I took quantitative samples of benthic macroinvertebrates monthly from December 2011-April 2012 and from December 2012- April 2014. Invertebrate abundance was assessed and biomass was obtained using published length-mass regressions. Year 1 (2011-2012) was characterized by severe drought. And Year 2 was characterized by a large flooding event. There was a significant difference between the communities. In year 1 the community was influenced by hydrology and high FBOM standing stocks. In year 2 the community was influenced by hydrology and low CBOM standing stocks. This study shows the importance of a flooding event in river floodplain systems and supports the idea that floodplains act as a source of organic matter to the main stem and are sites of high biological productivity especially from aquatic macroinvertebrates. As unimpounded rivers are becoming increasingly rare, it is important to understand how these systems function in both normal and abnormal (i.e., drought vs. flood) conditions.

INDEX WORDS: Aquatic macroinvertebrate, floodplain, biomass, coastal plain, flood pulse concept

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DEDICATION

This thesis is dedicated to anyone who has been my teacher in any capacity. I could not have come this far without you.

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CHAPTER 1

LITERATURE REVIEW

Floodplains are prominent physical features of many riverine landscapes. Floodplains of the Coastal Plain are highly abundant habitats (Hunt, 1967) that are low-gradient landscape adjacent to the main channel of a river that experience inundation or flooding. They are ecologically important features as they provide a multitude of resources (e.g., food, habitat) for aquatic and terrestrial biota. In the southeastern United States, riverine floodplains are an abundant habitat type that also acts as an important conduit for energy to the adjacent river and riparian areas (Hunt, 1967; Baxter, 2005). Increased demands on freshwater resources, alteration and modification of river systems, as well as natural disturbances such as drought are all factors that can negatively influence the ecological functioning of floodplain habitats. Understanding the temporal patterns of aquatic ecosystems during such disturbances is necessary to consider when dealing with management issues and conservation of riverine floodplain habitat.

Coastal plain floodplains become inundated annually in the winter months (December-March) due to decreased evapotranspiration and water usage from riparian vegetation (Smock, 1999). Seasonal flooding (the "flood pulse"), as described by Junk et al. (1989), is a key process in floodplain ecosystems. Inundation of floodplains provides essential habitat for aquatic biota (fish, macroinvertebrates) to spawn, develop, feed, and seek refugia. Flooding provides increased habitat and nutrient availability as well as organic matter transport to the main channel (Cuffney, 1988; Jones and Smock 1991). Flooding also increases surface area which makes floodplains a major energetic contributor to riverine ecosystems per unit area (Benke, 2001).

Ecosystem functions provided by riverine floodplains are associated with both riparian and riverine ecosystems. Riparian zones provide allochthonous inputs to floodplains which serve as a substantial energy and carbon subsidy. Coastal plain floodplains receive approximately 4643 g m^{-2} $yr^{-1}$of litter fall of which 55-80% is derived from autumnal leaf fall (Cuffney, 1988; Benfield, 1997; Meyer et al., 1997; Webster and Meyer, 1997). Studies conducted on the Ogeechee River suggest that coastal plain river floodplains act as sources of organic matter due to high transport of suspended particulates to the main channel (Benke and Meyer, 1988; Cuffney, 1988; Tockner et al., 1999). Breakdown of terrestrial litter fall in floodplains provides particulate organic matter to both the floodplain and the riverine system.

In addition to energy obtained from the riparian zone, riverine floodplains are sites of high biological productivity. Due to high surface area during inundation, biomass is higher per unit area in the floodplain than in the main channel (Benke, 2001). Fallen trees and large woody debris (commonly referred to as snags) are abundant in coastal plain river floodplains and are also a main driver of invertebrate biomass in floodplain systems by providing a stable substrate necessary for colonization (Meyer, 1990; Braccia and Batzer, 2001). Since annual net primary production in riverine floodplains of the Coastal Plain can be fairly low (Sharitz and Pennings, 2006), production from macroinvertebrates is vital to the overall productivity of the system.

Aquatic macroinvertebrates in floodplains form assemblages that are specially adapted to the periodic nature of flooding floodplain ecosystems and play a major role in ecosystem functions. Macroinvertebrate communities in coastal plain river floodplains are dominated by obligate wetland invertebrates such as predaceous beetles (Dytiscidae), amphipods (Crangonyctidae), and isopods (Asellidae) (Reese and Batzer, 2007). These organisms have developed specialized life history strategies that allow them to survive brief periods of inundation followed by longer periods of limited water availability (Wissinger, 1999). Some of these strategies include quick turn-over rates, resistance to desiccation, resting egg stages, or the ability to survive in the hyporheic zone (Smock et al., 1985; Smock, 1999; Griswold et al., 2008). Specialized life history strategies give these macroinvertebrates an advantage under stressful environmental conditions.

Aquatic macroinvertebrates play a major role in ecological functions in river floodplains as consumers of organic matter. Organic matter breakdown is an important process in stream ecosystems as it converts large items such as leaves into smaller, easily consumed particles. Previous studies have shown that fine benthic organic matter (FBOM; leaf litter and organic matter from 250 µm to 1mm) are important food sources to many of the invertebrates common to lentic river-floodplain habitat (Taylor and Batzer, 2010). The roles of macroinvertebrates in aquatic food webs can be described using functional feeding groups, or FFGs (Batzer and Wissinger, 1996; Wallace and Webster, 1996). Functional feeding groups classify aquatic macroinvertebrates based on their feeding habits (i.e., shredding, collecting, predation) rather than the food source (i.e., leaves, organic matter particles, animal tissue). Functional feeding groups are a relatively rapid classification method used to obtain relative trophic position within the macroinvertebrate food web as well as a way to link these organisms to ecosystem processes such as leaf breakdown (Lugthart and Wallace, 1992; Cummins et al., 2005).

Due to the high volume of terrestrial input from riparian forests, as well as the lentic nature of floodplains, organic matter breakdown is due to consumers more than physical breakdown from flowing water (Cuffney and Wallace, 1987). Since forested floodplains of the Coastal Plain do not contain preferred habitat for the suite of typical shredding macroinvertebrates (e.g., Plecoptera and Ephemeroptera), other invertebrates that are typically classified as omnivorous (e.g. Isopoda and Amphipoda) must assume the role of shredders. The functional plasticity of these macroinvertebrates is necessary in order for organic matter breakdown to occur.

Physical and biological processes in river floodplains depend on flooding. Hydrology is often referred to as the "master variable" in freshwater ecosystems that influences both physical and biological components of freshwater ecosystems (Poff et al., 1997). Flooding assists in organic matter accumulation, breakdown, and transport from the floodplain to the main channel (Benke and Meyer, 1988; Cuffney, 1988; Meyer et al., 1997; Golladay et al., 2000; Golladay et al., 2007). Additionally, natural flooding provides increased habitat availability in floodplains and promotes biological diversity (Ward 1998; Benke, 2001; Lytle and Poff, 2004).

Today many rivers in the United States are subject to alterations in flow that are either anthropogenic (dams and channelization) or natural (drought) in origin. Anthropogenic stressors (e.g. dams and channelization) are becoming increasingly common due to increasing demand on freshwater resources and human development. As a result approximately 2% of rivers in the United States are unmodified and naturally flowing (Graf, 1993). In the past decade natural disturbances, specifically drought, have gained attention as frequency of drought is predicted to increase as a result of climate change (Lake 2003; Lake 2008; Thorp, 2014). Alteration of the natural flow regime causes a shift in the magnitude, frequency, and duration of hydrologic events which can result in negative ecological responses such as reduced biological diversity and loss of ecosystem function (Poff et al., 1997; Cardinale et al., 2012).

