POTENTIAL EFFECTS OF ALTERED HYDROLOGY ON FLOODPLAIN FORESTS OF THE SAVANNAH RIVER

by

LINDA S. LEE

(Under the Direction of Rebecca R. Sharitz)

ABSTRACT

Two studies investigated floodplain forest vegetation composition with respect to hydrology. The first study compared floodplain vegetation on the Savannah River below Thurmond Dam with vegetation on the minimally regulated Altamaha River. Some vegetation differences were present between rivers, but did not appear to have been caused by dam construction. The second study analyzed longitudinal patterns in floodplain forests. The proportion of wetland to upland vegetation generally increased downstream in the Savannah and Altamaha watersheds. A literature review revealed similar patterns in other watersheds, but found no relationship between vegetation and streamflow across studies.

INDEX WORDS: Floodplain forests, Dams, Regulated river, Altamaha, Savannah, Longitudinal gradient, Wetland vegetation, Flood Pulse Concept, River Continuum Concept

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LINDA S. LEE

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LINDA S. LEE

Major Professor:	Rebecca Sharitz
Committee:	Darold Batzer Lisa Donovan Mary Davis

Electronic Version Approved:

Maureen Grasso
Dean of the Graduate School
The University of Georgia
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GENERAL INTRODUCTION

Floodplains support characteristic floras, distinct form the surrounding uplands, and shaped by their river's characteristic flow regime and morphology. Stream power (Bendix 1999), stream gradient (Hupp 1982), disturbance (Sigafoos 1964, Polzin and Rood 2006), hydroperiod (Townsend 2001), geomorphic surface (Shelford 1954, Hupp 1986, Scott et al. 1997) and sediment particle size (Frye and Quinn 1979) have all been noted as important determinants of floodplain vegetation composition. Streamflow can be thought of as the key variable (Poff et al. 1997) influencing or related to all of these factors.

Flow regimes naturally vary across systems, and also change with dam construction and other anthropogenic river modifications. Regulation by dams typically dampens the natural variability in flows, as floodwaters are stored in reservoirs and gradually released during what would have been much drier months. Regulation can alter all characteristics of the flow regime: magnitude, duration, seasonality, rise rate, frequency, predictability; though diminished flood pulses are often the most salient change, since flood control is often one of the goals of river management. Natural variations in flow regime include variations in flood pulse characteristics driven by basin size and stream gradient. Even within a single river system, pulse characteristics change as contributing basin area increases and river gradient flattens. In the headwaters, flows are driven by local precipitation; catchments are small, and floods are short and unpredictable. Further downstream the contributing watershed is much larger, and floods are usually longer and more predictable.

On large rivers of the southeastern United States, floodplains are typically a complex mosaic of meander scrolls, oxbows, and other geomorphic surfaces of various ages, accumulated and continually reworked over thousands of years (Wharton et al. 1982). Relict channels, backswamps, and other wet areas support cypress-tupelo forests, and higher areas with shorter hydroperiods support a mixture of bottomland hardwoods. Most of these large rivers are subject to regulation; the Altamaha and Pee Dee are the only ones that remain relatively unmodified (Dynesius and Nilsson 1994).

How do variations in streamflow and inundation patterns, both natural and anthropogenic, influence vegetation in southeastern floodplain forests? The goals of this thesis are twofold: the first chapter is an investigation of the effects of river regulation on the floodplain forests of the Savannah River, using the free-flowing Altamaha as a reference; the second chapter investigates downstream changes in floodplain forest vegetation that may be due to natural downstream changes in flood regime.

CHAPTER 1:

RIVER REGULATION AND FLOOD PULSE RESTORATION

INTRODUCTION

Though traditionally viewed negatively by humans, floods are now recognized as critical to many organisms (Junk et al. 1989, Poff et al. 1997). Floods are thought to supplement limited in-channel primary productivity and enhance floodplain nutrient cycling (Junk et al. 1989). Floodwaters allow fish to access rich feeding and spawning grounds in the floodplains (Hoover and Killgore 1998), and may provide birds with a refuge from nest predators (Kennamer 2001). Their ecological influence extends even to the river's estuary (Livingston et al. 1997). Floods may also be important in the maintenance of some kinds of instream habitats, removing silt accumulations in shoals and gravel bars that may be important for fish spawning (Wu 2000). In floodplain forests, floods disperse seeds (Schneider and Sharitz 1988, Andersson et al. 2000), provide moisture and establishment sites for seedlings (Rood et al. 2005), eliminate competitors (Howe and Knopf 1991), and may be an important ecological sorting mechanism (Townsend 2001). However, dams, levees, and other constructions have altered flood patterns on many of the world's rivers. To date, over 45,000 large (>15m height) dams have been constructed on rivers worldwide (World Commission on Dams 2000). As research on the ecological impacts of dams has grown, so have efforts to restore at least semi-natural flows on some of these systems. A great deal of research is now being devoted to developing ecological flow prescriptions (e.g., Poff et al. 1997, Hughes et al. 2005, Rood et al. 2005, Pearsall et al. 2005, Arthington et al. 2006, Richter et al. 2006). Flow restoration has become an important conservation priority in North America, Australia, and South Africa (Hughes and Rood 2003), and more recently, in the European Union (e.g., Hughes 2003).

In 2002 the US Army Corps of Engineers (USACE), which owns and operates over 600 dams across the United States, and The Nature Conservancy launched a partnership to improve management on USACE rivers. The TNC-USACE Sustainable Rivers Project (SRP) is an adaptive management process in which initial recommendations are developed and then refined by monitoring ecosystem response. The process is described in greater detail in Richter et al. (2006). The Savannah River is currently one of eleven rivers in the SRP, and one of the few that has already reached the implementation and monitoring stage. This chapter is part of that work.

In 2003 an interdisciplinary panel was convened to develop an initial set of flow recommendations for Thurmond Dam, USACE's lowermost facility on the Savannah River. Initial implementation has focused on pulsed water releases in the spring, designed to mimic natural spring floods. Spring pulses have been released in 2004-2006; 2007 was a very dry year, and artificial flood releases were deemed inappropriate. Ecosystem monitoring focused on fish, macroinvertebrates, rocky shoals spider lily (*Hymenocallis coronaria*) reproduction, estuary salinity levels, and floodplain forest regeneration; this chapter describes the forest component.

Researchers in southeastern floodplain forests have long noted relationships between forest composition and inundation (e.g., Wharton et al. 1982, Leitman et al.

1984, Townsend 2001). It follows that anthropogenic changes in flow regime and floodplain inundation patterns can be expected to impact forest composition, probably through gradual patterns in species replacement as less-flood-adapted species begin to replace flood-tolerant ones.

The first goal of this research was to analyze forest demographics for response to post-dam changes in hydrology; the second goal was to monitor seedlings for effects of SRP prescribed flood pulses. The nearby, minimally regulated Altamaha River was used as a reference. It was expected that: 1) Savannah forests will exhibit lower compositional similarity across age cohorts than forests of the Altamaha if regulation has affected regeneration patterns; 2) vegetation in communities at different elevations on the floodplain are likely to experience different degrees of hydrologic change, and should show differing degrees of compositional change relative to those same communities on the Altamaha floodplains; 3) if artificial flood pulses are wetting the floodplain adequately, seedling composition on the Savannah should resemble the older (pre-dam) age cohorts as closely as Altamaha seedlings resemble older Altamaha trees.

STUDY AREAS

The Savannah and Altamaha are both seventh-order alluvial rivers that flow from the base of the Appalachian Mountains to the Georgia coast. The Savannah is formed by the confluence of the Tugaloo and Seneca rivers; the Altamaha is formed by the Oconee and Ocmulgee. Their watersheds adjoin in the headwaters, and they are separated by approximately 100km when they meet the Atlantic.

The Savannah is a highly modified river (Dynesius and Nilsson 1993, Wrona et al. 2007). Among the major modifications, three large dam-and-reservoir systems have been constructed on the main stem of the river. The first, Thurmond, was completed in 1954. Dam construction has caused several modifications to the flow regime. Reservoir storage and gradual release of water has dampened overall variability; floods are smaller and less frequent, and summer low flows are higher (Meyer et al. 2003). Other modifications to the Savannah have included dredging and straightening for barge traffic. TNC and USACE are currently working to restore some aspects of pre-dam hydrology; experimental spring flood pulses have been released during 2004-2006. USACE may also have plans to reconnect some of the cutoff meanders (Hale and Jackson 2003).

The Altamaha River is a moderately impacted system (Dynesius and Nilsson 1993). Although two impoundments have been constructed on the Oconee River and one on the Ocmulgee, these reservoirs are not managed for flood control. Effects on peak flows appear minimal (Fig. 1.1). The Altamaha was never significantly modified for shipping. It contains the longest free-flowing stretch of river on the Atlantic coast (TNC 2005), and is one of The Nature Conservancy's 75 Last Great Places.

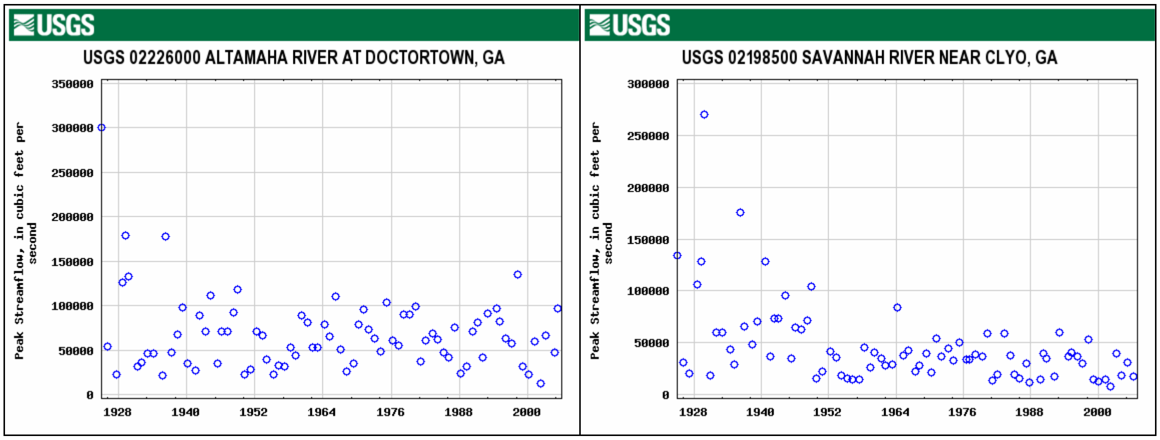

Figure 1.1. Peak flows on the Altamaha and Savannah rivers, 1928-2000. Hydropower dams were constructed in both watersheds in the early 1950s, but only the Savannah hydrograph shows a clear decrease in peak flows.

Three sites were chosen along the non-tidal coastal plain reaches of both rivers (Fig. 1.2). The uppermost site on the Savannah River was located on the Department of Energy's Savannah River Site (SRS). The middle site was located at Tuckahoe Wildlife Management Area, managed by the Georgia Department of Natural Resources. The lower site was at Webb Wildlife Management Area, managed by the South Carolina Department of Natural Resources. The uppermost Altamaha site was at Moody Forest Natural Area, which is owned by TNC. The middle site, Beards Bluff, is privately owned. The lower site was in Penholoway Swamp Wildlife Management Area, recently acquired by the Georgia Department of Natural Resources.

Figure 1.2. Study areas and impoundments on the Altamaha (GA) and Savannah (GA-SC border) rivers. Hartwell, Russell, and Thurmond are the three reservoirs upstream on the Savannah River. The dams on the tributaries of the Altamaha are also indicated.

METHODS

At each site, transects were established that spanned one side of the floodplain from channel to upland. Tree and seedling data were collected along the transects. Demographic analyses of the standing forest were used to assess the potential effects of regulation on Savannah River floodplains. Comparisons with Altamaha forests allowed us to separate trends from the results of regional influences. Seedling data were used to evaluate potential effects of artificial flood pulses on seedling establishment. Environmental characterization included soils and hydrology.

Environmental characterization

Hydrologic analysis of the sites was conducted by M. Davis of TNC. In brief, floodplains were surveyed for elevation, and a well and staff gauge used to correlate river stage data with conditions on the floodplain. Two to three elevation transects and one well were established per site. Long-term data from USGS were used to model inundation at points along the transects. Hydrologic data were compared to vegetation composition by indirect gradient analysis based on a non-metric multidimensional scaling (NMDS) ordination of plot vegetation. The hydrologic parameters for each plot were number of days flooded; minimum, maximum, and average number of consecutive flood days; and minimum, average, and maximum depth of flooding. Following Townsend (2001), data were summarized for 10th percentile (driest), median, and 90th percentile (wettest year) averages. The available hydrologic data spanned 1989-2006. Years with more than 14 consecutive days of missing data were omitted.

Soil samples were taken from four locations per site, two in swamp forest and two in bottomland hardwood forest. At each location three 20-cm cores were taken with an Oakfield soil probe, and the three cores bulked. Soils were analyzed for texture, Ca, K, Mg, Mn, Zn, P, C, N, and pH. Samples were compared using NMDS.

Vegetation sampling

Trees were sampled in 20x50m Carolina Vegetation Survey-style plots (Peet et al. 1998) located every ~100m along the elevation transects, oriented perpendicular to the transect line. When necessary, plots were shifted to avoid sampling across obvious topographic or compositional gradients. Within each plot all trees and saplings >1.4m in height were identified and measured for diameter at breast height (DBH), at the standard height of 1.4m. Species with swollen bases (*Taxodium distichum* and *Nyssa* spp.) were measured above the swell. DBH of secondary stems for multi-stemmed individuals were recorded and included in basal area calculations, but only the largest stem was used in all other analyses. Additionally, 10 - 15 trees were cored at each of the Savannah sites to provide general size/age relationships for pre-dam/post-dam cohort designations. Sixteen species were cored, with individual stems ranging from 19 - 60.5cm DBH (Appendix 4).

Seedlings were sampled in $30m^2$ circular subplots within the 20x50m vegetation plots. One seedling subplot was located at the 30m mark of each vegetation plot. All tree seedlings <30cm tall were recorded. Seedlings were counted during July - August 2006 and July - September 2007.

Vegetation assemblage assignments

Plots were assigned to forest types using a divisive hierarchical clustering algorithm. Relative basal area (RBA) was used for this analysis since RBA gives more weight to larger trees, ensuring that Savannah plot assignments were based mostly on pre-dam vegetation.

Demographic analysis

Table 1.1. Cohort designations used for the demographic analyses.

Younger	Older	Species
≤ 2.5cm	> 2.5cm	all
≤ 2.5cm	> 2.5cm	canopy
≤ 10cm	>10cm	canopy
2.5-10cm	>10cm	canopy
≤ 10cm	> 40cm	canopy
2.5-10cm	> 40cm	canopy

Forest demographics were used to determine whether Savannah floodplain forests are changing in response to river regulation. Savannah forests should exhibit lower compositional stability across age cohorts than Altamaha forests if regulation has been influencing regeneration patterns. Trees were grouped into two cohorts, approximating pre-dam and post-dam establishment, and the compositional similarity between the two cohorts compared. Altamaha forests were used as a reference. Compositional stability on both rivers was evaluated at the plot level and at the community level. Diameter class was used as a proxy for age cohort. General size/age estimates were based on 41 trees cored at the Savannah sites.

Analyses were repeated using six different cohort designations to determine whether results were dependent on the choice of size classes (Table 1.1). The 2.5cm comparison was modeled after a demographic analysis by Rice and Peet (1997) on the Roanoke River floodplain in North Carolina; although it does not approximate the date of dam construction, this comparison permits inclusion of all species. Understory species were excluded from other comparisons since they are naturally uncommon in the larger diameter classes. Designation as understory or canopy was subjective, and was based on previous field experience on the Congaree River, South Carolina. For species with data available, our designations were generally well supported by the growth rates reported from floodplains in northern Florida by Darst and Light (2008); understory species had the slowest growth rates. A species list with designations is provided in Appendix 1.