From 2009 to 2012 Georgia experienced a multi-year drought (US Drought Monitor, 2014). This type of multi-year, unpredictable drought event is referred to as a supraseasonal drought and is less well understood than the more predictable seasonal drought (Lake, 2003). Supraseasonal droughts are becoming more prevalent with human modified flow regimes and low precipitation years (Lake, 2008). Disturbances such as drought have the potential to affect standing crop biomass (macroinvertebrates and benthic organic matter), taxonomic richness, and trophic-functional diversity and it is therefore necessary to examine these factors when investigating the impact of drought (Resh et al., 1988).

The purpose of this study is to identify trends in aquatic macroinvertebrate community composition and function and benthic organic matter standing stock in a river floodplain of the Altamaha River in southeastern Georgia during severe drought and flooding conditions. The Altamaha River basin consists of approximately 738,000 hectares of which 44% is forested cover, 17% is wetlands, 1.4% is urbanized and 19% is agricultural (Georgia DNR, 2003). It is the largest river basin in the state, draining approximately 25% of Georgia. Its two major tributaries are the Oconee and the Ocmulgee Rivers that originate in the Piedmont physiographic region of the state and converge in the Coastal Plain region to form the main stem of the Altamaha. While there are several small dams on the Oconee and the Ocmulgee Rivers, there are no impoundments on the main stem of the Altamaha which allows the flow regime to occur naturally. This large river is a valuable resource as it falls within the 2% of rivers in the United States that flow naturally.

The Altamaha River supports animal life that is of economic, recreational and conservation importance. Approximately 93 species of fish including many sport fish (redbreast, bluegill, warmouth and other centrarchids), the economically important American shad and the endangered Atlantic and shortnose sturgeon inhabit the Altamaha (Benke and Cushing, 2010). In total there are 25 endangered species in the Altamaha River including several fish and invertebrates species such as the Altamaha spinymussel which was listed as an endangered species in 2011 (Benke and Cushing, 2010; USFWS, 2011). The lower reaches of the Altamaha are characterized by a wide, meandering main channel that is bordered by large bottomland hardwood forests, swamp and floodplain habitat. Approximately 10,000 hectares of riparian forest along the Altamaha are designated as wildlife management areas (WMAs) by the Georgia Environmental Protection Division. This acreage is divided into three WMAs (upstream to downstream): Bullard Creek WMA, Moody Forest Natural Area, and Big Hammock WMA. Wildlife management areas provide hunting and recreation opportunities as well as minimally developed habitat for scientific investigation.

Research on aquatic ecosystems has been conducted at both Bullard Creek and Big Hammock WMA. Reese and Batzer (2007) identified longitudinal patterns in aquatic macroinvertebrate communities by investigating a series of habitat ranging from the headwaters of the Oconee River in northern Georgia to Big Hammock WMA. Results of this study concluded that there are predictable differences in community composition from the headwaters to the lower reaches of the Altamaha (Reese and Batzer, 2007). In a study that included data from Bullard Creek and Big Hammock WMA, Bright et al. (2010) identified unique fish and macroinvertebrate communities in the river-floodplain and the upland-floodplain ecotones. Both of these studies have provided spatial analysis of aquatic macroinvertebrate communities in river-floodplain areas of the Altamaha however assessments of temporal patterns in these communities are still lacking.

Due to the prevalence of drought disturbance in the state, there is a need to characterize aquatic communities and their response to this disturbance since this is still a growing area of research (Lake, 2008). Sampling for this study occurred during the 2011-2012 and the 2012-2013 flood pulse. The 2011-2012 flood pulse was characterized by lower than average flows at the main stem, followed by a small flooding event. The 2012-2013 flood pulse was characterized by a wet summer and a large flooding event in the winter. This contrast between drought and flood provided a unique research opportunity to determine the potential resiliency of the aquatic macroinvertebrate communities that inhabit the floodplains of the Moody Forest.

I addressed the question of how aquatic macroinvertebrate communities and their associated food resources change throughout the course of the annual flood pulse in the river floodplain area of the Altamaha River. Since river-floodplains depend on a predictable flood event, the temporal aspect of this study makes it unique compared to previous research that has been conducted in similar habitats. I predicted that there would be discernible differences in community structure and function between sampling years. These changes are predicted to be driven by variation in food resource availability as well as gauge height in the main channel of the river.

CHAPTER 2

BENTHIC MACROINVERTEBRATE COMMUNITY RESPONSE TO FLOODING AND DROUGHT

Introduction

Floodplains are low gradient areas adjacent to the main channel of a river that can be both ecologically and economically valuable. Floodplains provide habitat, food resources, and ecosystem functions such as organic matter processing and nutrient cycling (Junk et al., 1989; Benke, 2001). Ecosystem functions provided by floodplains are valued at approximately \$19,500 ha^{-1} yr^{-1}, which is second only to ecosystem services provided by estuaries (Costanza et al., 1997). Freshwater coastal floodplains are characterized by a predictable hydrological event in which lateral overbank flooding occurs. In the Southeastern Coastal Plain of the United States seasonal flooding typically begins in the winter months (December-March) and is coupled with decreased evapotranspiration and water usage from riparian vegetation (Smock, 1999). This flood pulse event, as described by Junk et al. (1989), provides increased habitat and nutrient availability as well as organic matter transport to the main channel (Cuffney, 1988; Jones and Smock 1991). Due to their large surface area during inundation, floodplains are highly productive making them a major energetic contributor to riverine ecosystems (Benke, 2001).

The aquatic consumer communities (e.g., fish, macroinvertebrates) that inhabit floodplains are highly productive. Snag habitat (i.e., deposited woody debris), which is characteristic of river floodplains in the southeastern US, facilitates high macroinvertebrate production that can at times exceed that of the main channel (Benke et al., 1984; Benke, 2001). Benthic macroinvertebrate communities in southeastern floodplains are dominated in abundance and biomass by Oligochaeta, Isopoda, chironomid larvae, mollusks and crustaceans (Smock, 1999; Batzer and Wissinger 1996; Benke 2001). This macroinvertebrate biomass can be an important energetic source that links basal resources to higher trophic levels (Ross and Baker, 1983; Batzer and Wissinger 1996;

The Altamaha River Basin is one of the largest watersheds in the U.S. Atlantic coast, originating in the northern Piedmont physiographic region, continuing through the coastal plain region, and terminating at the Atlantic Ocean. The Altamaha River is a 6th order river with low topographic relief with abundant floodplain habitat. Furthermore, unlike in other major river basins in the southeastern Coastal Plain (e.g., Savannah River), there are no major impoundments on the main stem of the Altamaha River making it an ideal system for studying natural flow regimes in the Coastal Plain.

From 2009- 2013, Georgia experienced a multi-year, supraseasonal drought disturbance (US Drought Monitor, 2013). Supraseasonal droughts are becoming more prevalent with human modified flow regimes and low precipitation years (Lake, 2003; Lake, 2008). During this time, discharge on the main stem of the Altamaha River near Baxley, Georgia, was well below the 42-year average (USGS, 2013). Human-mediated or natural disturbances can have impacts on the floodplain ecosystem and thus affect the ecosystem function and services they provide.

In this study I assessed temporal patterns of aquatic macroinvertebrate community structure in a floodplain of the Altamaha River, at the Moody Forest Natural Area in Appling Co., Georgia. The study was conducted over the course of an annual flooding event during a two year period (December 2011-April 2012 and December 2012-April 2013). December 2011-April 2012, hereafter referred to as "year 1", was characterized by severe to extreme drought while December 2012-April 2013, hereafter referred to as "year 2", was characterized by higher than average discharge at the main stem. I examined macroinvertebrate community abundance and biomass as well as quantified benthic organic matter standing stocks. I hypothesized that aquatic macroinvertebrate abundance and biomass would differ between the two years and that hydrology at the main channel and organic matter resource availability would be the most influential mechanisms determining the structure of macroinvertebrate communities.