Four measures of compositional similarity were used to compare tree size (age) cohorts. Two were traditional vegetation indices: percent similarity (also known as Bray-Curtis), and the Jaccard Index of Similarity. Two additional indices addressed vegetation change with respect to hydrologic conditions. These were created from the National Wetland Inventory (NWI) wetland indicator classifications (Reed 1996), and the Floodplain Species Category (FSC) classifications of Darst and Light (2008). All comparisons were restricted to plots with at least five stems in both classes.

NWI indicators are based on frequency of occurrence in wetlands versus uplands (Table 1.2). Ratings do not address hydroperiod length; no distinction is made between temporary and permanent wetlands. Numeric equivalents were used for this study.

Table 1.2. NWI and FSC classification systems. National Wetland Inventory wetland indicator status (Reed 1996) and Floodplain Species Category (Darst and Light 2008).

Status	Value	NWI Indicator Descriptor
OBL	1	Obligate Wetland (OBL). Almost always occur in wetlands (est. probability >99%)
FACW	2	Facultative Wetland (FACW). Usually occur in wetlands (67%-99%)
FAC	3	Facultative (FAC). Equally occur in wetlands or uplands (34%-66%).
FACU	4	Facultative Upland (FACU). Occasionally occur in wetlands (1%-33%).
UPL	5	Obligate Upland (UPL). Less than 1% for region specified.
FSC	**FSC Descriptor**	
1	More dominant in swamps	
2	More dominant in low bottomland hardwood	
3	More dominant in high bottomland hardwood	
4	Atypical bottomland hardwood or upland sp.	

The FSC classifications are specific to southeastern floodplains, and were intended to reflect tolerance to flooding and saturated conditions (Darst and Light 2008). Species category assignments were based on their dominance at different elevations on the Apalachicola River floodplain.

Stems on each plot were divided into two size cohorts, and species relative abundances or species presence calculated within each cohort. Percent similarity was calculated as the sum of the minimum shared RA for all species. Jaccard IS was calculated as the number of shared species divided by the total number of species in both cohorts. For NWI and FSC, each species RA was multiplied by the species NWI or FSC. The resulting values were then summed for each cohort to give an average NWI or FSC score, weighted by RAs. The score for the younger cohort was subtracted from the older to get the change in NWI (Δ NWI) or FSC (Δ FSC) for each plot. A negative Δ NWI or Δ FSC indicated the younger cohort contained more plants common to drier habitats.

Because many plots had <5 stems in one class for some comparisons, all analyses were repeated using whole vegetation communities instead of plots as the unit of analysis. Within each research site, all plots of the same community type were pooled. Results are reported for both plot-based and community-based analyses.

Mean between-cohort similarity was compared by river with a t-test. In addition, two-way ANOVA was used to look for an interaction between river and vegetation community, since changes in hydrology are likely to affect different parts of the floodplain differently. ANOVA was conducted only on the 2.5cm data, which had the greatest number of plots with ≥ 5 stems in each class, and high and low swamps were lumped to provide adequate sample sizes for each category. With the use of both of these statistical methods it should be recognized that our plots are only subsamples of the true unit of study (river); interspersion of treatments is impossible. Although our plots are not independent samples, it is hoped that since floodplains are naturally heterogeneous environments, intrinsic covariation will be minimal.

Seedling analysis

Seedlings were compared to tree cohorts using the same four indices of compositional similarity described above: percent similarity, Jaccard IS, Δ FSC, and Δ NWI. We expected that if the artificial flood pulses were effective, seedling composition on the Savannah should closely resemble that of the pre-dam canopy. Altamaha sites were used as a reference. As with the demographic analysis, comparisons were repeated using several different size classes of trees. By comparing seedlings to several different tree cohorts we hoped to gain a better understanding of the temporal dynamics in the forest. As a conservative measure, trees difficult to identify to species as small seedlings (*Quercus*, *Carya*, *Fraxinus*) were lumped for the percent similarity and Jaccard analyses. However, since FSC and NWI values cannot be assigned at the generic level, many seedlings were eliminated from those analyses. So many data were lost that Δ FSC and Δ NWI were deemed unreliable, and are not included here.

The 2006 and 2007 seedling cohorts were compared to each other in a NMDS ordination. For each site, plot data from both years were placed in a single ordination, and vectors were drawn to track each plot's movement in ordination space from 2006 to 2007. Vectors were then analyzed subjectively by visual inspection to determine whether any overall trends were present, evident as general concordance among the vectors.

RESULTS

Environmental characterization

The initial ordination of site soils revealed one extreme outlier (Beards Bluff swamp #1). That sample was removed, and the analysis re-run. NMDS returned a 2-D solution with final stress of 17.74 and a final instability of 0.00 (Fig. 1.3). Axis 1 is correlated with calcium (r=.92), magnesium (r=.85), pH (r=.80) and potassium (r=.76). Axis 2 is negatively correlated with nitrogen (r=-.86), carbon (r=-.83), and clay (r=-.81), and positively correlated with sand (r=.69) and silt (r=.57). A multi-response permutation procedure (MRPP), which tests distance within groups against distance between groups, indicated that Altamaha and Savannah floodplain soils differ significantly (p=0.0058). The rivers separate mostly on Axis 2, with higher clay and organic content (C and N) at Savannah sites, and higher sand and silt at Altamaha sites. Soil chemical properties were similar between the rivers (Table 1.3). The Beards Bluff sample was probably an outlier because of its texture (94% sand, compared to 56% for the next highest site, and an average of 28%). This sample also had the lowest C and N.

The indirect gradient analysis of vegetation composition and hydrology indicated that most flood variables were positively correlated with both vegetation ordination axes, as were swamp species (*Taxodium distichum*, *Nyssa aquatica*, *N. ogeche*, *Fraxinus caroliniana*). No single metric performed exceptionally well (most r=0.4-0.6; highest r=.72), and a few, such as maximum depth in wettest (90th percentile) years, showed almost no correlation. Most of the correlation seemed to be driven by the strong difference in hydrology and vegetation between swamp and bottomland hardwood forests. Results were similar whether vegetation data were RA or RBA.

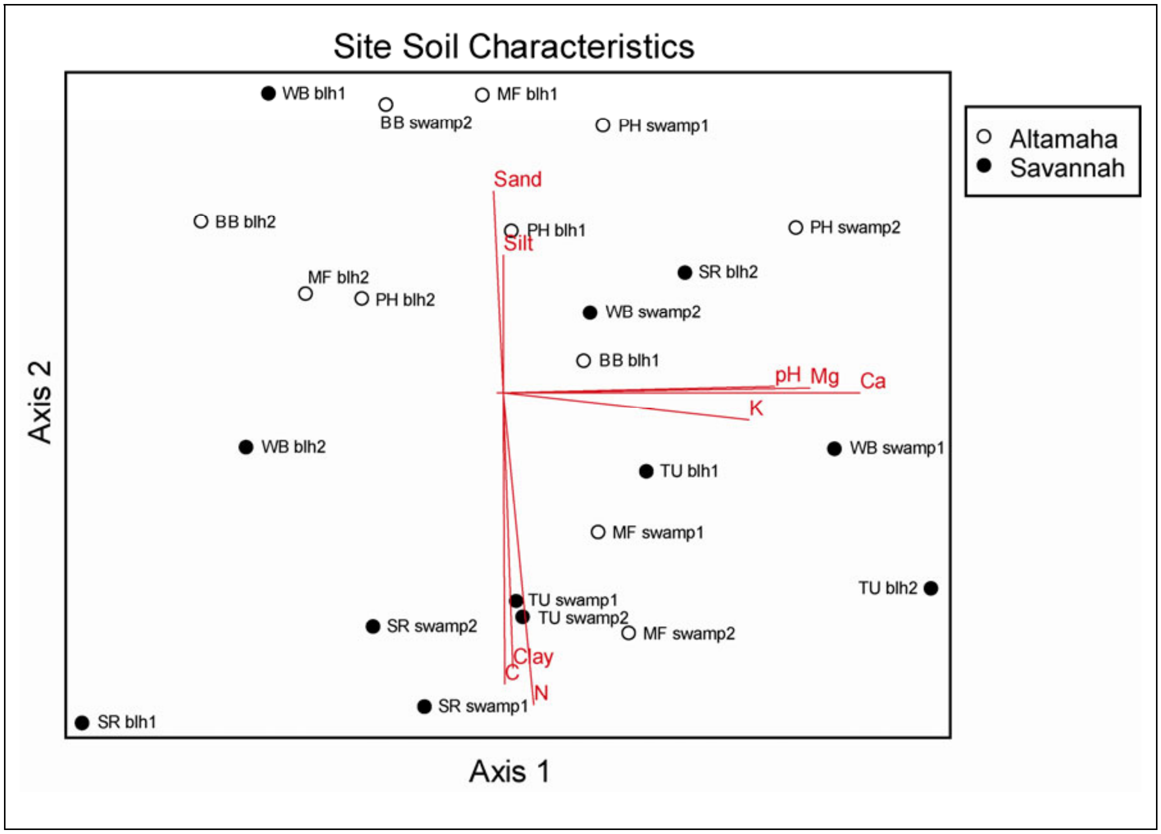

Figure 1.3. NMDS ordination of site soils. Axis 1 is positively correlated with Ca, K, Mg, and pH. Axis 2 is positively correlated with sand and silt, and negatively correlated with clay, C, and N. BB=Beards Bluff; MF=Moody Forest; PH=Penholoway; SR=SRS; TU=Tuckahoe WMA; WB=Webb WMA. Blh=bottomland hardwood forest; swamp=swamp forest.

Table 1.3. Physical and chemical properties of floodplain soils by forest type. Standard deviations are enclosed in parentheses. Cation concentrations are kg/ha.

	pH	Ca	K	Mg	Mn	P	Zn	%N	%C	%Sand	%Silt	%Clay
Altamaha BLH	4.68 (0.24)	955.23 (355.90)	83.48 (14.52)	207.46 (51.72)	109.89 (63.93)	10.64 (4.32)	12.30 (3.45)	0.12 (0.03)	1.63 (0.29)	32.4 (10.04)	22.33 (4.08)	45.27 (12.18)
Altamaha Swamp	4.89 (0.20)	1191.79 (496.81)	93.50 (33.02)	212.58 (92.55)	86.82 (43.14)	17.24 (9.34)	15.58 (7.82)	0.13 (0.07)	1.76 (1.00)	41.07 (33.66)	17.00 (9.53)	41.93 (26.33)
Savannah BLH	4.95 (0.34)	915.73 (574.08)	80.74 (33.53)	214.49 (110.61)	274.08 (190.00)	9.95 (1.66)	7.48 (3.62)	0.18 (0.06)	2.77 (1.24)	28.67 (11.41)	19.17 (8.79)	52.17 (12.88)
Savannah Swamp	4.91 (0.32)	1194.54 (404.56)	96.40 (6.25)	206.94 (102.38)	99.04 (75.78)	19.30 (7.04)	7.25 (1.18)	0.17 (0.04)	2.57 (0.99)	9.33 (9.32)	15.53 (2.07)	75.13 (10.30)

General forest characterization

Cluster analysis yielded four forest types, designated high bottomland hardwood, low bottomland hardwood, high swamp, and low swamp (Fig. 1.4). High bottomland hardwoods were dominated by *Liquidambar styraciflua*, *Quercus* spp., *Carpinus caroliniana*, *Ulmus americana*, and others. Low bottomland hardwoods were dominated by *Quercus* spp., *Liquidambar styraciflua*, *Nyssa sylvatica*, *Carya aquatica*, and others. High swamps were dominated by *Quercus lyrata*, *Nyssa ogeche* (Altamaha only), *Carya aquatica*, *Fraxinus caroliniana*, and others. Low swamps were dominated by *Nyssa aquatica* and *Taxodium distichum*.

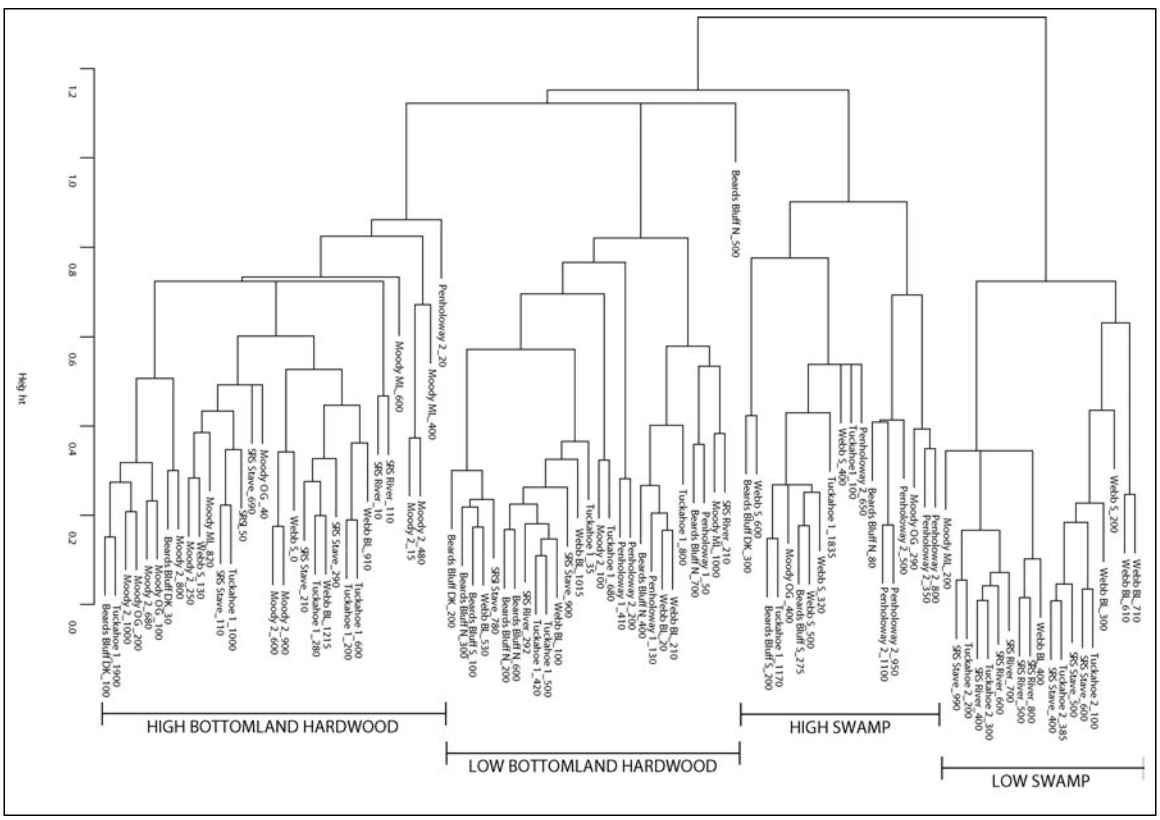

Figure 1.4. Cluster diagram of plots with the resulting vegetation designations. Plot data were species RBAs.

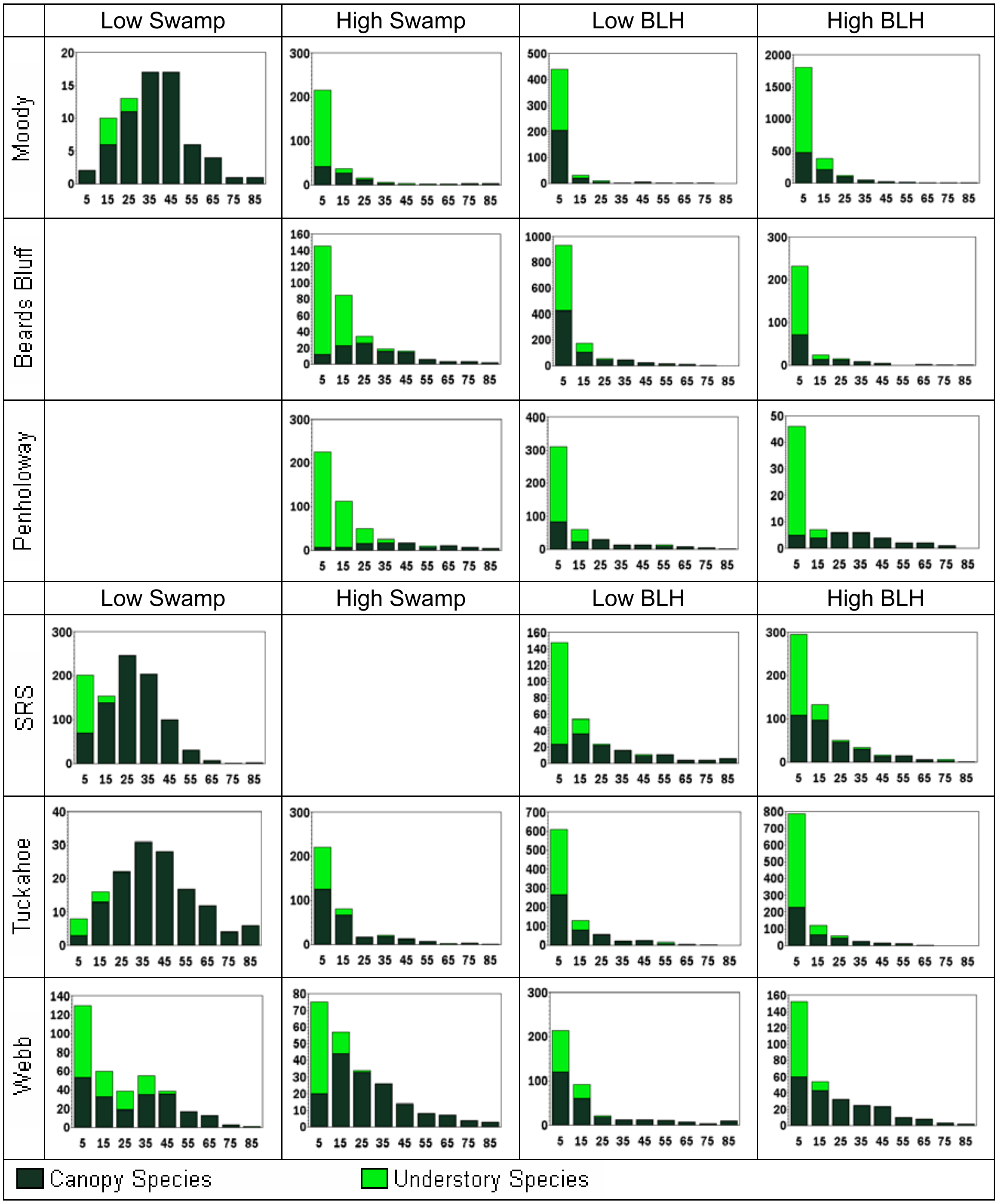

Figure 1.5. Tree demographics by site and forest type. Y-axis represents the number of stems in each diameter class; x-axis values are the midpoints of each class. The 80-90cm group also includes all stems with DBH > 90cm. Top three sites are Altamaha; bottom three sites are Savannah. Sites are also arranged in order from upstream to downstream.

Low swamps exhibited different demographic patterns from other forest types (Fig. 1.5). Regeneration in these habitats appears limited, as might be expected for areas that remain inundated for long periods (Kozlowski 1997). When only canopy species are considered, some high swamps also show limited regeneration, though the understory still shows a typical reverse-J demographic distribution, characteristic of forests with continual recruitment.

Savannah and Altamaha floodplains differed most strikingly in the character of their swamp forests. Even from field observations it was evident that most Altamaha swamp plots tended to have sandier soils and more shrubs than swamp forests on the Savannah. Both observations were supported by the data. Only one Altamaha plot grouped with the low swamps on the Savannah in the cluster analysis (Fig. 1.4). This plot, at Moody Forest, was located in a deep slough with a high clay/silt content similar to that of the low swamps on the Savannah.

As a whole, Altamaha sites tended to have greater abundance of understory trees than Savannah sites. Just three major understory species (*Carpinus caroliniana, Ilex decidua*, and *Fraxinus caroliniana*) accounted for 45-54% of all stems at Altamaha sites (Fig. 1.6). Understory species were also abundant at Tuckahoe (35% RA), but less important at the other two Savannah sites. In terms of relative basal area, understory species are only minor components at all sites (Fig. 1.7).

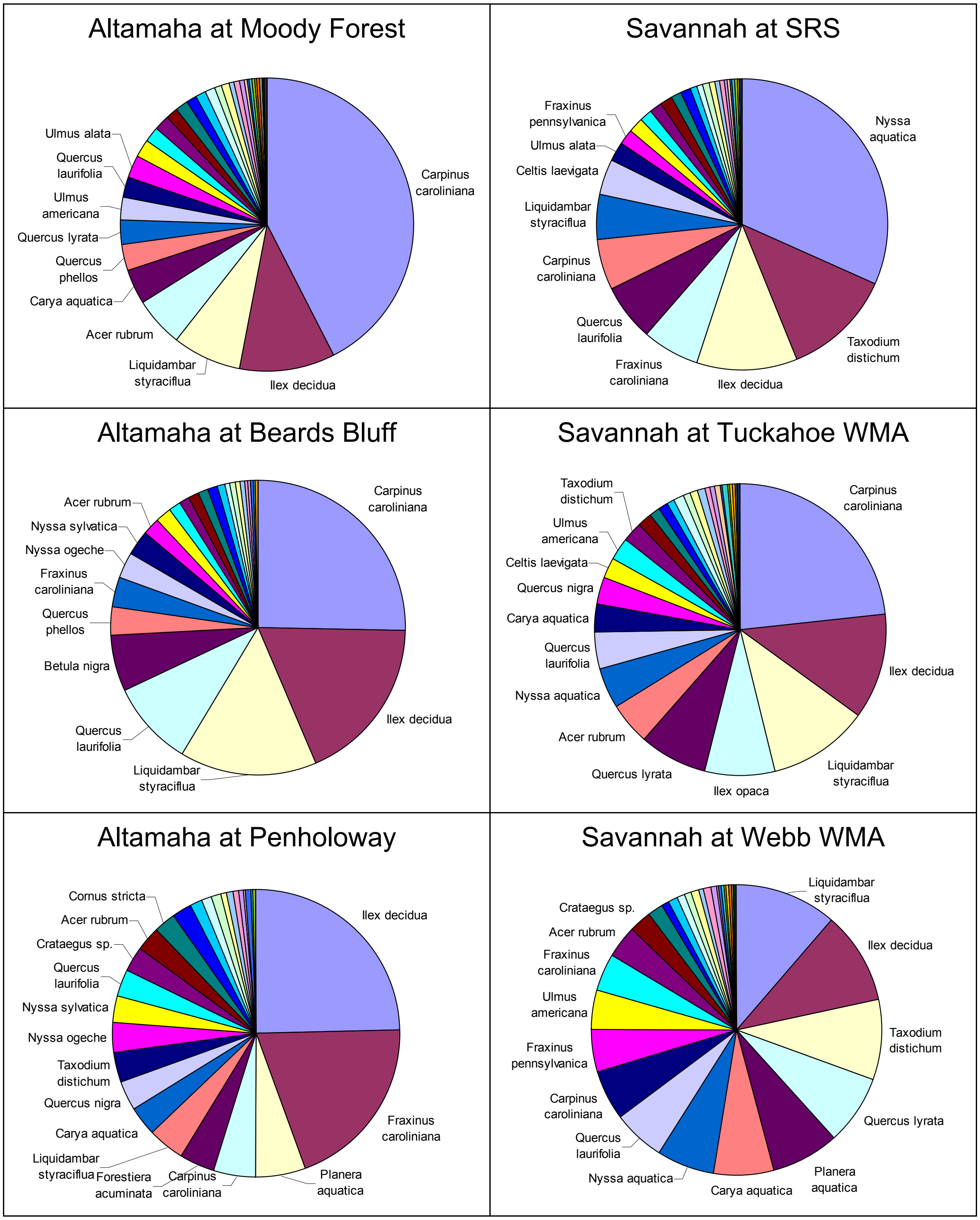

Figure 1.6. Species importance by relative abundance. Understory species include *Ilex decidua*, *Fraxinus caroliniana*, *Planera aquatica*, *Forestieria acuminata*, and *Crataegus* spp. A list of species RAs is provided in Appendix 2.

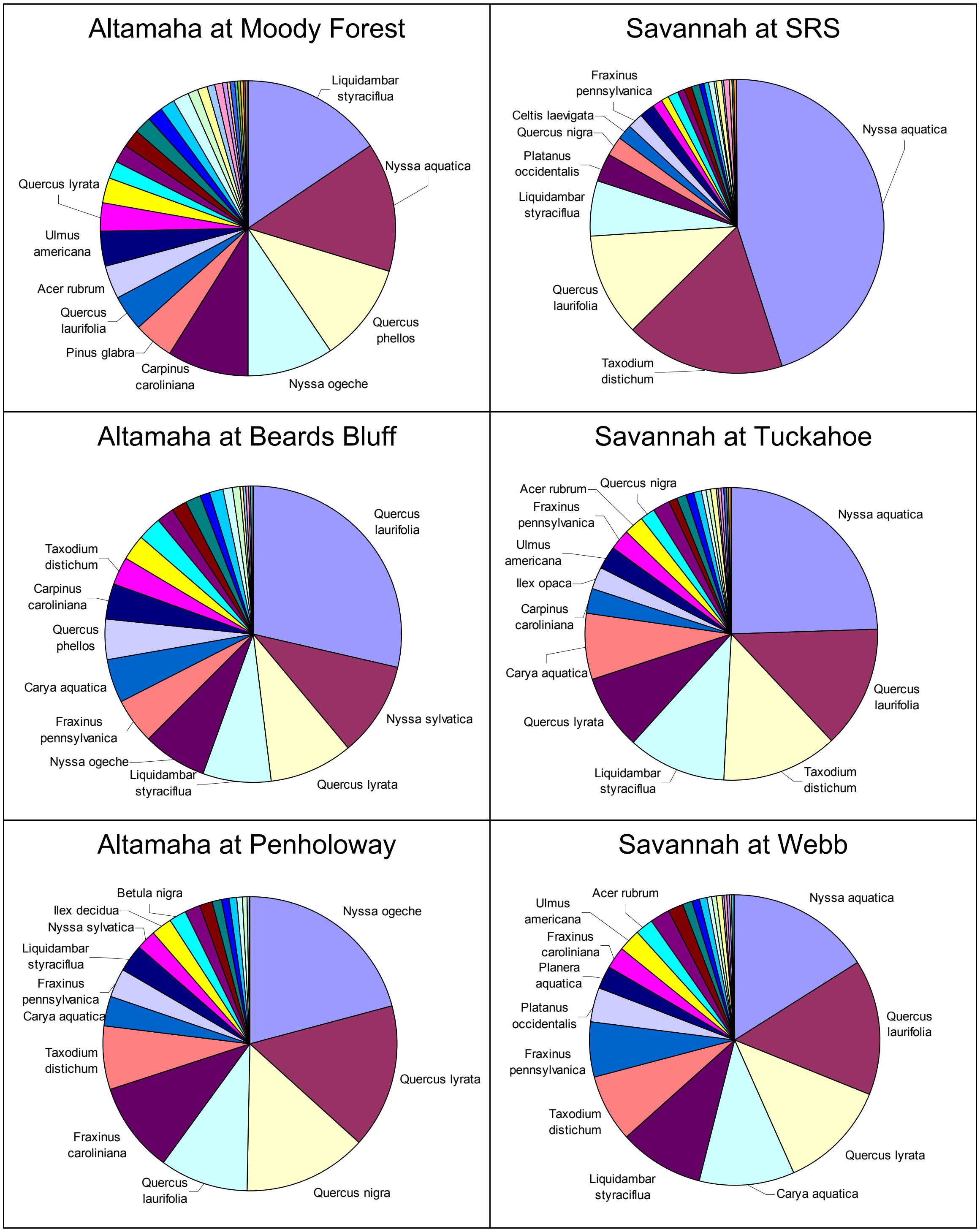

Figure 1.7. Species importance by relative basal area. A list of species RBAs is provided in Appendix 2.

Demographic analysis

Some analyses indicated lower similarity between size classes on the Savannah, as expected, but the trend was not robust. In the plot-based analysis, three of the four indices (percent similarity, Jaccard, and FSC) were significantly different between rivers, but the effect was highly dependent on the size classes (age cohorts) compared. For the Jaccard IS and one of the percent similarity comparisons, the trend was actually opposite the expected (Table 1.4). Initially the ≤2.5cm DBH versus > 2.5cm DBH comparison for percent similarity appears to give strong support to the predictions of lower similarity on the Savannah, but it actually seems to be due to a greater relative abundance of understory species on the Altamaha. When these species are excluded, results are not significant, even if only the plots with enough stems to qualify for both analyses are used.

Table 1.4. Within-plot cohort similarity on the Altamaha and Savannah floodplains. Asterisks denote means that are significantly different (* = p<0.05, ** = p<0.01, *** = p<0.001). Green indicates difference is in the direction predicted; red indicates opposite.

A. Compositional indices		**Percent Similarity**		**Jaccard IS**		**Number of Plots**	
YOUNGER (DBH)	OLDER (DBH)	Altamaha	Savannah	Altamaha	Savannah	Altamaha	Savannah
≤ 2.5cm	>2.5 cm	**55.00*** **	**35.11*** **	35.36	30.59	37	35
Canopy species only							
≤ 2.5cm	>2.5 cm	50.06	42.96	39.97	34.33	13	16
≤ 10cm	>10cm	48.75	45.20	48.07	49	27	36
2.5-10cm	>10cm	49.76	47.71	50.05	48.06	23	35
≤ 10cm	> 40cm	27.08	33.66	**21.15***	**31.16***	11	33
2.5-10cm	> 40cm	**20.75***	**35.57***	**15.70****	**30.72****	9	32
B. Wetland indices		**Δ NWI**		**Δ FSC**		**Number of Plots**	
YOUNGER (DBH)	OLDER (DBH)	Altamaha	Savannah	Altamaha	Savannah	Altamaha	Savannah
≤ 2.5cm	>2.5 cm	-0.0159	-0.1260	-0.21524	0.018083	37	35
Canopy species only							
≤ 2.5cm	>2.5 cm	0.0751	-0.1226	-0.0973	-0.0706	13	16
≤ 10cm	>10cm	0.1193	-0.1405	0.0640	-0.0262	27	36
2.5-10cm	>10cm	0.0712	-0.1182	0.0572	-0.0058	23	35
≤ 10cm	> 40cm	-0.0559	-0.1500	**0.3215***	**-0.0990***	11	33
2.5-10cm	> 40cm	-0.1332	-0.1249	**0.3627***	**-0.0702***	9	32

In the community-level analysis, the 2.5cm comparison indicated significantly lower percent similarity on the Savannah, with or without understory species. When only the largest and smallest trees are compared, the trend reverses (Table 1.5). Two NWI comparisons were significant; both used 10cm as the lower bound for the large size class. Jaccard and FSC show no significant differences between the rivers for any size class.