Methods

Study Location

The study site was located in a floodplain area at the Moody Forest Natural Area (Moody Forest) in Appling County, GA (31° 55' 47.24" N, 82° 16' 12.14" W). The Moody Forest consists of approximately 1,780 hectares of land designated as Wildlife Management Area (GA DNR). Land cover is comprised of primarily old-growth longleaf pine forests, bottomland hardwood forests, and cypress-tupelo sloughs. Dominant tree species at the Moody Forest include bald cypress (*Taxodium distichum*), water tupelo (*Nyssa aquatica*), and overcup oak (*Quercus lyrata*). Approximately, three river kilometers of the Altamaha River and adjoining floodplains run though the Moody Forest. The area has been co-managed by the Georgia Department of Natural Resources and The Nature Conservancy since 2001 (The Nature Conservancy, 2005). The sampling area for the study was a backwater slough that consistently retains water throughout the year and experiences an increase in water level continuously.

Hydrology and Water Quality

Temperature (°C), dissolved oxygen (mg/L), conductivity (µS/cm), and pH were recorded monthly using a handheld YSI Professional Plus Multi-parameter Water Quality Meter (YSI, Inc). Hydrologic data (discharge, gauge height, multi-year averages) were obtained from USGS gauge 02225000 near Baxley, GA (waterdata.usgs.gov/nwis). This gauge is located at the bridge crossing the Altamaha River on US Highway 1, approximately 5-10 km upstream of the site. Temperature was monitored continuously every 90 minutes using a HOBO pendant temperature logger. Diel oxygen curves were also obtained during year 1 of the study using a YSI XLM900 multi-parameter sonde.

Benthic Macroinvertebrate and Organic Matter Standing Stocks

Macroinvertebrates were collected monthly using a benthic corer (sampling area 0.032 m^2) from December 2011 to April 2012 and December 2012 to April 2012. During collections, the core was placed into the water, inserted and secured into the substrate, and all benthic macroinvertebrates and organic matter down to approximately 10 cm below the substrate surface were removed and placed into a 5 gal bucket. Three samples were taken each month in approximately the same place each month. The volume of sample material removed from the core and placed in the bucket was recorded and contents of the bucket were poured through a 250µm sieve. To collect very fine benthic organic matter (VFBOM; < 250µm) a 50-100 ml subsample of water filtered through the sieve was collected and frozen until further processing. All other materials retained in the sieve were placed in a plastic bag, preserved with ~70% ethanol and transported to the laboratory for further processing.

At the laboratory, samples were washed through stacked 1mm and 250µm sieves to further separate the sample into coarse benthic organic matter (CBOM; >1mm) and fine benthic organic matter (FBOM; <1mm, but >250µm). CBOM was further separated into wood, leaves, or miscellaneous components. All macroinvertebrates were sorted from organic matter, identified to the lowest taxonomic level possible (usually genus for insects, order/family for non-insects) using Merritt et al. 2008 and Thorp and Covich 2010, and preserved in ~70% ethanol. To estimate biomass, individual invertebrates were measured to the nearest 1mm. Biomass was estimated using published length-mass regressions for specific taxa (when available) or length-mass regressions for a similarly-sized taxon within the same classification group (Pace and Orcutt, 1981; Hodar, 1996; Benke et al. 1999; Mercer et al., 2001; Sabo et al., 2002; Stead et al., 2003; Chimney et al., 2007). After all macroinvertebrates were removed, organic matter components were placed in a drying oven at 60°C for at least 48h and weighed to the nearest 0.01g to obtain dry mass (DM). Organic materials were later combusted in a muffle furnace at 500°C for 1h and weighted to obtain ash free dry mass (AFDM; Benfield 2006).

Statistical analysis

Biomass and Abundance data were log transformed to meet assumptions of equal variance and normality. After transformation equal variance and normality were tested using Levene's test and the Shapiro-Wilk test, respectively. Differences between sampling months and sampling years were tested using a factorial Analysis of Variance (ANOVA) in JMP Pro 10 and differences between groups were assessed with a Tukey-Kramer post-hoc test (SAS Institute Inc., Cary, NC, USA). Differences in aquatic macroinvertebrate communities between sampling years were examined with nonmetric multi-dimensional scaling (NMDS) based on abundance and biomass data using PRIMER6 software (McCune and Grace, 2002; Primer-E Ltd., Plymouth, UK). Community dissimilarities were calculated using the Bray-Curtis Index (Bray and Curtis 1957).

When a grouping among sampling years was suggested by NMDS, Analysis of Similarity (ANOSIM) was used to determine significant results. Similarity Percentages (SIMPER) was used to identify the percent of the total community each taxon were contributing during both sampling years. Both ANOSIM and SIMPER tests were run with Primer 6 software (Primer-E Ltd., Plymouth, UK)

In order to determine the amount of variation that environmental factors were contributing to the overall biomass and abundance of the invertebrate community, a Principal Components Analysis (PCA) was performed (Gauch, 1982). The environmental factors used were: temperature, dissolved oxygen, discharge at the main stem, as well as CBOM, FBOM and VFBOM standing stock data. PCA was run with JMP Pro 10 (SAS Institute Inc., Cary, NC, USA). Scree plots and vector scores were examined to determine which axes were contributing a majority of the variance.

Results

Hydrology and Water Quality

While there was a noticeable hydrologic event, gauge height in the main stem of the Altamaha near the study site did not reach or exceed flood stage during year 1(Figure 2.1). During the second year of the study, 2012-2013, the main stem of the Altamaha exceeded flood stage in March and April (Figure 2.2).

Temperature increased in both years, as expected, as the sampling period progressed. Overall, dissolved oxygen rates in year 1 were lower compared to year 2 and ranged from 2.9-5.4 mg/L (Table 2.1). In year 2 dissolved oxygen ranged from 3.6-10.8 mg/L which was, at times, twice as high as dissolved oxygen from Year 1. Conductivity in year 1 remained constant, but in year 2 there was a drop in conductivity coupled with the flooding event. pH at the study site remained stable in both years.

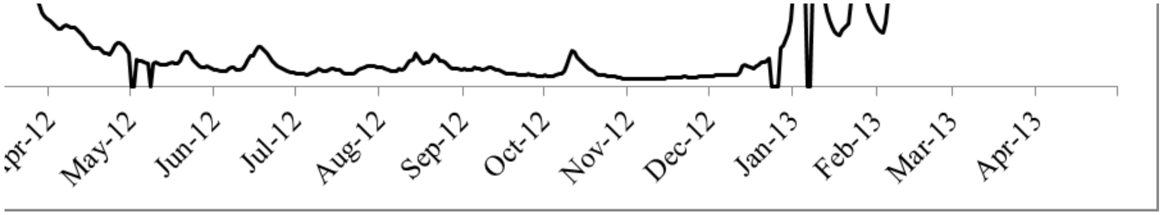

Figure 2.1. Gauge height (solid line) from November 2011- May 2013 at USGS gauge 02225000 near Baxley, Ga. Flood stage is indicated by the dashed line.

19.417 (0.054)	5.498 (0.354)	0.113 (0.0003)	6.483 (0.020)
20.017 (0.120)	2.943 (0.174)	0.143 (0.142)	5.695 (0.017)
15.150 (0.160)	5.310 (0.156)	0.118 (0.130)	6.177 (0.100)
15.120 (0.124)	10.884 (0.166)	0.1408 (0.085)	6.464 (0.086)
11.483 (0.162)	7.167 (0.215)	0.076 (0.021)	5.525 (0.033)
14.367 (0.136)	6.933 (0.196)	0.083 (0.142)	6.033 (0.110)
21.500 (0.226)	3.673 (0.268)	0.087 (0.175)	6.810 (0.074)

Benthic Organic Matter Standing Stocks

Organic matter was highly variable within samples (Table 2.2). Overall there was a trend towards higher standing stocks of CBOM during year 1 than during year 2. Both years showed a similar trend of less CBOM in March than in any other month. In both years FBOM standing stocks were lowest during December and April and highest in March. There was low VFBOM availability (< mg/m^2) during all months in both years except for December of year 1.

Table 2.2. Benthic organic matter standing stocks at Moody Forest during both sampling years. CBOM (> 1mm); FBOM (< 1mm, > 250µm); VFBOM (< 250µm)

Sample Month	Sampling Year	CBOM	FBOM	VFBOM
December	2011-2012	591.446 (472.626)	9.534 (3.428)	14.781 (5.583)
January	2011-2012	395.948 (503.661)	33.681 (11.048)	5.230 (1.552)
February	2011-2012	674.698 (746.417)	90.475 (24.079)	2.529 (1.695)
March	2011-2012	80.114 (112.134)	108.633 (45.490)	1.240 (0.181)
April	2011-2012	915.021 (299.920)	32.961 (11.478)	2.910 (0.551)
December	2012-2013	388.031 (169.926)	1.695 (0.191)	4.427 (1.887)
January	2012-2013	214.898 (176.016)	85.730 (79.173)	3.023 (0.986)
February	2012-2013	152.4588 (5.327)	77.954 (22.936)	1.915 (0.561)
March	2012-2013	23.053 (1.204)	3.147 (0.066)	1.900
April	2012-2013	97.601 (65.618)	15.3190 (8.144)	1.640 (0.540)

Benthic Macroinvertebrate Communities

In year 1, macroinvertebrate mean monthly abundance was highest at the beginning of the sampling period (December) and lowest during the rest of the sampling period (Figure 2.2). The opposite pattern was seen in year 2, when there was highest macroinvertebrate biomass at the end of the sampling period (April). There was a significant correlation between discharge and abundance for both sampling years (Figure 2.3; r^2= 0.373, p = 0.006). In year 1 Oligochates contributed to 20.5% of the total abundance, whereas copepods contributed 18.9%, non-Tanypodinae chironomids contributed 9.6% and ostracods contributed 7.9%. These four taxa contributed to 50% of the total abundance in year 1. In year 2 copepods contributed 17.72% of the total abundance, oligochaets contributed 15.3%, non-Tanypodinae chironomids contributed 12% and clacadocerans contributed 10.6%

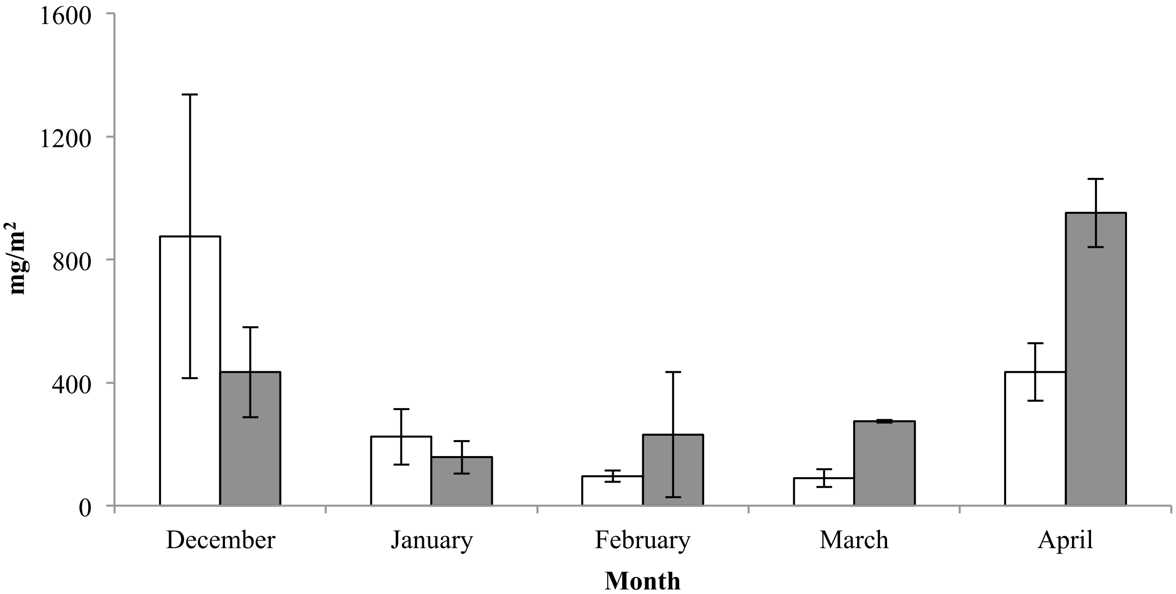

Figure 2.2. Average monthly benthic invertebrate abundance (±SE) at Moody Forest. Year 1 (2011-2012) indicated by white bars. Year 2 (2012-2013) indicated by solid bars.

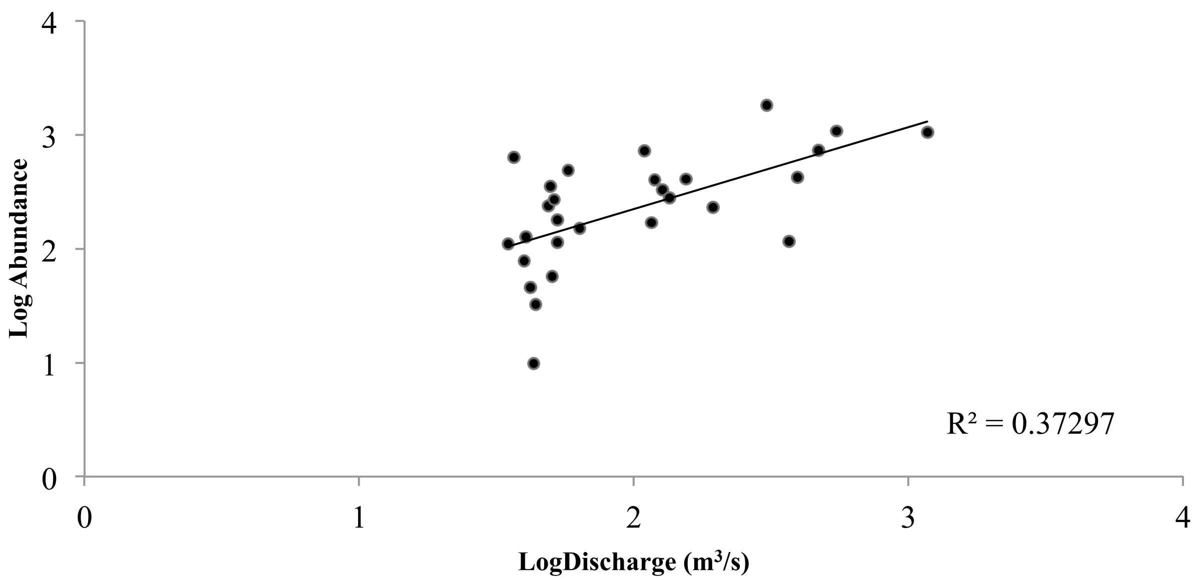

Figure 2.3. Regression of macroinvertebrate abundance and discharge for year 1 and year 2. Discharge data was obtained from USGS gauge 02225000 near Baxley, Georgia.

Overall, average monthly biomass was less than 50 mg/m^2 during the entirety of year 1. There were no significant differences in biomass between months in year 1. In year 1 Oligochaeta contributed 16.5% of the total macroinvertebrate biomass, Copepoda contributed 14.9%, non-Tanypodinae chironomids contributed 12%, and asellid isopods contributed 10.6%. These five taxa represented 54% of the total biomass for year 1.In year 2 average monthly biomass ranged from 9.9-145.5 mg/m^2 (Figure 2.2). There was significantly more biomass in April of year 2 than in December, January, February, and March of year 1 (ANOVA; $F_{9,18}$= 6.0895; p= 0.0006). Non-Tanypodinae chironomids contributed 16.7% of the total biomass, asellid isopods contributed 14.2%, Oligochaeta contributed 13.2% and copepods contributed 12.7%. These four taxa contributed 56% of the total biomass to the community in year 2.