Table 1.5. Within-community cohort similarity on the Altamaha and Savannah floodplains. In this analysis each vegetation community within each site was considered one unit of analysis, in order to give a larger sampling area than that afforded by single plots. Asterisks denote means that are significantly different (* = p<0.05, ** = p<0.01, *** = p<0.001). Green indicates difference is in the direction predicted; red is opposite.

A. Compositional indices		**Percent Similarity**		**Jaccard IS**		**Number of Plots**	
YOUNGER (DBH)	OLDER (DBH)	Altamaha	Savannah	Altamaha	Savannah	Altamaha	Savannah
≤ 2.5cm	>2.5 cm	**56.19****	**36.57****	46.5782	36.9530	9	11
Canopy species only							
≤ 2.5cm	>2.5 cm	**60.07***	**45.90***	52.8788	38.9090	5	8
≤ 10cm	>10cm	48.91	56.32	54.4372	63.2833	9	11
2.5-10cm	>10cm	50.46	58.45	57.8517	62.1841	8	11
≤ 10cm	> 40cm	**30.98***	**47.96***	36.0245	44.8849	9	11
2.5-10cm	> 40cm	**32.13***	**49.08***	37.1539	44.6086	8	11
B. Wetland indices		**Δ NWI**		**Δ FSC**		**Number of Plots**	
YOUNGER (DBH)	OLDER (DBH)	Altamaha	Savannah	Altamaha	Savannah	Altamaha	Savannah
≤ 2.5cm	>2.5 cm	0.1140	-0.0796	-0.1076	0.1092	5	8
Canopy species only							
≤ 2.5cm	>2.5 cm	0.1140	-0.0796	-0.1076	0.1092	5	8
≤ 10cm	>10cm	**0.2330***	**-0.1340***	0.1761	-0.0383	9	11
2.5-10cm	>10cm	**0.1659***	**-0.1337***	0.1413	-0.0686	8	11
≤ 10cm	> 40cm	0.1351	-0.1454	0.1759	-0.0856	9	11
2.5-10cm	> 40cm	0.0407	-0.1451	0.0810	-0.1159	8	11

ANOVA indicated that within-plot percent similarity differed significantly between rivers ($p < .0001$, $F=20.03$, d.f.=1) and among forest types ($p = .0012$, $F = 7.48$, d.f. = 2), but the interaction was not significant. A posthoc means separation test (Tukey's HSD) indicated that swamps on both rivers have inherently lower cohort similarity than either high or low bottomland hardwood forests.

Seedlings

The total number of seedlings was lower in 2007 than in 2006 on both the Savannah and the Altamaha floodplains, though the reduction was greater on the Savannah. Altamaha seedling abundance in 2007 was 76% of abundance the previous year; Savannah seedling abundance in 2007 was 64% of that in 2006. Within individual plots, the majority of Savannah plots (38 to 14) had higher abundances in 2006, while about half of the Altamaha plots had greater abundances in 2006. Beards Bluff, the privately owned site, had been logged when we returned in summer of 2007; only the four recoverable seedling plots are included here.

On the Altamaha, Penholoway high swamps had very high seedling abundances both years, as did one of the Beards Bluff high swamp plots (Fig. 1.8) On the Savannah, Tuckahoe low swamps had noticeably higher regeneration during the drier conditions in 2007, though low swamps at Webb and SRS did not show this trend. Seedling abundances in Webb low swamps were much greater in 2006, and moderately greater in SRS low swamps. In general, the upper sites on both rivers, Moody Forest and SRS, both had relatively low numbers of seedlings both years, while the lower sites had the highest abundances. (Although limited data were available for Beards Bluff in 2007, plot seedling abundances in 2006 were within comparable range to Tuckahoe, with the exception of one plot.)

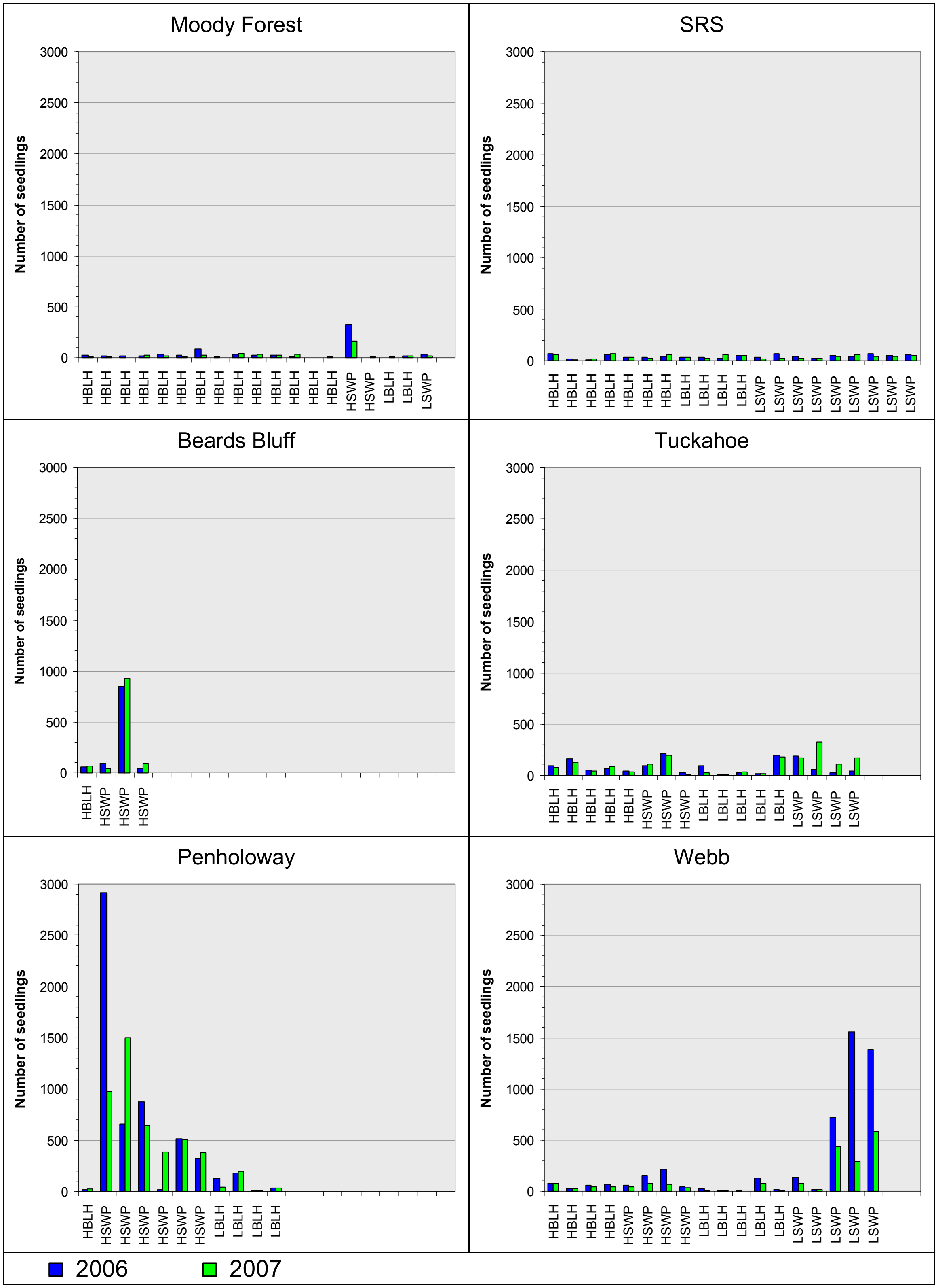

Figure 1.8. Seedling abundance in 2006-2007. Plots are labeled by their vegetation types. HBLH=high bottomland hardwood; LBLH=low bottomland hardwood; HSWMP=high swamp; LSWP=low swamp.

For most sites, seedling trajectories in the NMDS did not appear to present unified patterns (Fig. 1.9). Webb WMA was the only site in which a general trend was evident. The majority of species in Webb plots were present in both years, but abundances were lower in 2007. Webb plots with nonconforming vectors had greater abundances of seedlings in 2007 than in 2006, unlike the other plots at this site.

For most comparisons, Savannah seedlings were significantly more similar to the forest than Altamaha seedlings were. This was true for both the 2006 and 2007 cohorts, and for both the quantitative (percent similarity) and presence/absence (Jaccard) indices (Table 1.6). Similarity between Savannah seedlings and smaller (<10cm) trees was much lower than for other Savannah cohorts, but not statistically different from the Altamaha. The patterns were similar for the community-level comparisons, although most of the differences were not statistically significant.

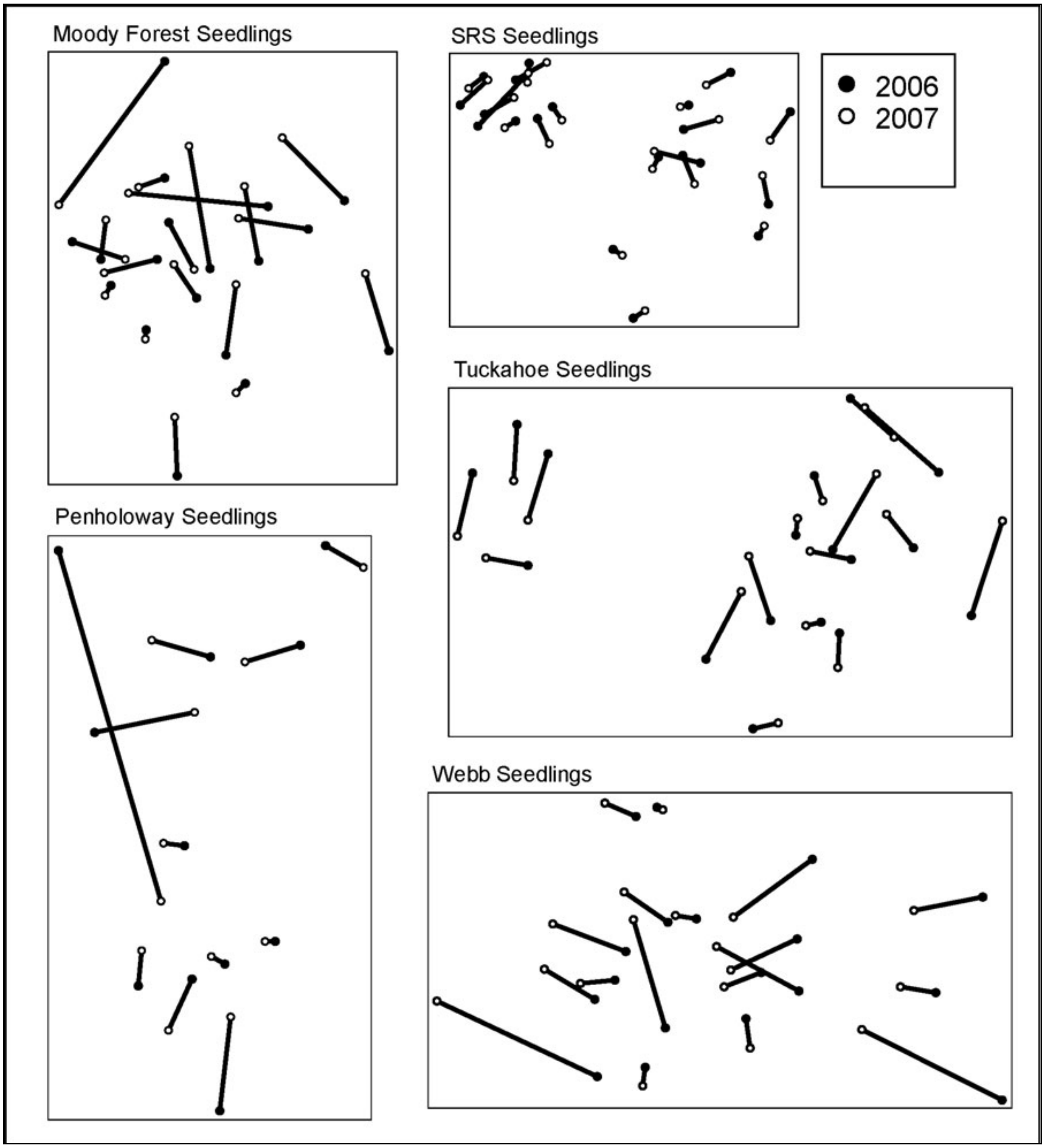

Figure 1.9. NMDS ordination of seedling plots showing trajectories from 2006-2007. Savannah River sites are on the right. One Altamaha site (Beards Bluff) was not included because it was logged in winter 2006.

Table 1.6. Seedling-tree similarity on the Altamaha and Savannah floodplains. Asterisks denote means that are significantly different (* = p<0.05, ** = p<0.01, *** = p<0.001). Red indicates difference is opposite expected. Canopy denotes that only canopy species of trees and seedlings were included.

2006 Seedlings	**Percent Similarity**		**Jaccard IS**		**Number of Plots**	
Tree size cohort	Altamaha	Savannah	Altamaha	Savannah	Altamaha	Savannah
All spp., all DBH	**33.99****	**46.25****	**40.74***	**48.50***	39	55
All spp. DBH < 2.5cm	26.16	22.35	28.96	26.55	32	35
All spp. <10cm	29.03	29.47	34.27	40.26	37	50
Canopy spp., all DBH	**35.70*****	**51.51*****	**42.51****	**53.53****	35	55
Canopy spp. < 2.5cm	34.06	34.78	41.34	40.38	13	19
Canopy spp. <10cm	33.10	39.56	42.85	48.73	21	37
Canopy spp. <20cm	**33.78***	**46.41***	42.83	50.42	27	52
Canopy spp. >10cm	**34.71*****	**51.23*****	**39.87*****	**55.17*****	35	55
Canopy spp. >20cm	**35.42****	**49.68****	**38.29****	**51.40****	35	55
Canopy spp. >40cm	**30.38***	**44.36***	**27.79*****	**41.68*****	21	50
2007 Seedlings	**Percent Similarity**		**Jaccard IS**		**Number of Plots**	
Tree size cohort	Altamaha	Savannah	Altamaha	Savannah	Altamaha	Savannah
All spp., all DBH	**37.95***	**47.31***	**40.8**	**46.79**	30	54
All spp. DBH < 2.5cm	29.18	22.48	31.31	27.32	27	35
All spp. <10cm	30.88	33.21	33.85	40.65	29	49
Canopy spp., all DBH	**39.73***	**51.08***	**42.29***	**53.42***	26	53
Canopy spp. < 2.5cm	39.29	34.03	48.99	40.7	8	19
Canopy spp. <10cm	36.53	39.74	41.02	47.87	15	36
Canopy spp. <20cm	39.59	46.63	46.99	51.86	17	50
Canopy spp. >10cm	**37.61****	**50.79****	**40.63****	**53.46****	26	53
Canopy spp. >20cm	**37.1***	**49.02***	**38.41****	**51.41****	26	53
Canopy spp. >40cm	**31.4***	**46.13***	**25.81*****	**44.72*****	17	48

DISCUSSION

This research did not find strong evidence that floodplain forests of the Savannah River are shifting towards a drier suite of species since the construction of the Thurmond Dam. Although in some comparisons Altamaha plots did have significantly greater similarity between older and younger trees, the effect depended on how the "pre-dam" and "post-dam" cohorts were defined. Based on growth rate estimates from the Apalachicola by Darst and Light (2008), ~15-20 cm is probably a good estimate of the upper size range of the post-dam cohort for most trees; estimates from our tree cores suggest ~25cm. However, only when "post-dam" was defined as ≤2.5cm did results indicate significantly lower similarity on the Savannah. Additionally, the results from the percent similarity comparisons were not in congruence with the results from the wetland vegetation indices. Had the difference in percent similarity been due to Savannah floodplains shifting towards more upland species, FSC and NWI indices should also have shown a shift for the same cohort definitions.