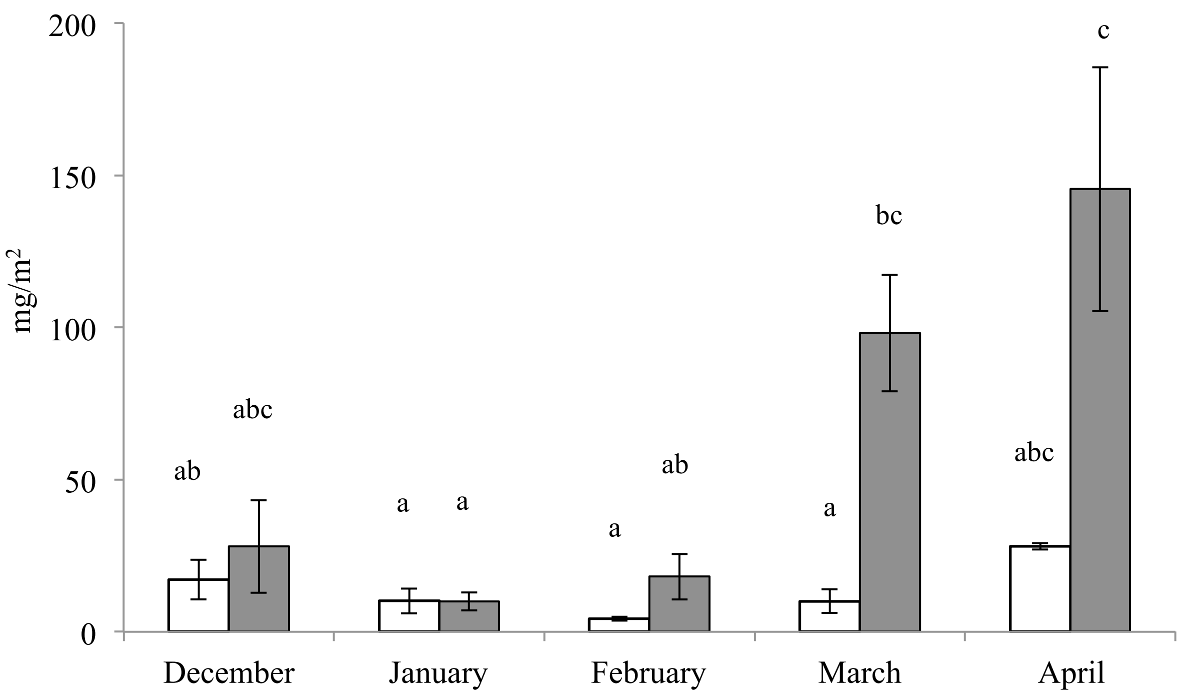

Figure 2.4. Average monthly benthic invertebrate biomass (±SE) at Moody Forest. Year 1 (2011-2012) indicated by white bars. Year 2 (2012-2013) indicated by solid bars.

Aquatic macroinvertebrate communities were significantly different in year 1 and year 2 based on abundance (ANOSIM; Global R= 0.151; p= 0.005) and biomass (ANOSIM; Global R= 0.176; p= 0.003). NMDS ordination plots suggest a distinct clustering of macroinvertebrate communities based on abundance (Figure 2.2) and biomass (Figure 2.4) data for each sampling year.

PCA analysis of physiochemical parameters (temperature, dissolved oxygen, and pH), discharge at the main stem and organic matter standing stocks (CBOM, FBOM, and VFBOM) during year 1revealed that principal component axis 1 (PC1) is characterized by high discharge and high VFBOM standing stock (Table 2.3). PC2 was characterized by high dissolved oxygen, high VFBOM, high CBOM, low temperature and explains 30.4% of the total variation in macroinvertebrate biomass for year 1.

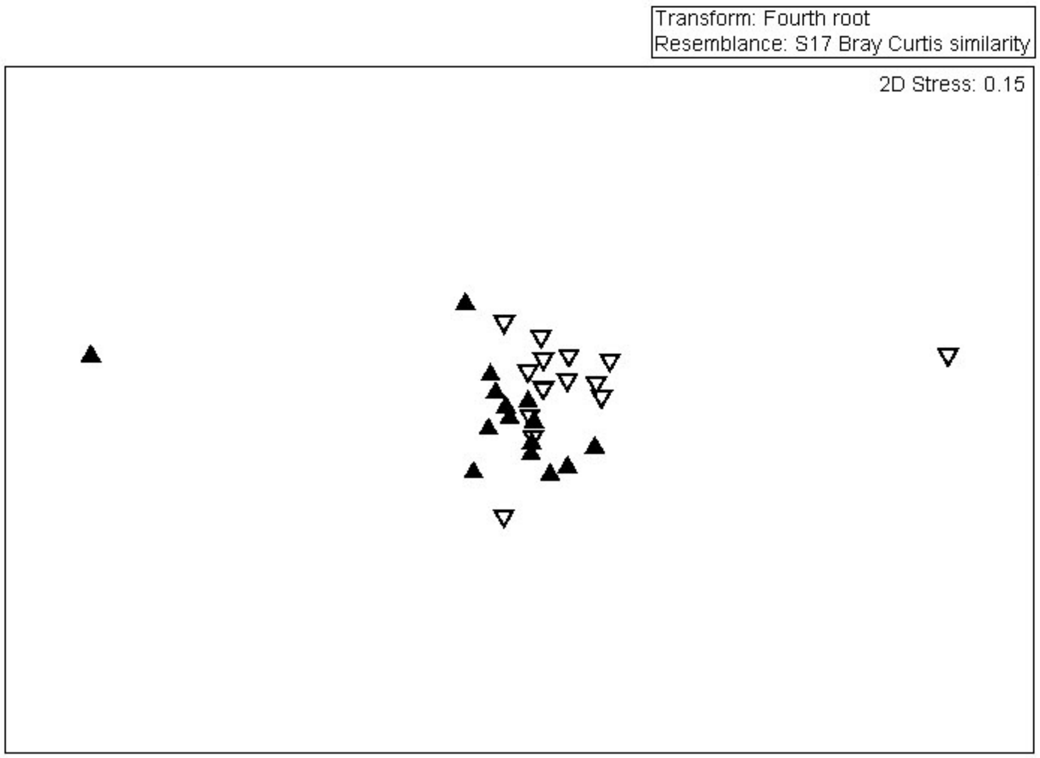

Figure 2.5. Non-metric multidimensional scaling (NMDS) ordinations in terms of macroinvertebrate abundance for year 1 (solid triangles) and year 2 (open triangles)

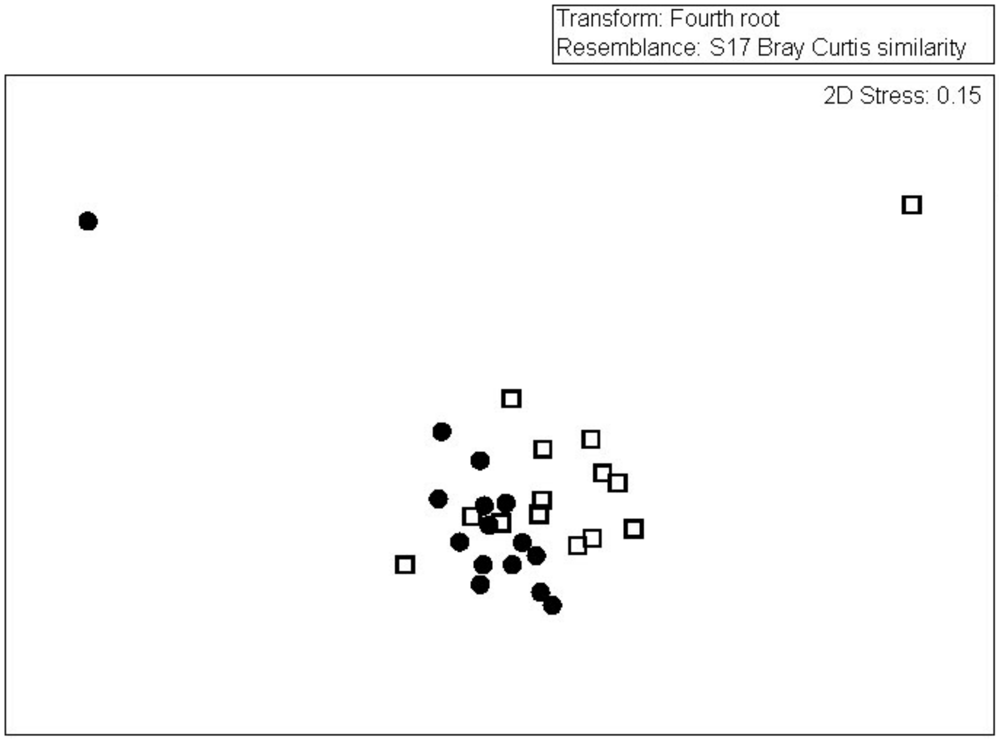

Figure 2.6. Non-metric multidimensional scaling (NMDS) ordinations in terms of macroinvertebrate biomass for year 1 (solid circles) and year 2 (open circles).

Table 2.3. Eigen loadings for each principal component (PC) vector of year 1 based on physiochemical parameters and invertebrate biomass standing stocks.

	PC1	PC2
Temperature	0.276	**-0.502**
DO	0.295	**0.542**
pH	-0.056	0.280
Discharge	**0.570**	0.044
VFBOM	-0.210	**0.515**
FBOM	**0.611**	-0.035
CBOM	0.302	0.328
Percent Variation to Biomass	32.806	27.063
Total Percent Variation	32.806	59.869

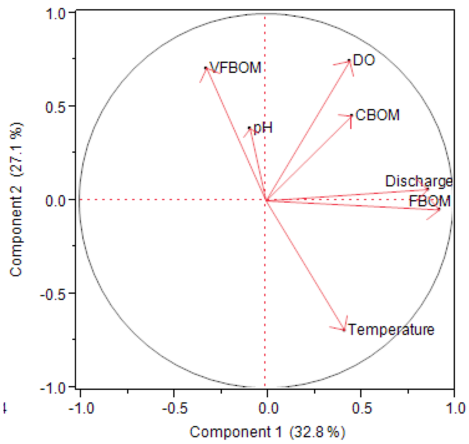

Figure 2.7. Principal component vectors for year 1. PC axis 1 was characterized by high discharge and high FBOM standing stocks.

In year 2 PC1 explained 38.6% of the total variation in macroinvertebrate biomass on and was characterized by high discharge, high dissolved oxygen, and high VFBOM (Table 2.6, Figure 2.8). Principal Component axis 2 (PC2) was characterized by high dissolved oxygen, high VFBOM, and low discharge.

Table 2.4. Eigen loadings for principal component (PC) axes1 and 2 for 2012-2013. Analysis was based on physiochemical data and mean aquatic invertebrate biomass across all months.

	PC1	PC2
Temperature	**0.458**	0.206
DO	-0.263	0.289
pH	**0.515**	0.330
Discharge	**-0.453**	0.219
VFBOM	0.309	0.355
FBOM	-0.377	0.319
CBOM	0.114	**-0.699**
Percent Variation to Biomass	39.721	21.658
Total Percent Variation	39.721	61.379

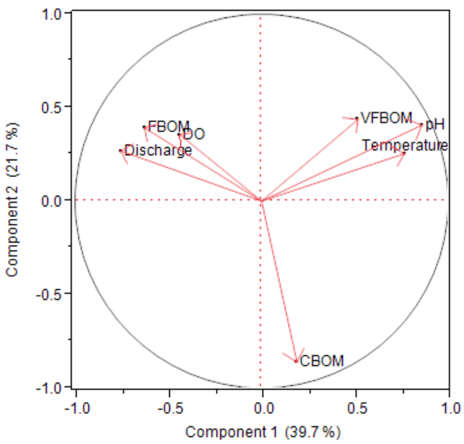

Figure 2.8. Principal component vectors for year 2. PC axis 1 was characterized by high discharge and low CBOM standing stocks.

In year 1 there was a significant positive relationship between discharge and FBOM standing stocks; there was a significant negative relationship between discharge and CBOM and total organic matter standing stocks (Table 2.7)

Table 2.5. Regression values for discharge at USGS gauge 02225000 near Baxley, GA and organic matter standing stocks at Moody Forest

Size	Sampling Year	r^2	p
CBOM	2011-2012	0.0197	0.9491
FBOM	2011-2012	0.645	0.0128*
VFBOM	2011-2012	-0.3337	0.2437
All OM	2011-2012	-0.6158	0.6663
CBOM	2012-2013	-0.6045	0.0374*
FBOM	2012-2013	0.3412	0.2539
VFBOM	2012-2013	-0.3051	0.3349
All OM	2012-2013	-0.5377	0.0474*

Discussion

This this study supports the hypothesis that invertebrate abundance and biomass would differ during flooding and drought and that those differences would be due in part to seasonal hydrologic variation and availability of organic matter standing stocks. Poff et al. (1997) identified magnitude, frequency, duration, timing, and rate of change in the flow regime as the five master variables in freshwater ecosystems upon which ecosystem processing and biodiversity depend on. In both years of this study hydrology was an important component in driving the variation in abundance and biomass of aquatic macroinvertebrates. My results showed that discharge and abundance were positively correlated and there was a strong trend towards higher biomass in the second year of the study which was characterized by a large flood.

Furthermore, benthic macroinvertebrate community abundance and biomass was significantly different between the drought (year 1) and flood (year 2) year. Despite the significant differences in overall aquatic macroinvertebrate community abundance and biomass, the assemblage of dominant taxa (Oligochaeta, non-Tanypodinae Chironomidae, Asellidae, and Copepoda) was similar for both years. This suite of taxa is characteristic of the temporarily flooded habitat as in Moody Forest, with many of them having specialized life history characteristics (resting egg stages, ability to live in the hyperheos) that are advantageous for habitat that experiences periodic wetting and drying (Smock 1999). The assemblage of invertebrates found in the Moody Forest floodplain are predominantly obligate wetland occupants that are tolerant of low dissolved oxygen (Batzer and Wissinger, 1999; Reese and Batzer, 2007). Other studies in floodplain ecosystems such as Tronstead et al. (2005) suggest that survival in the floodplain is due to an organism's ability to follow the receding waters and/or retreat into the exposed soil. It is important to note that the flood event in the Tronstead et al., (2005) study was of a much shorter duration (~8d) than the one observed at Moody Forest in my study. Nonetheless, these findings highlight the importance of adaptation to a changing environment as a key mechanism for survival especially with the increasing prevalence of extended drought and a rapidly changing climate (Lytle and Poff, 2004)

Since both years exhibited similarities in dominant taxa, it is possible that the ecosystem functions provided by the benthic macroinvertebrate assemblages were similar as well. Oligochaetes and non-Tanypodinae chironomids, both collector-gatherers, consume smaller size fractions of deposited organic matter and, according to this study, comprised a large amount of biomass especially in the early stages of the flood pulse. Asellid isopods, which were predominant in the later stages of the flood (March and April), are considered shredders in floodplain ecosystems that play a major role in organic matter breakdown from CBOM to FBOM (Golladay et al., 1999: Griffith et al., 2012). Battle and Golladay (2001) found similar results in a seasonally flooded wetland where shredding invertebrate biomass and leaf decomposition in litter bags was high during flooding and that litter decomposition was accelerated by flooding events. The high density and biomass of shredding macroinvertebrates suggests that organic matter resources are crucial to the productivity of the Moody Forest floodplain.