Evaluating the effects of artificial flood pulses on seedling recruitment proved difficult, since trees and seedlings were more similar overall on the Savannah River than at the reference sites. No obvious compositional differences in seedling cohorts were evident between the pulse year (2006) and non pulse year (2007). Seedling patterns at the reference sites also changed little from 2006-2007. Some differences in seedling abundance were evident, with higher abundance in 2006 for most Savannah plots, and higher abundance in about half of the Altamaha plots. Most of our Savannah plots were inundated during the 2006 prescribed pulse, but at present we do not have the data to determine hydrologic conditions at the plots during 2007. Additionally, though 2006 was a wetter spring, both 2006 and 2007 were very dry summers. We do not know how much summer conditions influenced seedlings, and whether extremely dry summers could have been a more powerful influence than the spring pulses. We also cannot be sure that all seedlings were first-year germinants.

Similar research on the floodplain of the Congaree River in South Carolina also found no conclusive evidence that forests are changing in response to dam construction upstream on the Saluda River (Minchin and Sharitz 2007). Some forest areas showed compositional trends towards more upland species, but other factors such as increased sedimentation might also be responsible. That study also found little change in seedling composition during run-of-river (marginally regulated) Saluda Dam operations in 2003-2004. However, recent research has also questioned whether the Saluda River influences Congaree River hydrology as much as has been previously thought (Feaster 2005).

Our work, and that on the Congaree, both contrast with research on other rivers in the southeastern US. Darst and Light (2008) found evidence that floodplain forests of the Apalachicola River in northern Florida are shifting towards drier species, while studies from the Roanoke River in North Carolina suggest a compositional shift at higher elevations combined with regeneration failure in cypress-tupelo forests (Rice and Peet 1997). However, these two rivers face a somewhat different set of hydrologic issues than those most evident on the Savannah. The Savannah has experienced higher low (base) flows and reduced peak flows (Meyer et al. 2003). The main hydrologic impacts to the Apalachicola have been reduced low to moderate flows, through increased withdrawals during dry months, without much change in flooding (Darst and Light 2008). Though the Roanoke may have experienced reduced peak flows as well, the primary concern for floodplain communities may be growing season inundation caused by water releases during peak electrical demands (Pearsall et al. 2005). Detailed hydrologic monitoring on the Roanoke indicates that inundation now extends well into the growing season in some habitats (Pearsall et al. 2005). In the past, cypress and tupelo seedling mortality from growing season flooding has been reported from the Savannah (Sharitz and Lee 1985), but based on hydrologic records those levels of summer flows do not appear to have been a regular occurrence in the intervening years. During 2006-2007 Savannah floodplain swamps dried adequately to permit cypress and tupelo germination.

Our work also contrasts with studies in the western US. Merritt and Cooper (2000) found major vegetation differences between the regulated Green River, Colorado, and the nearby, unregulated Yampa River, although there changes in hydrology were also accompanied by major changes in geomorphology from the altered flows. Studies of other riparian cottonwood forests have shown that river regulation and dewatering can promote invasion of exotic species (Howe and Knopf 1991) or cause lack of regeneration (Scott et al. 1997). Rood and others (2005) describe three successful restoration projects on cottonwood systems in Canada and the western US in which implementation of recommended flows led to extensive cottonwood and willow seedling recruitment.

It should be noted that floodplain forests were only one component of the flow restoration efforts on the Savannah River. Target flows were designed for each part of the regulated reach (shoals, floodplains, estuary), based on what is known about the needs of the organisms that are dependent on each habitat. Different flows were also designed for dry, wet, and average years, and included recommendations not only for high flows and floods, but also low flows. The full recommendations are described in Duncan and EuDaly (2003). Savannah pulse flow recommendations were designed primarily for instream organisms, particularly fishes such as the endangered shortnose sturgeon, Atlantic sturgeon, and robust redhorse (believed extinct until 1991), though they were thought to benefit vegetation as well, as long as they occurred in the dormant season. Restoration efforts on Kentucky's Green River, the SRP's pilot site, also focused on instream organisms, particularly reproduction of endangered mussels, with success (Turner and Byron 2006).

The differing hydrologic issues evident in just three regulated rivers within the same region (Savannah, Apalachicola, Roanoke) indicate that there is indeed no one-size-fits-all solution (Poff et al. 1997, Naiman et al. 2002, Arthington et al. 2006), and that an adaptive management approach is critical (Arthington et al. 2006, Richter et al. 2006). In addition, the three southeastern studies reviewed here focused only on vegetation; in reality ecologists are tasked with the formidable challenge of developing flow recommendations suitable for all organisms. Managers sometimes face potential biological tradeoffs, such as providing floods that are late enough (therefore warm enough) to signal migration and spawning of anadromous fishes, but early enough to avoid seedling mortality; these are in addition to potential tradeoffs with human demands. Perhaps in the future, through the iterative process of adaptive management, flow prescriptions within a region will begin to converge, and general patterns will emerge. Manipulation and monitoring through adaptive management certainly provides opportunity to learn more about relationships between hydrology and biological processes in big rivers, hopefully before irreversible changes take place.

CHAPTER 2:

DOWNSTREAM VARIATION IN FLOODPLAIN VEGETATION

INTRODUCTION

Several models have been proposed to explain variations in ecological processes and the distributions of different organisms across gradients in river/stream ecosystems and their floodplains. The River Continuum Concept (RCC) as originally conceived (Vannote et al. 1980) applied mostly to aquatic insect communities and instream processes, while the Flood Pulse Concept (FPC; Junk et al. 1989) focused on lateral exchange of organisms and materials between the river and its floodplain, with an emphasis on fish. Though generally presented as separate concepts (e.g., Johnson et al. 1995, Junk et al. 1989), there has been at least one direct effort to combine these ideas, Ward's (1989) four-dimensional conceptualization of lotic ecosystems (longitudinal, horizontal [flooding], vertical [hyporheic], temporal). However, this synthesis lacked specificity on the nature of the interaction between these four dimensions, and like the RCC, focused primarily on instream processes and invertebrate assemblages.

By contrast, floodplain vegetation has often been studied in relation to physical, rather than ecological, processes. Geomorphology (e.g., Shelford 1954, Hupp 1986, Hupp and Osterkamp 1996), flood disturbance (e.g., Sigafoos 1964, Polzin and Rood 2006), and hydroperiod (e.g., Townsend 2001) have all been common areas of research. Traditionally the focus has been on lateral (across floodplain) gradients, with Hupp

(1982, 1986) and Nilsson and others (1989, 1994) as notable exceptions. Although interest in longitudinal variation in vegetation does appear to be increasing in recent decades (e.g., Baker and Wiley 2004), often these ideas have remained vegetation-specific, focused on physical processes, and isolated from ecosystem theories such as the RCC and FPC.

Batzer and Sharitz have been developing a concept that combines aspects of the FPC and RCC, predicting that as floods become longer and more predictable farther downstream, the floodplain becomes less of a terrestrial-lotic ecotone and more of a distinct wetland ecosystem (D. Batzer, R. Sharitz, pers. comm.). Unlike the RCC or vegetation-landform relationships, this idea is easily applicable to several groups of organisms – plants, fish, invertebrates – since all have suites of species that characteristically inhabit wetlands. Reese and Batzer (2007) examined longitudinal variation in proportions of wetland taxa of invertebrates in the Altamaha River system. This chapter is intended as a companion to that study, examining downstream variation in the proportion of wetland vegetation in floodplain forests. The first section is a field study of woody vegetation along two major drainage systems of the southeastern United States, the Altamaha and the Savannah; the second is a literature review that examines whether our findings are supported by existing studies in other regions. We expected to find an increase in the prevalence of wetland vegetation with higher streamflow, since larger streams are usually lower in the watershed and therefore likely to flood longer and more predictably. The field study and literature review are treated together in the discussion section.

I. FIELD STUDY

STUDY AREAS

Three sites on the main stems of the Savannah and Altamaha rivers were sampled in 2006 for the first chapter of this thesis. From downstream to upstream, the three Savannah sites were Webb Wildlife Management Area (SCDNR), Tuckahoe Wildlife Management Area (GADNR), and the Department of Energy's Savannah River Site (SRS). The Altamaha sites were Penholoway Swamp Wildlife Management Area (GADNR), Beards Bluff (privately owned), and Moody Forest Natural Area (TNC preserve). In summer of 2007 two additional sites were chosen upstream on tributaries of each river.

In the Savannah watershed the lower tributary site was located on Stevens Creek, which flows into the Savannah River just below Thurmond Dam; the upper site was on Turkey Creek, a tributary of Stevens Creek (Fig. 2.1). Sampling sites on both tributaries were located within the Sumter National Forest. In many places Stevens Creek and Turkey Creek are steeply banked with no floodplain development. As a conservative measure, only areas with well-developed floodplains were sampled.

In the Altamaha watershed the lower tributary site was located on the Oconee River, just south of Hwy 15, in the Oconee National Forest; the upper site was located on the North Oconee River, a tributary of the Oconee, at Sandy Creek Nature Center (Fig. 2.1). Most of the sites in the Altamaha watershed were previously sampled for aquatic invertebrates by Reese and Batzer (2007). North Oconee and Oconee correspond to Reese #4 and #5, respectively. Reese #8 lies between two of the Beards Bluff transects;

Penholoway is roughly 5 air km upstream from Reese #9. Moody Forest is about 21 air km downstream of Reese #7.

Figure 2.1. Site locations in the Altamaha (GA) and Savannah (GA-SC border) watersheds.

METHODS

Only vegetation data were collected at the tributary sites. Because tributary floodplains were much narrower (~100-250m on one side) than those on the main stems (~1-2km), vegetation was sampled in continuous 20m-wide transects rather than the discrete 20x50m plots used at the main stem sites. Transects spanned the width of one side of the floodplain, from channel to floodplain edge. Edge of the floodplain was determined subjectively by the upper limits of physical evidence of flooding, such as silt on tree bark, piles of flood debris, and obvious changes in soil, especially when coupled with an evident rise in topography. Although this method is subjective, any errors were conservative, restricting sampling to the wettest areas. A minimum of 250m of transect (the equivalent of 5 20x50m plots) was sampled at each of the tributary sites. As at the main stem sites, all trees and saplings > 1.4m in height were identified to species and measured for diameter at breast height (DBH; 1.4m above ground). Sampling methods for the main stem sites are described in Chapter 1.

Table 2.1. NWI wetland indicator categories with numeric assignments. Definitions from Reed (1996).

Status	Value	Definition
OBL	1	Obligate Wetland (OBL). Occur almost always (estimated probability >99%) under natural conditions in wetlands.
FACW+ FACW FACW-	2	Facultative Wetland (FACW). Usually occur in wetlands (estimated probability 67%-99%), but occasionally found in non wetlands.
FAC+ FAC FAC-	3	Facultative (FAC). Equally likely to occur in wetlands or non wetlands (estimated probability 34%-66%).
FACU+ FACU FACU-	4	Facultative Upland (FACU). Usually occur in non wetlands (estimated probability 67%-99%), but occasionally found on wetlands (estimated probability 1%-33%).
UPL	5	Obligate Upland (UPL). Occur in wetlands in another region, but occur almost always (estimated probability >99%) under natural conditions in non wetlands on the region specified. If a species does not occur in wetlands in any region, it is not on the National List.

Tributary and main stem vegetation data sets were combined, and numerical wetland indicator values were assigned to each species by creating numerical equivalents for the National Wetland Inventory Wetland Indicator Status rankings (Table 2.1). Plants excluded from the NWI list were counted as upland species and given a value of 5.

Wetland scores for each site were determined by weighted averages of these indicator values. Averages were applied to four different metrics of vegetation prevalence: relative abundance (RA), relative basal area (RBA), relative frequency (relFQ), and importance value (IV) which combines the first three metrics. For comparison, scores were also calculated as an unweighted average of the species present, since this was sometimes the only method possible for data from the literature review.

RESULTS

In general, sites followed the expected pattern, with higher values (less wetland vegetation) further upstream, although the relationship is not exact (Fig. 2.2). Two sites on the Savannah floodplain, SRS and Tuckahoe WMA, exhibited some degree of spread between weighted averages using different metrics, but otherwise patterns were roughly the same regardless of the type of quantitative data used. Even the unweighted averages, based on species presence alone, generally gave results similar to the quantitative data.

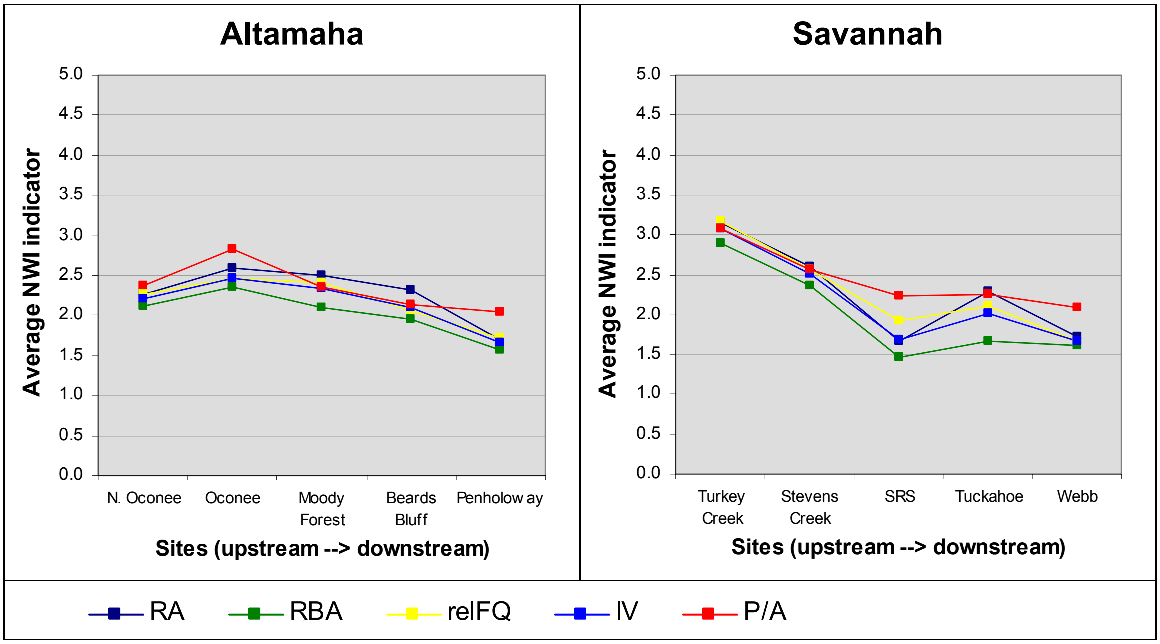

Figure 2.2. Downstream variation in prevalence of wetland vegetation at five sites in the Altamaha and Savannah watersheds. Averages were weighted by four metrics of species importance, or unweighted, for comparison. RA = relative abundance; RBA = relative basal area; relFQ = relative frequency; IV = importance value; P/A = presence / absence (unweighted). 1=wetland obligate; 5=upland obligate.

In addition to the generally decreasing (more wetland) NWI averages downstream, wetland obligates as a class were nearly absent from both Altamaha tributary sites, and completely absent from Turkey Creek, the uppermost Savannah tributary (Fig. 2.3). Stevens Creek had a total of 13 stems classified as wetland obligates, including some *Taxodium distichum*, but these were still rare. The only wetland obligates observed at the Altamaha tributary sites were a few *Salix nigra* and *Quercus lyrata*. Wetland obligates were present at all main stem sites. Upland obligates were essentially absent from all sites, with tributaries dominated by a mix of the three facultative classes. Facultative upland species were a significant presence only at tributary sites.

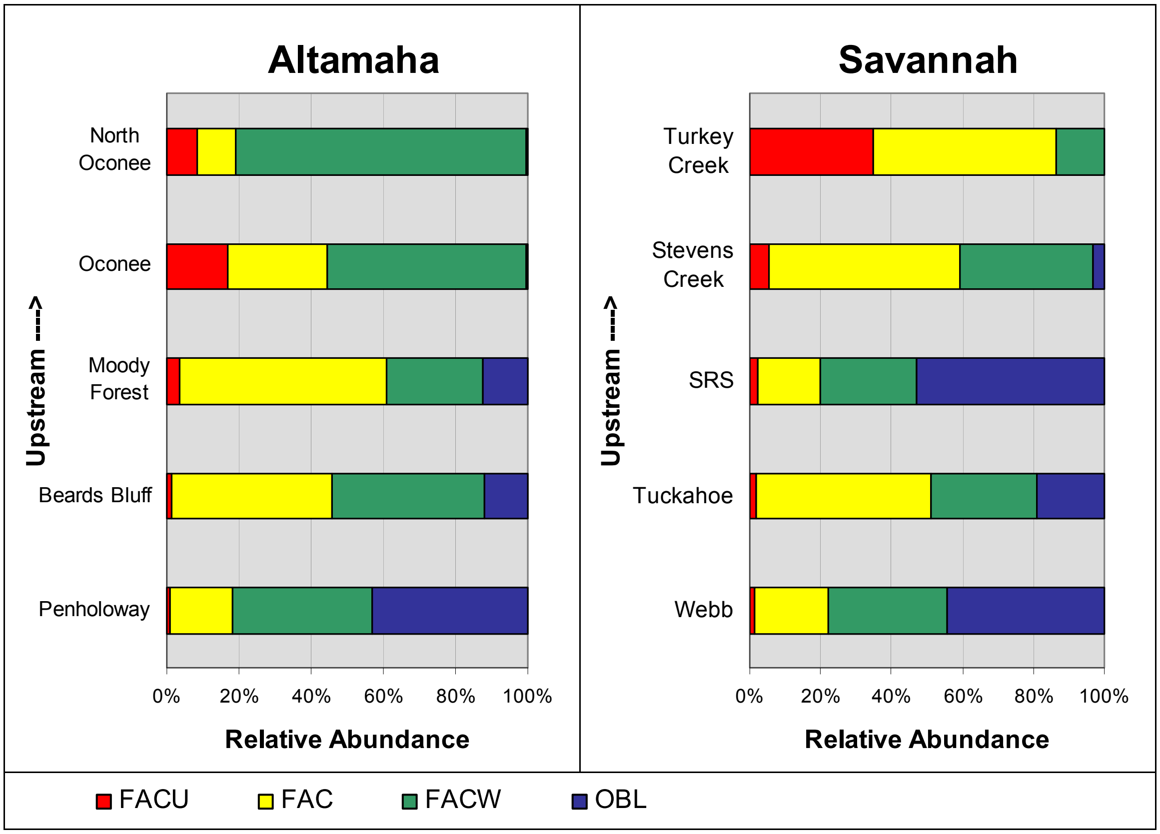

Figure 2.3. Upstream variation in abundance of wetland indicator species on floodplains. OBL=wetland obligate; FACW=facultative wetland; FAC=facultative; FACU=facultative upland.

II. LITERATURE REVIEW

To be included in the review, publications had to provide adequate information on stream size and vegetation composition. Papers were first screened for information on vegetation composition; only studies providing comprehensive species lists, rather than dominants or associations, were included. Publications were then assessed for information on stream size. Mean annual flow was chosen as the metric for comparison since basin size is poorly comparable across ecoregions, and stream order was not commonly reported in the vegetation literature. To be included, publications had to provide either mean annual flow data or a detailed location description for which a nearby USGS gauge could be found. River gradient was originally to be taken into consideration as well, but due to the difficulty in finding publications that included adequate information on all three variables, the one deemed least critical was dropped. Due to the difficulty in determining which plants are wetland species in different parts of the world, the literature review has been restricted to the US, where such information is easily available through the National Wetland Inventory's List of Plant Species that Occur in Wetlands (Reed 1996).

Nine publications were found that met the criteria for the review (Limber Jim Creek and West Chicken Creek were reported in the same publication). For publications that included quantitative measures of species presence, the average NWI indicator was weighted by the quantitative metric provided, e.g., relative abundance (RA), relative basal area (RBA), or importance value (IV). Since the measures varied, and because some publications only included species presence, prevalence of wetland vegetation was also calculated as an unweighted average of the species present. Publications that included quantitative information by landform or community, but did not describe the spatial extent of these features, were also treated as presence/absence data. Among the publications found to have sufficient data for this analysis, the prevalence of wetland vegetation, represented by the average NWI indicator value, did not appear to have a strong relationship to annual flow (Fig. 2.4).

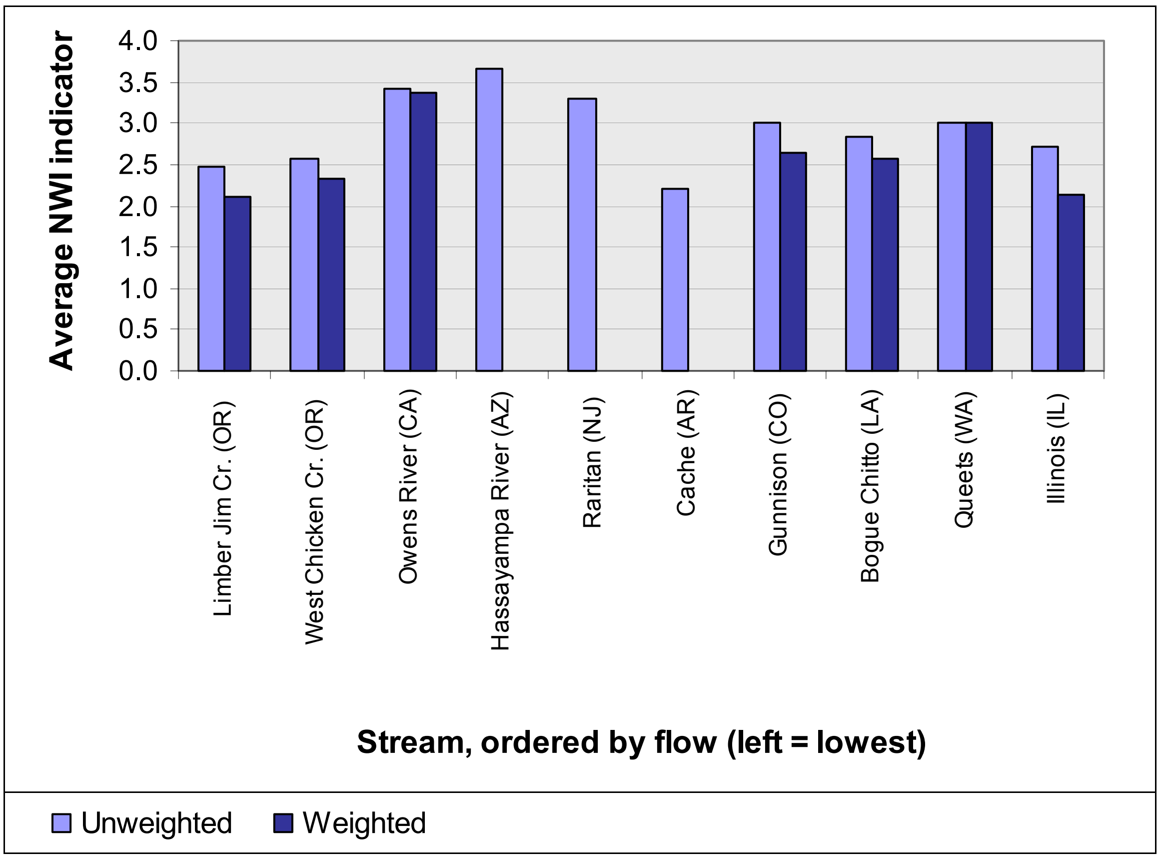

Figure 2.4. Average wetland indicator value for streamside vegetation on 10 streams, ordered from lowest to highest annual flow. Data from: Limber Jim and West Chicken Creek -- Dwire et al. 2006; Hassayampa River -- Stromberg et al. 1993; Owens River -- Brothers 1984; Raritan River – Frye and Quinn 1979; Cache – Smith 1996; Gunnison – Auble et al. 1994; Bogue Chitto – Robertson and Augspurger 1999; Queets – Van Pelt et al. 2006; Illinois – Nelson and Sparks 1998.

In addition, several studies reporting data from different sized streams within the same drainage system or same general habitat were found. They did not contain the requisite information to be included in the comparative analysis above, but have been analyzed on an individual basis for patterns within their respective watersheds or habitats. Although more geographically limited, this case study approach has the advantage of internal consistency.

Danzer and colleagues (2001) sampled woody vegetation along 15 mostly intermittent or ephemeral high-elevation streams in the mountains of southeastern Arizona. Stream size was described in terms of basin area, which ranged from 3 – 46 km^2. Six different vegetation types were identified by cluster analysis. Though these vegetation types were described only by dominants, the authors commented unequivocally on the importance of facultative upland species, and the relatively low incidence of traditional riparian obligates, in these habitats. Further, they found that small watersheds were dominated by upland species such as *Abies concolor* or oaks, while more traditional riparian communities dominated by *Baccharis*, *Fraxinus*, or *Salix* were found on large, lower elevation streams with low or moderate gradients.

Hupp (1986) researched upstream variation in vegetation in the Massanutten Mountain area of northwest Virginia, sampling first-to-fifth-order streams, and comparing patterns in species presence with several geomorphic

Table 2.2. Presence/absence data from Hupp (1986) analyzed for average wetland indicator values. Study examined upstream variation in woody vegetation in NW Virginia.

Stream Order	Fluvial Landform		
	Basin Head	Channel Shelf	Floodplain
NA	3.57	NA	NA
1	NA	2.60	3.20
2	NA	2.63	3.11
3	NA	2.36	3.00
4	NA	2.31	3.00
5	NA	2.22	2.88

properties, including stream order, stream gradient, fluvial landform, and basin area. He found distinct upstream variation in species occurrences, much of which he attributed to changes in the prevalence of different fluvial landforms. However, he also found clear evidence of longitudinal variation in vegetation within each landform, corresponding with variation in stream order. When NWI indicator values were applied to the species lists he reported, both channel shelves and floodplains generally showed the pattern expected (Table 2.2), with values decreasing as stream order increased. Additionally, floodplains, which are higher above the channel and therefore less frequently flooded than channel shelves, had a higher average NWI indicator than channel shelves across all stream orders.

Rheinhardt and colleagues (1998) examined vegetation characteristics of first-to-fourth-order streams on the North Carolina Coastal Plain. In contrast to Massanutten Mountain, river gradients on the Coastal Plain change little from headwaters to larger streams, but like Hupp (1986), these researchers also found important vegetational differences between headwater (1-2 order) and mid-reach (3-4) streams. When wetland indicator values are applied, scores generally follow the expected pattern (Table 2.3).

Table 2.3. Data from Rheinhardt et al. (1998) analyzed for average wetland indicator values. Study sampled forests on 22 low-order streams on the NC coastal plain. Scores were calculated two ways: 1) unweighted average of all species present; 2) weighted by importance value (IV).

Stream Order	Wetland Score		# sites
	Pres/Abs	Weighted (IV)	
1	2.82	2.78	12
2	2.63	2.18	5
3	2.10	1.29	2
4	1.95	1.67	3

In summary, studies within watersheds were in general agreement that a downstream trend towards greater abundance of wetland plants does exist, though this trend is not apparent in the comparison across watersheds. Though ample publications on floodplain vegetation exist, few fulfilled the criteria for the review. The primary obstacles to this review were insufficient environmental information, and data aggregation. Data were often presented as ordination figures, cluster diagrams, vegetation classes described by a few dominants, or as composite species lists for studies that sampled across a gradient of streamflow. Additionally, lack of information on wetland status of plants in other countries eliminated all vegetation studies outside the US, regardless of their content.

DISCUSSION

From our own work on the Altamaha and Savannah rivers, floodplain forests do seem to exhibit a general trend toward greater dominance of wetland plants downstream, evidenced by decreasing average wetland indicator values. Other case studies in the mountains of northwestern Virginia (Hupp 1982), the Coastal Plain of North Carolina (Rheinhardt et al. 1998), and the mountains of southeastern Arizona (Danzer et al. 2001) all support these findings; though a comparison of data from different sources, ranked by streamflow, failed to detect any pattern. It seems likely that trends may exist but were obscured by other sources of variability such as differences in sampling protocol, or more important, by variation in climatic or other physical factors that should be addressed by future work in this area. For example, stream gradient was not included in this analysis because of limited data, though it is an additional source of variation (Hupp 1982, Hupp 1986).

Our findings also matched the general trend found in floodplain macroinvertebrates by Reese and Batzer (2007), who reported that assemblages varied predictably downstream, with greater abundances of lentic taxa lower in the watershed, and greater abundance of terrestrial taxa in the upper reaches. Although unlike Reese and Batzer our upper sites were dominated by facultative species rather than upland (terrestrial) species, we also began our sampling lower in the watershed. Our uppermost site in the Altamaha watershed is equivalent to Reese #4, which was considered "mid-reach" by that study. Both vegetation and invertebrate assemblages seemed to indicate that terrestrial or upland species are uncommon in the mid-reach of the river, and that wetland obligates or lentic species assume greater importance in the lower (coastal plain) reach.

Vegetation also suggests that at least in the Altamaha and Savannah watersheds, mid-reach floodplains may be considered wetlands, even though wetland obligates are infrequent or absent until further downstream. Wentworth and others (1988) evaluated the use of average NWI wetland indicator values for wetland delineation, using the same scale employed here. According to that research, areas with wetland prevalence values ≤ 3 should be considered wetlands. By this criterion all of our sites are wetlands except Turkey Creek (3.16, Fig. 2.3). For comparison, values ranged from 2.88 (5^{th} order floodplains) to 3.57 (basin heads) in the mountains of VA, and all values from 1^{st}-4^{th} order streams on the NC Coastal Plain were below 3.

Though our findings did show a downstream increase in wetland vegetation, the relationship was not exact. The North Oconee and SRS sites both appeared to be somewhat anomalous (Fig. 2.2). The SRS site may have had lower average wetland indicator values because of its extensive backswamp, much larger than the swamps sampled at the other sites. The results of our hydrologic analyses also suggest that water levels at this site may be significantly influenced by factors other than the river; we suspect there is significant groundwater influence from the high bluff on the floodplain edge. It is not clear why the North Oconee site did not fit the pattern well. Nonetheless, although site idiosyncrasies may obscure patterns to some degree, on a broad level the floodplain continuum concept does appear to be a useful model for describing floodplain vegetation. More work is needed to better establish the actual variation in floodplain hydroperiod, and to develop this model further in terms of wetland ecological processes.

SUMMARY

Within watersheds, river floodplains do appear to exhibit downstream transitions toward greater importance of wetland vegetation that suggests change in hydrology, even if no patterns across watersheds are evident. Some floodplain forests, particularly cottonwoods (e.g. Scott et al. 1997, Merritt and Cooper 2000, Rood et al. 2005), also clearly show changes in vegetation when flood pulses are reduced or eliminated through regulation, although no differences were seen in the present study. In both contexts (natural downstream patterns and effects of regulation), assessment of the influence of flood pulse characteristics on vegetation is complicated by the difficulty in determining how much floodplain hydroperiod has actually changed, since some parts of the floodplain become inundated well before the river reaches bankfull ("flood") stage. Variations in topography and water holding capacity of soils within the floodplain contribute additional complexity.