Terrestrial litter and organic matter are known to be important basal food resources in floodplain ecosystems (Roach, 2013). Forested floodplains receive a large input of energy from terrestrial vegetation. In the southeastern coastal floodplains, a substantial amount of litter fall is deposited to the floodplain annually (4643 g m^{-2} yr^{-1}) and is a major carbon subsidy that can be transported to the main channel or retained in the floodplain (Cuffney, 1988; Benfield, 1997). In the Moody Forest there was higher trend of organic matter standing stocks overall in year 1 than in year 2. Since year 1 was characterized as being the last year of a multi-year drought, the greater organic matter availability in year 1 may have been due to the accumulation of leaf litter in the dry floodplain that becomes available to consumers upon flooding. The only causal relationship found between organic matter and discharge in year 1 was in FBOM standing stocks. This may explain the high abundance of gatherer-collector invertebrates (non-Tanypodinae chironomids and oligochaetes).

Tockner et al. (1999) identified three distinct phases of the flood pulse: biotic interaction, primary productivity, and transport. The transport phase occurs when there is high water level in the main stem of the river and consequent overflow into the floodplain. This is supported by the significant negative relationship between discharge and CBOM standing stocks. There was also a significant negative relationship of total organic matter standing stock and discharge in year 2, however this is believed to be caused by the fact that CBOM makes up a majority of the total organic matter standing stock. Low CBOM standing stock was characteristic of year 2 of the study, further supporting the idea that river-floodplains act as sources of organic matter during flooding.

The periodic nature of floodplains makes them disturbance-dependent systems (Tockner et al., 2000, King et al., 2012). The results of my study support the idea that the predictable disturbance (flooding) is advantageous for the system to function as both a site of high biological productivity by macroinvertebrates, as well as a source of organic matter resources within the floodplain and to the main channel. In the first year of my study, I observed low macroinvertebrate biomass compared to the second year. I was able to determine that both the magnitude of flooding and the organic matter resource availability were the most probable drivers of differences between the two years.

CHAPTER 3

DISCUSSION

A natural flow regime is important for ecosystem health and biodiversity. Lateral flow from the main channel to floodplain areas is necessary to provide nutrient transport and maintain structure and function of floodplain communities (Bunn and Arthington, 2002). In addition, high flow conditions have been identified as contributing to high sexton quality in a southeastern US floodplain system (Atkinson et al., 2009). Low flow and altered flow conditions, such as that associated with dams and channelization have been hypothesized to have negative synergistic impacts on freshwater systems with respect to diversity and distribution of biota as well as energy transport from wetlands to rivers (Rolls et al., 2013)

River-floodplain ecosystems in the southeastern United States are unique habitats that are at high risk for anthropogenic disturbances such as habitat alteration and ecosystem destruction (Malmqvist and Rundle, 2002). Forests associated with river floodplains provide habitat for fire dependent plant taxa, as well as endangered species such as the red-cockaded woodpecker, and are highly susceptible to alteration for agricultural and silvicultural uses (Brinson and Malvarez, 2002). Protected areas, such as Moody Forest, help to protect floodplain habitat as well as the ecosystem functions they provide.

In addition to human-mediated disturbance on freshwater systems, there is an increased risk of extended periods of drought due to climate change with the southeastern US being particularly vulnerable (Mulholland et al., 1997). Due to the unpredictable nature of onset and duration, biotic responses to drought are relatively understudied (Lake, 2003). Despite the difficulties presented by the unpredictability of drought, the information garnered can provide valuable information on the resiliency of a system to drought.

Today approximately 2% of the rivers in the United States flow freely (Postel and Richter, 2003). Currently, the Altamaha River is part of this small percentage that experiences natural flooding and has not been impounded or channelized. The Altamaha has the potential to serve as a reference to other, more heavily managed rivers due to the fact that it is free flowing and contains some of the region's most unique and biologically productive habitat.

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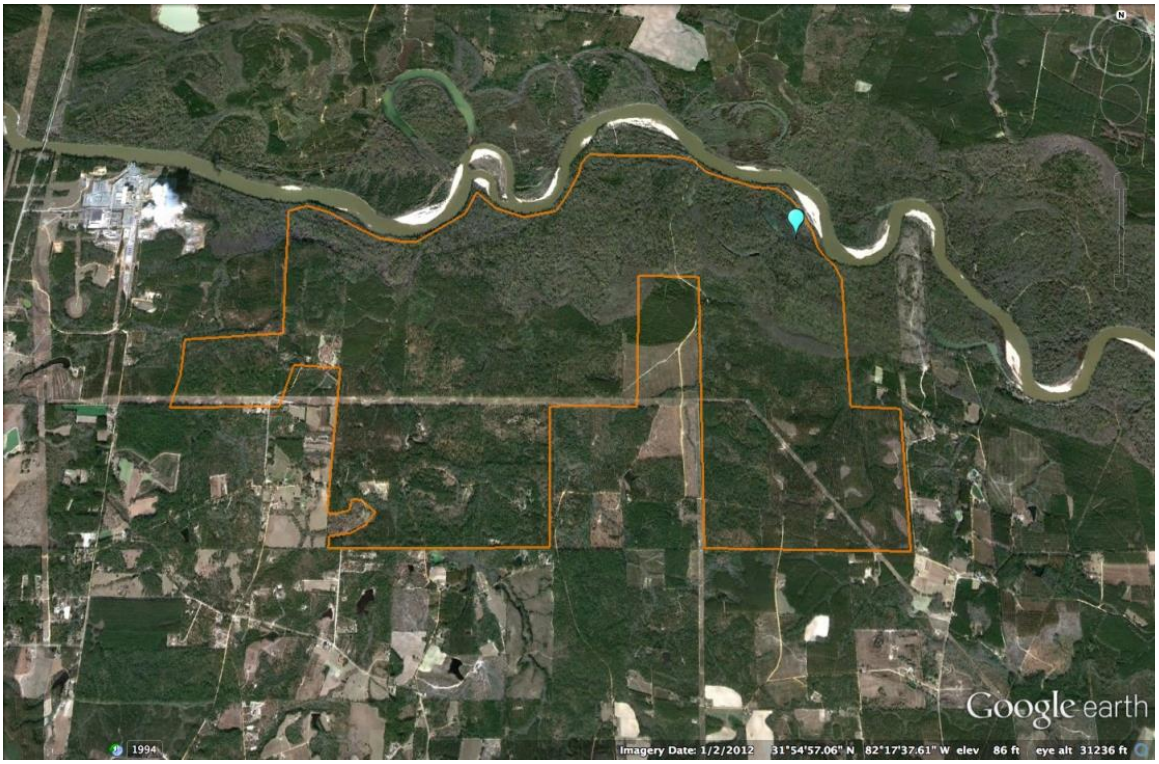
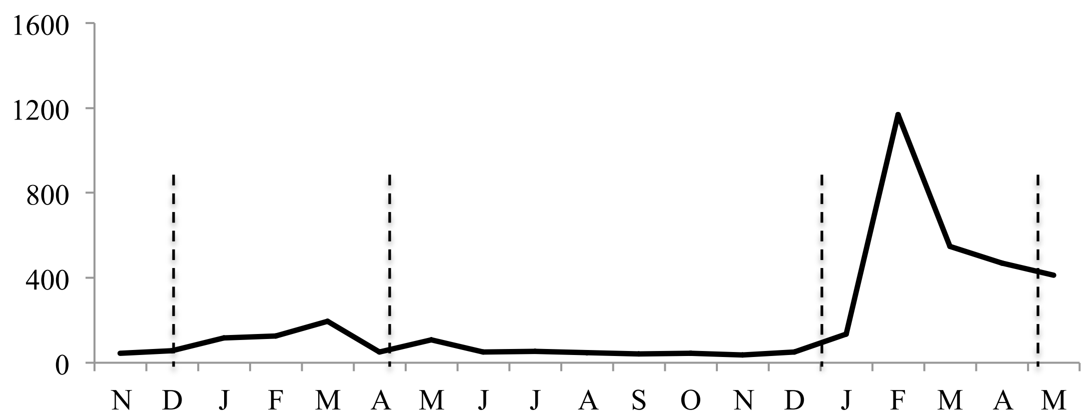
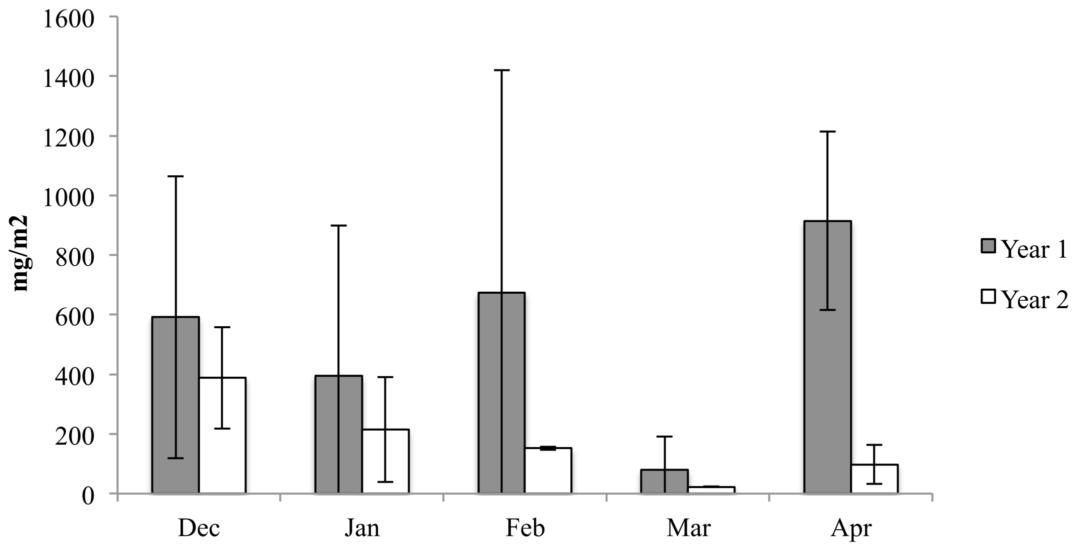
APPENDIX