Work on the Apalachicola River also suggests that low and medium flows can be critical determinants of vegetation as well (Darst and Light 2008). It would be useful to know how all aspects of the natural flow regime outlined by Poff and others (1997) change on floodplains downstream, and with river regulation. Future research may be able to benefit from the ecosystem perspective provided by adaptive management, as the responses of multiple suites of organisms to the same flow events are monitored in tandem. Perhaps the SRP will prove to be a unique opportunity to better understand dynamics in what are fundamentally highly variable systems.

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APPENDICES

APPENDIX 1: CANOPY AND UNDERSTORY SPECIES DESIGNATIONS

Canopy species	Understory species
Acer floridanum	*Aesculus pavia*
Acer negundo	*Asimina triloba*
Acer rubrum	*Carpinus caroliniana*
Acer saccharinum	*Cornus florida*
Betula nigra	*Cornus stricta*
Carya aquatica	*Crataegus marshalli*
Carya cordiformis	*Crataegus* sp.
Carya glabra	*Diospyros virginiana*
Carya tomentosa	*Forestiera acuminata*
Celtis laevigata	*Fraxinus caroliniana*
Fraxinus pennsylvanica	*Fraxinus* sp.
Juniperus virginiana	*Gleditsia aquatica*
Liquidambar styraciflua	*Ilex decidua*
Nyssa aquatica	*Ilex opaca*
Nyssa biflora	*Maclura pomifera*
Nyssa ogeche	*Melia azedarach*
Nyssa sylvatica	*Morus rubra*
Pinus glabra	*Planera aquatica*
Pinus taeda	*Salix nigra*
Platanus occidentalis	*Styrax americana*
Populus heterophylla	*Styrax grandifolia*
Quercus austrina	*Viburnum obovatum*
Quercus laurifolia	
Quercus lyrata	
Quercus michauxii	
Quercus nigra	
Quercus pagoda	
Quercus phellos	
Quercus virginiana	
Taxodium distichum	
Ulmus alata	
Ulmus americana	

APPENDIX 2: LIST OF SPECIES BY SITE

Altamaha - N. Oconee R.	Basal area	No. stems	Rel. BA	Rel. abund.
Acer negundo	1567.26	48	0.0078	0.1182
Acer rubrum	99717.98	121	0.4992	0.2980
Betula nigra	952.69	5	0.0048	0.0123
Carpinus caroliniana	3083.67	25	0.0154	0.0616
Cornus stricta	142.65	10	0.0007	0.0246
Crataegus sp. 1	12.57	1	0.0001	0.0025
Elaeagnus umbellata	0.20	1	0.0000	0.0025
Fraxinus pennsylvanica	68231.07	88	0.3416	0.2167
Ilex decidua	1607.07	44	0.0080	0.1084
Liquidambar styraciflua	5996.71	8	0.0300	0.0197
Morus rubra	102.89	3	0.0005	0.0074
Nyssa sylvatica	1038.30	2	0.0052	0.0049
Platanus occidentalis	333.79	2	0.0017	0.0049
Quercus laurifolia	201.06	1	0.0010	0.0025
Quercus lyrata	4094.28	1	0.0205	0.0025
Quercus nigra	6388.43	5	0.0320	0.0123
Ulmus alata	5147.79	35	0.0258	0.0862
Ulmus americana	1139.61	6	0.0057	0.0148
Total	199758.02	406	1.0000	1.0000

Altamaha – Oconee R.	Basal area	No. stems	Rel. BA	Rel. abund.
Acer floridanum	2045.62	50	0.0158	0.0838
Acer negundo	10753.18	79	0.0829	0.1323
Acer rubrum	36794.04	112	0.2836	0.1876
Aesculus pavia	2.41	1	0.0000	0.0017
Betula nigra	4474.41	4	0.0345	0.0067
Carpinus caroliniana	7411.12	115	0.0571	0.1926
Carya cordiformis	2301.95	12	0.0177	0.0201
Carya ovata	346.36	1	0.0027	0.0017
Celtis laevigata	90.57	6	0.0007	0.0101
Cornus alterifolia	28.27	1	0.0002	0.0017
Cornus florida	28.47	2	0.0002	0.0034
Cornus stricta	2.80	3	0.0000	0.0050
Crataegus sp. 1	113.10	1	0.0009	0.0017
Crataegus sp. 2	50.27	1	0.0004	0.0017
Diospyros virginiana	22.24	3	0.0002	0.0050
Fraxinus pennsylvanica	12403.65	67	0.0956	0.1122
Ilex decidua	93.27	19	0.0007	0.0318
Liquidambar styraciflua	19832.09	14	0.1528	0.0235
Liriodendron tulipifera	201.06	1	0.0015	0.0017
Maclura pomifera	34.61	2	0.0003	0.0034
Ostrya virginiana	271.26	22	0.0021	0.0369
Platanus occidentalis	16884.49	15	0.1301	0.0251
Prunus serotina	532.50	8	0.0041	0.0134
Quercus michauxii	95.03	1	0.0007	0.0017
Quercus nigra	6934.08	16	0.0534	0.0268
Quercus phellos	807.05	4	0.0062	0.0067
Quercus shumardii	2081.31	2	0.0160	0.0034
Salix nigra	2331.85	2	0.0180	0.0034
Sambucus canadensis	0.20	1	0.0000	0.0017
Sassafras albidum	2.41	1	0.0000	0.0017
Ulmus alata	1615.22	12	0.0124	0.0201
Ulmus americana	1172.94	18	0.0090	0.0302
Viburnum prunifolium	2.41	1	0.0000	0.0017
Total	129760.20	597	1.0000	1.0000

Altamaha - Moody	Basal area	No. stems	Rel. BA	Rel. abund.
Acer rubrum	21185.33	180	0.0379	0.0551
Acer saccharinum	1661.90	1	0.0030	0.0003
Acer sp.	66.22	3	0.0001	0.0009
Betula nigra	22.04	2	0.0000	0.0006
Carpinus caroliniana	49208.34	1391	0.0880	0.4259
Carya aquatica	11195.85	122	0.0200	0.0374
Carya cordiformis	2499.73	18	0.0045	0.0055
Carya glabra	5153.78	2	0.0092	0.0006
Celtis laevigata	1436.54	6	0.0026	0.0018
Cornus stricta	32.10	6	0.0001	0.0018
Crataegus marshalli	59.69	6	0.0001	0.0018
Crataegus sp. 1	220.75	8	0.0004	0.0024
Diospyros virginiana	943.12	54	0.0017	0.0165
Forestiera acuminata	972.37	8	0.0017	0.0024
Fraxinus caroliniana	459.65	3	0.0008	0.0009
Fraxinus pennsylvanica	28.27	1	0.0001	0.0003
Fraxinus sp.	12.57	1	0.0000	0.0003
Gleditsia aquatica	2.41	1	0.0000	0.0003
Ilex decidua	7210.35	344	0.0129	0.1053
Ilex opaca	2179.33	36	0.0039	0.0110
Juniperus virginiana	10721.72	39	0.0192	0.0119
Liquidambar styraciflua	86622.74	246	0.1550	0.0753
Maclura pomifera	63.62	1	0.0001	0.0003
Morus rubra	1361.29	11	0.0024	0.0034
Nyssa aquatica	79004.77	51	0.1413	0.0156
Nyssa ogeche	52474.02	18	0.0939	0.0055
Nyssa sylvatica	2107.42	13	0.0038	0.0040
Pinus glabra	25131.07	31	0.0450	0.0095
Pinus taeda	5405.11	4	0.0097	0.0012
Planera aquatica	9587.99	70	0.0172	0.0214
Quercus austrina	530.93	1	0.0009	0.0003
Quercus laurifolia	21896.07	76	0.0392	0.0233
Quercus lyrata	17159.82	88	0.0307	0.0269
Quercus michauxii	8741.78	31	0.0156	0.0095
Quercus nigra	9972.84	44	0.0178	0.0135
Quercus pagoda	14945.49	32	0.0267	0.0098
Quercus phellos	61171.82	94	0.1094	0.0288
Quercus virginiana	4944.87	3	0.0088	0.0009
Styrax americana	69.36	7	0.0001	0.0021
Styrax grandifolia	19.63	1	0.0000	0.0003
Taxodium distichum	11099.10	46	0.0199	0.0141
Ulmus alata	10474.02	74	0.0187	0.0227
Ulmus americana	20764.65	84	0.0371	0.0257
Viburnum obovatum	164.25	8	0.0003	0.0024
Total	558984.71	3266	1.0000	1.0000

Altamaha - Beards Bluff	Basal area	No. stems	Rel. BA	Rel. abund.
Acer rubrum	2554.02	33	0.0058	0.0177
Acer saccharinum	2010.62	2	0.0046	0.0011
Betula nigra	7940.42	111	0.0181	0.0595
Carpinus caroliniana	17158.69	474	0.0391	0.2539
Carya aquatica	20840.64	23	0.0475	0.0123
Carya glabra	745.34	3	0.0017	0.0016
Cornus florida	132.73	1	0.0003	0.0005
Cornus stricta	110.25	9	0.0003	0.0048
Crataegus sp. 1	1104.47	15	0.0025	0.0080
Diospyros virginiana	38.58	5	0.0001	0.0027
Fraxinus caroliniana	12188.59	63	0.0278	0.0337
Fraxinus pennsylvanica	22493.80	19	0.0513	0.0102
Fraxinus sp.	1153.41	15	0.0026	0.0080
Gleditsia aquatica	380.13	1	0.0009	0.0005
Ilex decidua	11292.11	343	0.0257	0.1837
Liquidambar styraciflua	32407.93	280	0.0739	0.1500
Morus rubra	283.53	1	0.0006	0.0005
Nyssa aquatica	7362.32	8	0.0168	0.0043
Nyssa ogeche	30321.87	54	0.0691	0.0289
Nyssa sylvatica	44506.16	51	0.1015	0.0273
Planera aquatica	5631.99	15	0.0128	0.0080
Quercus laurifolia	126104.95	176	0.2875	0.0943
Quercus lyrata	40628.70	31	0.0926	0.0166
Quercus nigra	5445.95	6	0.0124	0.0032
Quercus phellos	19052.63	61	0.0434	0.0327
Styrax americana	521.55	4	0.0012	0.0021
Taxodium distichum	12994.41	28	0.0296	0.0150
Ulmus alata	5768.99	21	0.0132	0.0112
Ulmus americana	7369.39	10	0.0168	0.0054
Viburnum obovatum	144.56	4	0.0003	0.0021
Total	438688.76	1867	1.0000	1.0000

Altamaha - Penholoway	Basal area	No. stems	Rel. BA	Rel. abund.
Acer rubrum	8051.51	27	0.0169	0.0271
Betula nigra	8545.92	6	0.0179	0.0060
Carpinus caroliniana	2361.64	47	0.0049	0.0472
Carya aquatica	15947.61	34	0.0334	0.0341
Cornus florida	103.67	4	0.0002	0.0040
Cornus stricta	217.46	27	0.0005	0.0271
Crataegus sp. 1	5296.14	28	0.0111	0.0281
Diospyros virginiana	75.05	8	0.0002	0.0080
Forestiera acuminata	658.95	40	0.0014	0.0402
Fraxinus caroliniana	47375.51	197	0.0993	0.1978
Fraxinus pennsylvanica	14894.49	13	0.0312	0.0131
Fraxinus sp.	2995.12	5	0.0063	0.0050
Gleditsia aquatica	2.41	1	0.0000	0.0010
Ilex decidua	10182.98	245	0.0213	0.2460
Ilex opaca	119.53	5	0.0003	0.0050
Liquidambar styraciflua	14058.87	39	0.0295	0.0392
Nyssa aquatica	4071.50	1	0.0085	0.0010
Nyssa ogeche	99742.43	32	0.2090	0.0321
Nyssa sylvatica	11352.98	32	0.0238	0.0321
Planera aquatica	6988.13	56	0.0146	0.0562
Quercus laurifolia	47418.90	29	0.0994	0.0291
Quercus lyrata	75051.27	21	0.1573	0.0211
Quercus nigra	64658.69	34	0.1355	0.0341
Styrax americana	132.14	9	0.0003	0.0090
Taxodium distichum	32871.61	33	0.0689	0.0331
Ulmus alata	5.40	5	0.0000	0.0050
Ulmus americana	3773.94	14	0.0079	0.0141
Viburnum obovatum	212.06	4	0.0004	0.0040
Total	477165.91	996	1.0000	1.0000

Savannah – Turkey Cr.	Basal area	No. stems	Rel. BA	Rel. abund.
Acer floridanum	321.38	50	0.0013	0.0588
Acer leucoderme	1453.87	46	0.0060	0.0541
Acer negundo	799.88	54	0.0033	0.0635
Acer rubrum	609.13	8	0.0025	0.0094
Asimina triloba	131.16	96	0.0005	0.1129
Carpinus caroliniana	3997.97	89	0.0166	0.1047
Carya cordiformis	4910.55	14	0.0204	0.0165
Carya ovata	296.88	3	0.0012	0.0035
Celtis laevigata	0.59	3	0.0000	0.0035
Cornus florida	1313.43	35	0.0055	0.0412
Crataegus sp. 2	0.20	1	0.0000	0.0012
Fagus grandifolius	1894.77	7	0.0079	0.0082
Fraxinus americana	296.10	4	0.0012	0.0047
Fraxinus pennsylvanica	84.04	6	0.0003	0.0071
Lindera benzoin	12.57	1	0.0001	0.0012
Liquidambar styraciflua	47226.92	158	0.1965	0.1859
Liriodendron tulipifera	41154.08	41	0.1712	0.0482
Ostrya virginiana	2883.15	108	0.0120	0.1271
Pinus taeda	47985.47	16	0.1996	0.0188
Platanus occidentalis	22764.77	5	0.0947	0.0059
Poncirus trifoliatus	33.23	18	0.0001	0.0212
Prunus serotina	0.39	2	0.0000	0.0024
Quercus alba	1170.24	2	0.0049	0.0024
Quercus michauxii	8864.00	8	0.0369	0.0094
Quercus nigra	6265.17	9	0.0261	0.0106
Quercus pagoda	25319.08	4	0.1053	0.0047
Quercus shumardii	16127.37	5	0.0671	0.0059
Ulmus alata	2083.22	31	0.0087	0.0365
Ulmus americana	2383.19	26	0.0099	0.0306
Total	240382.79	850	1.0000	1.0000

Savannah – Stevens Cr.	Basal area	No. stems	Rel. BA	Rel. abund.
Acer floridanum	834.09	3	0.0050	0.0072
Acer negundo	12821.13	70	0.0766	0.1687
Acer rubrum	4830.98	14	0.0289	0.0337
Carpinus caroliniana	2930.91	56	0.0175	0.1349
Carya cordiformis	3872.01	17	0.0231	0.0410
Celtis laevigata	4688.43	18	0.0280	0.0434
Crataegus sp. 1	69.90	1	0.0004	0.0024
Fraxinus pennsylvanica	19335.72	10	0.1155	0.0241
Ilex decidua	12.57	1	0.0001	0.0024
Juglans nigra	1382.30	3	0.0083	0.0072
Juniperus virginiana	283.53	1	0.0017	0.0024
Lindera benzoin	40.10	4	0.0002	0.0096
Liquidambar styraciflua	45860.18	134	0.2740	0.3229
Liriodendron tulipifera	2416.67	2	0.0144	0.0048
Melia azedarach	314.16	1	0.0019	0.0024
Morus rubra	702.93	4	0.0042	0.0096
Pinus taeda	14714.43	7	0.0879	0.0169
Platanus occidentalis	15843.05	13	0.0947	0.0313
Populus heterophylla	7264.93	2	0.0434	0.0048
Quercus lyrata	479.29	3	0.0029	0.0072
Quercus michauxii	0.20	1	0.0000	0.0024
Quercus pagoda	226.98	1	0.0014	0.0024
Quercus phellos	2463.01	1	0.0147	0.0024
Taxodium distichum	17130.32	8	0.1023	0.0193
Ulmus alata	4889.99	15	0.0292	0.0361
Ulmus americana	3962.33	24	0.0237	0.0578
Viburnum prunifolium	2.41	1	0.0000	0.0024
Total	167372.57	415	1.0000	1.0000

Savannah - SRS	Basal area	No. stems	Rel. BA	Rel. abund.
Acer negundo	1017.88	1	0.0011	0.0006
Acer rubrum	8484.71	19	0.0089	0.0107
Acer sp.	3631.68	1	0.0038	0.0006
Aesculus pavia	325.79	24	0.0003	0.0135
Carpinus caroliniana	9273.29	101	0.0097	0.0567
Carya aquatica	4306.34	5	0.0045	0.0028
Carya cordiformis	1114.48	3	0.0012	0.0017
Carya ovata	1134.11	1	0.0012	0.0006
Carya sp.	1138.83	2	0.0012	0.0011
Carya tomentosa	1276.27	2	0.0013	0.0011
Celtis laevigata	16115.58	67	0.0169	0.0376
Crataegus marshalli	201.50	24	0.0002	0.0135
Crataegus sp. 1	378.56	11	0.0004	0.0062
Diospyros virginiana	2.41	1	0.0000	0.0006
Fraxinus caroliniana	4110.92	116	0.0043	0.0651
Fraxinus pennsylvanica	15975.78	30	0.0168	0.0168
Ilex decidua	4605.72	198	0.0048	0.1111
Ilex opaca	4165.21	21	0.0044	0.0118
Liquidambar styraciflua	58390.38	89	0.0612	0.0499
Melia azedarach	12.57	1	0.0000	0.0006
Morus rubra	673.09	3	0.0007	0.0017
Nyssa aquatica	429300.21	565	0.4501	0.3171
Nyssa sylvatica	8637.81	10	0.0091	0.0056
Pinus taeda	5674.50	1	0.0059	0.0006
Planera aquatica	5522.13	15	0.0058	0.0084
Platanus occidentalis	29232.52	13	0.0307	0.0073
Populus heterophylla	535.74	3	0.0006	0.0017
Quercus austrina	9191.71	13	0.0096	0.0073
Quercus laurifolia	108216.18	112	0.1135	0.0629
Quercus lyrata	1595.14	5	0.0017	0.0028
Quercus michauxii	5874.78	11	0.0062	0.0062
Quercus nigra	20943.13	27	0.0220	0.0152
Quercus sp.	1520.53	1	0.0016	0.0006
Salix nigra	95.03	1	0.0001	0.0006
Taxodium distichum	165749.94	216	0.1738	0.1212
Ulmus alata	9673.75	41	0.0101	0.0230
Ulmus americana	15645.13	28	0.0164	0.0157
Total	953743.35	1782	1.0000	1.0000

Savannah - Tuckahoe	Basal area	No. stems	Rel. BA	Rel. abund.
Acer floridanum	1440.42	3	0.0021	0.0013
Acer rubrum	14726.36	113	0.0219	0.0472
Aesculus pavia	39.86	5	0.0001	0.0021
Carpinus caroliniana	19875.04	558	0.0296	0.2331
Carya aquatica	47102.73	78	0.0701	0.0326
Carya cordiformis	4345.90	26	0.0065	0.0109
Carya tomentosa	2.41	1	0.0000	0.0004
Celtis laevigata	11684.22	57	0.0174	0.0238
Cornus stricta	33.77	2	0.0001	0.0008
Crataegus marshalli	96.06	12	0.0001	0.0050
Crataegus sp. 1	1095.83	23	0.0016	0.0096
Diospyros virginiana	1188.60	19	0.0018	0.0079
Fraxinus caroliniana	2927.62	14	0.0044	0.0058
Fraxinus pennsylvanica	14734.17	25	0.0219	0.0104
Fraxinus sp.	756.44	24	0.0011	0.0100
Gleditsia aquatica	1251.14	3	0.0019	0.0013
Ilex decidua	6353.13	279	0.0095	0.1165
Ilex opaca	16774.14	183	0.0250	0.0764
Liquidambar styraciflua	72524.65	269	0.1079	0.1124
Morus rubra	756.34	3	0.0011	0.0013
Nyssa aquatica	165115.83	106	0.2456	0.0443
Nyssa sylvatica	19.63	1	0.0000	0.0004
Pinus glabra	1176.53	10	0.0018	0.0042
Planera aquatica	4428.27	15	0.0066	0.0063
Platanus occidentalis	1992.56	6	0.0030	0.0025
Quercus laurifolia	90894.87	101	0.1352	0.0422
Quercus lyrata	57052.01	178	0.0849	0.0744
Quercus michauxii	1607.91	22	0.0024	0.0092
Quercus nigra	12765.47	69	0.0190	0.0288
Quercus pagoda	6833.75	11	0.0102	0.0046
Quercus phellos	6448.22	18	0.0096	0.0075
Styrax americana	66.46	10	0.0001	0.0042
Taxodium distichum	85711.29	54	0.1275	0.0226
Ulmus alata	4519.28	41	0.0067	0.0171
Ulmus americana	15910.25	55	0.0237	0.0230
Total	672251.15	2394	1.0000	1.0000

Savannah - Webb	Basal area	No. stems	Rel. BA	Rel. abund.
Acer rubrum	16622.17	46	0.0218	0.0359
Acer saccharinum	507.37	3	0.0007	0.0023
Aesculus pavia	20.76	9	0.0000	0.0070
Asimina triloba	22.24	12	0.0000	0.0094
Betula nigra	2121.36	2	0.0028	0.0016
Carpinus caroliniana	6557.88	68	0.0086	0.0531
Carya aquatica	81623.98	86	0.1069	0.0672
Carya glabra	1832.33	6	0.0024	0.0047
Carya sp.	1256.64	1	0.0016	0.0008
Cornus stricta	25.13	1	0.0000	0.0008
Crataegus sp. 1	2140.55	33	0.0028	0.0258
Diospyros virginiana	14.33	3	0.0000	0.0023
Forestiera acuminata	78.59	2	0.0001	0.0016
Fraxinus caroliniana	18419.80	55	0.0241	0.0430
Fraxinus pennsylvanica	46580.49	60	0.0610	0.0469
Fraxinus sp.	215.44	19	0.0003	0.0148
Gleditsia aquatica	40.89	2	0.0001	0.0016
Ilex decidua	5808.17	134	0.0076	0.1047
Ilex opaca	226.19	1	0.0003	0.0008
Liquidambar styraciflua	71723.25	145	0.0940	0.1133
Nyssa aquatica	123306.73	83	0.1615	0.0648
Nyssa biflora	1901.45	2	0.0025	0.0016
Nyssa sylvatica	3525.65	1	0.0046	0.0008
Pinus glabra	104.16	8	0.0001	0.0063
Planera aquatica	20332.93	94	0.0266	0.0734
Platanus occidentalis	29108.43	10	0.0381	0.0078
Populus heterophylla	13253.59	7	0.0174	0.0055
Quercus laurifolia	114585.13	75	0.1501	0.0586
Quercus lyrata	91942.64	100	0.1204	0.0781
Quercus michauxii	4539.60	2	0.0059	0.0016
Quercus nigra	16385.76	10	0.0215	0.0078
Quercus pagoda	7902.68	4	0.0104	0.0031
Styrax americana	241.90	12	0.0003	0.0094
Taxodium distichum	57210.07	113	0.0749	0.0883
Ulmus alata	4543.43	13	0.0060	0.0102
Ulmus americana	18324.12	56	0.0240	0.0438
Ulmus sp.	289.81	2	0.0004	0.0016
Total	763335.64	1280	1.0000	1.0000

APPENDIX 3: FLOODPLAIN SOILS

Altamaha floodplain soil characteristics (all samples). Cation concentrations are kg/ha.

	MOODY				PENHOLOWAY				BEARDS BLUFF			
	Swamp		BLH		Swamp		BLH		Swamp		BLH	
	#1	#2	#1	#2	#1	#2	#1	#2	#1	#2	#1	#2
pH	4.61	4.71	4.84	4.48	5.16	4.96	4.99	4.47	5.01	4.87	4.86	4.45
Ca	1490.72	1339.52	1082.70	718.26	1358.56	1674.40	1281.28	633.25	282.13	1005.42	1423.52	592.37
K	112.56	111.56	67.29	74.18	90.65	127.34	93.61	94.83	34.08	84.75	100.74	70.24
Mg	302.29	278.21	196.11	143.36	185.81	261.86	241.02	206.98	47.81	199.47	288.29	169.01
Mn	85.06	67.46	221.20	113.68	112.45	153.89	106.47	78.80	26.41	75.67	113.23	25.96
P	15.76	30.06	9.76	11.78	19.21	24.42	7.81	18.76	5.69	8.25	8.87	6.84
Zn	16.50	17.42	14.35	9.39	19.50	26.77	9.43	11.66	5.79	7.51	18.26	10.70
%N	0.20	0.22	0.14	0.12	0.09	0.14	0.10	0.10	0.03	0.08	0.15	0.09
%C	2.45	3.12	2.10	1.65	1.55	2.05	1.44	1.55	0.35	1.04	1.78	1.28
%Sand	7.60	5.60	45.60	31.60	53.80	29.80	41.80	29.80	93.80	55.80	17.80	27.80
%Silt	22.00	20.00	30.00	22.00	18.00	28.00	18.00	22.00	0.00	14.00	22.00	20.00
%Clay	70.40	74.40	24.40	46.40	28.20	42.20	40.20	48.20	6.20	30.20	60.20	52.20

Savannah floodplain soil characteristics (all samples). Cation concentrations are kg/ha.

	TUCKAHOE				SRS				WEBB			
	Swamp		BLH		Swamp		BLH		Swamp		BLH	
	#1	#2	#1	#2	#1	#2	#1	#2	#1	#2	#1	#2
pH	4.91	4.81	5.08	5.45	4.56	4.65	4.59	5.15	5.45	5.05	4.81	4.62
Ca	1270.08	1357.44	1025.70	1952.16	756.78	695.07	292.88	973.28	1768.48	1319.36	652.06	598.30
K	88.93	98.03	89.17	144.03	105.66	91.64	53.51	72.95	93.36	100.74	68.28	56.47
Mg	141.90	158.82	285.49	357.73	143.70	129.14	50.68	270.37	375.87	292.21	163.07	159.60
Mn	33.15	57.03	301.39	275.97	169.01	218.74	296.46	601.66	62.79	53.51	88.79	80.17
P	22.83	28.48	8.52	10.81	23.44	14.26	10.37	10.81	8.96	17.79	11.78	7.37
Zn	7.27	7.31	5.35	5.75	8.67	8.39	10.94	13.06	5.63	6.23	5.75	4.07
%N	0.20	0.19	0.21	0.26	0.22	0.17	0.22	0.15	0.13	0.10	0.09	0.16
%C	2.66	2.59	3.50	3.81	3.63	3.68	4.27	1.89	1.49	1.40	1.25	1.89
%Sand	1.60	5.60	17.60	37.60	7.60	5.60	41.60	25.60	7.80	27.80	35.80	13.80
%Silt	18.40	14.40	24.40	12.20	14.20	14.20	10.20	16.20	14.00	18.00	34.00	18.00
%Clay	80.00	80.00	58.00	50.20	78.20	80.20	48.20	58.20	78.20	54.20	30.20	68.20

APPENDIX 4: SAVANNAH FLOODPLAIN TREE CORES*

SRS	Diameter (cm)	Ring count	Coring height (m)
Carya cordiformis	46.5	135	1.40
Liquidambar styraciflua	34.0	62	1.40
Nyssa aquatica	29.0	94	1.40
Nyssa aquatica	36.0	77	1.40
Nyssa aquatica	37.0	121	1.40
Nyssa aquatica	42.0	134	1.66
Nyssa aquatica	42.0	134	1.68
Quercus laurifolia	56.3	77	1.40
Quercus lyrata	49.3	100	1.40
Quercus lyrata	57.8	151	1.40

Tuckahoe WMA	Diameter (cm)	Ring count	Coring height (m)
Acer rubrum	42.5	76	1.40
Carya aquatica	32.0	69	1.40
Carya aquatica	36.5	55	1.40
Carya glabra	46.5	99	1.40
Celtis laevigata	36.0	60	1.40
Fraxinus pennsylvanica	41.5	59	1.40
Nyssa aquatica	49.0	113	2.30
Nyssa aquatica	60.0	>327 (hollow)	2.45
Quercus laurifolia	60.5	69	1.40
Quercus lyrata	48.0	59	1.40
Quercus lyrata	56.0	74	1.40
Quercus nigra	23.8	20	1.40
Taxodium distichum	36.0	101	2.70
Taxodium distichum	42.5	86	1.40
Taxodium distichum	60.0	88	1.40

Webb WMA	Diameter (cm)	Ring count	Coring height (m)
Acer rubrum	33.5	52	1.40
Carya aquatica	43.0	70	1.40
Carya aquatica	49.0	63	1.40
Crataegus sp.	19.0	90	1.40
Fraxinus caroliniana	25.0	100	1.40
Fraxinus pennsylvanica	42.0	88	1.40
Liquidambar styraciflua	57.0	119	1.40
Nyssa aquatica	41.5	77	2.80
Planera aquatica	24.5	58	1.40
Platanus occidentalis	56.5	70	1.40
Quercus lyrata	26.0	48	1.40
Quercus lyrata	58.0	92	1.40
Quercus nigra	29.5	20	1.40
Taxodium distichum	34.0	83	2.60
Taxodium distichum	38.0	70	1.40
Taxodium distichum	54.0	110	2.80

*Rings of some species were difficult to distinguish, so ages are approximate.

APPENDIX 5: TRANSECT LOCATIONS

SAVANNAH	Length (m)	LAT	LON	Loc. (m)	Bearing (°)
Turkey Creek	100	33.79151	-82.15478	0	330
Turkey Creek	100	33.79184	-82.15414	0	0
Turkey Creek	100	33.79144	-82.15333	0	40
Stevens Creek	150	33.63677	-82.09847	0	45
Stevens Creek	100	33.63380	-82.09510	0	60
SRS	970	33.12782	-81.67315	50	180
SRS	817	33.10889	-81.67289	10	30
Tuckahoe WMA	2300	32.80070	-81.42914	35	270
Tuckahoe WMA	385	32.79848	-81.43901	100	0
Webb WMA	1235	32.57194	-81.31616	20	0
Webb WMA	665	32.56972	-81.30003	0	0

ALTAMAHA	Length (m)	LAT	LON	Loc. (m)	Bearing (°)
North Oconee	70	33.98743	-83.38604	0	90
North Oconee	200	33.98780	-83.38672	0	70
Oconee	250	33.67756	-83.29018	0	90
Moody Forest	425	31.92628*	-82.31630*	0	0
Moody Forest	1000	31.93738	-82.29476	10	315
Moody Forest	1142	31.92740	-82.27527	200	0
Beards Bluff	300	31.79083	-81.99134	30	45
Beards Bluff	780	31.79052	-81.96945	80	0
Beards Bluff	330	31.78903*	-81.96848*	0	180
Penholoway	800	31.55156*	-81.68312*	0	210
Penholoway	1360	31.54142	-81.67102	350	225

* Indicates coordinates were estimated from aerial imagery
Length = transect length
Location = coordinate position on transect