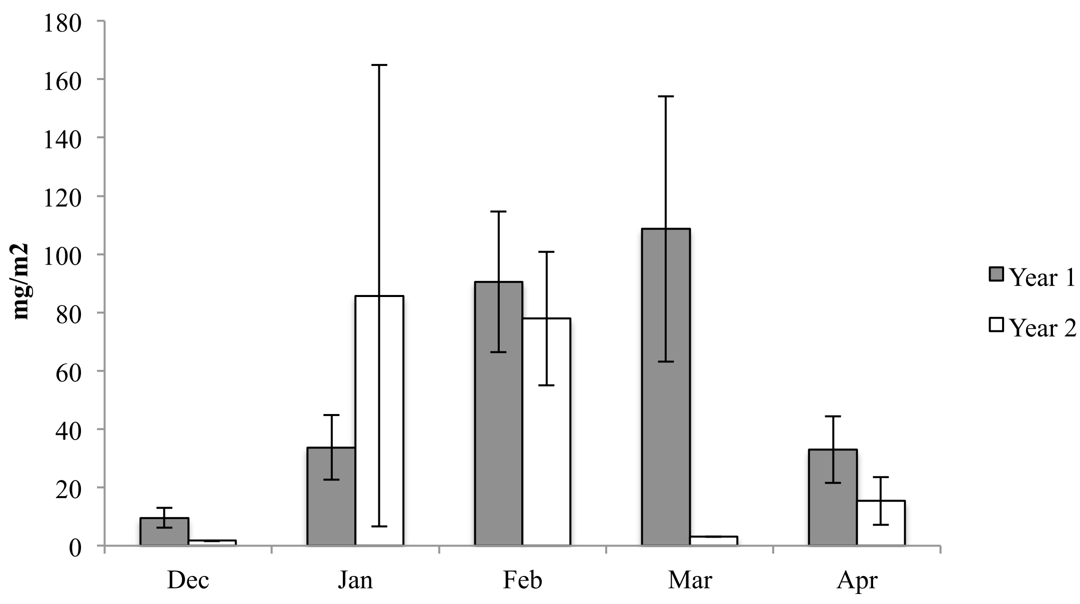
Appendix 1. Aerial view of Moody Forest Natural Area. Perimeter of Moody Forest is outlined in orange and the blue marker denotes the sampling area



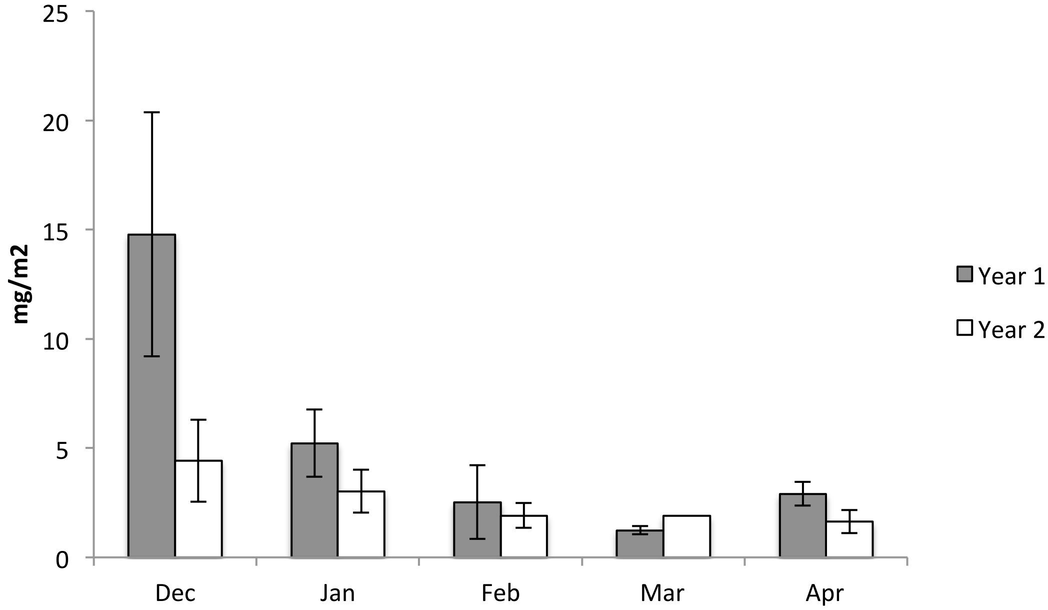
Appendix 2. Average monthly discharge at USGS gauge 02225000 near Baxley, Ga during the two sampling periods (denoted by black dashed horizontal bars).



Appendix 3. CBOM (±SE) standing stocks during drought (year 1) and flooding (year 2) at Moody Forest.



Appendix 4. FBOM (±SE) standing stocks during drought (year 1) and flooding (year 2) at Moody Forest.



Appendix 5. VFBOM (±SE) standing stocks during drought (year 1) and flooding (year 2) at Moody Forest.