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LARGE WOOD DEBRIS RECRUITMENT ON DIFFERING RIPARIAN LANDFORMS ALONG A GULF COASTAL PLAIN (USA) STREAM: A COMPARISON OF LARGE FLOODS AND AVERAGE FLOWS

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ABSTRACT

In southeastern Coastal Plain streams, wood debris can be very abundant and is recruited from extensive forested floodplains. Despite importance of wood debris, there have been few opportunities to examine recruitment and redistribution of wood in an undisturbed setting, particularly in the southeastern Coastal Plain. Following extensive flooding in 1994, measurements of individual downed trees (species, dbh, orientation, distance from base-flow channel and condition) were made across replicated riparian landforms in a Gulf Coastal Plain 5th-order stream. Annually, the fate of these trees was determined and newly recruited trees were noted. More than 300 downed trees have been recorded. Recruitment varied across landforms with more constrained reaches having greatest mortality. Total tree mortality varied substantially across years. Generally, tree recruitment was greatest in years with substantial floods (1994 and 1998). For each riparian landform type, tree mortality was correlated with the maximum daily flow during the period preceding annual debris surveys. This relationship was particularly strong for sand ridges ($r^2 = 0.942$) and low terraces ($r^2 = 0.915$), but was significant for floodplains ($r^2 = 0.413$). Greatest rates of debris recruitment per maximum daily flow were observed for sand ridges followed by low terraces. Flood characteristics also influenced debris recruitment. The 1994 flood was caused by a tropical storm and resulted in a rapid rise in streamflow. Much of the debris recruited during this flood was from toppled trees and was oriented parallel to the stream channel. In contrast, the 1998 flood was preceded by a wetter than average winter with more gradually rising flows and there was no relationship between riparian landform and debris characteristics. These results indicate that wood recruitment dynamics in Coastal Plain streams are complex. Wood recruitment rates are controlled by cyclical variations in climate interacting with riparian geomorphology. Infrequent high flows appear critical in the maintenance of the instream debris pool.

KEY WORDS: large wood debris; floods; coastal plain; riparian; geomorphology; climate cycles

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INTRODUCTION

Throughout North America and most of the world, there has been a long history of wood removal from streams and rivers (Sedell and Froggatt, 1984; Triska, 1984; Gippel *et al.,* 1996; Benke, 2001; Montgomery and Piegay, 2002). In addition, extensive riparian deforestation combined with flow regulation and channelization has reduced overbank flooding and limited potential sources of large wood debris (LWD) recruitment into larger streams and rivers (Sedell and Froggatt, 1984; Gippel *et al*., 1996; Benke, 2001).

Yet, numerous studies (see Gurnell and Sweet, 1998) have documented the importance of LWD in streams and rivers (e.g. habitat for fishes and invertebrates, bank stabilization, sediment retention, altering water flow, structuring instream and riparian habitat, and enhancing productivity). While there is widespread recognition of the role of wood debris, there have been few opportunities to examine its dynamics in an undisturbed setting, particularly in larger streams and rivers.

In southeastern Coastal Plain, USA streams, LWD appears to be particularly important in contributing to stream foodwebs. Invertebrate diversity, habitat-specific abundance, biomass and productivity are greater on submerged

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wood debris compared to other habitats (Benke *et al*., 1985; and reviewed by Benke, 2001). Many streams and rivers of the southeastern Coastal Plain have a long history of human-caused degradation. Beginning in the early 1800s with snagging operations and continuing through the 1900s with river regulation and pollution, streams have been managed for human benefit with little thought to ecological consequences (Benke, 1990, 2001).

While human degradation is prevalent, many free flowing streams remain in the southeast. For example, Georgia has five rivers with segments of greater than 200 km that are considered unregulated (Benke, 1990). Many of their major tributaries have little flow regulation on their main stems. Also, in some areas the distribution of human populations has changed dramatically during the past 100 years. For example, since 1920 the population of many rural counties in southwest Georgia has been declining. This has resulted in decreasing numbers of small farms and livestock, particularly along stream corridors (e.g. Craft and Casey, 2000). It has also resulted in the consolidation of farms into large operations concentrated in the uplands (Craft and Casey, 2000). As a result, riparian forests have recovered to some degree from extensive disturbance in the late 1800s and early 1900s (Craft and Casey, 2000) and are approaching maturity (Lynch *et al*., 1986). As a consequence of changing human land use, extensive and intact riparian areas occur along many streams. These rivers and their tributaries offer an opportunity to examine the recovery of stream/riparian interactions under minimally altered flow regimes.

This paper represents a continuation of a previous study examining the influence of riparian geomorphology on wood debris recruitment in a Gulf Coastal Plain stream (Palik *et al*., 1998). Previous work suggested that debris recruitment was pulsed in nature and associated with a large flood. Floodwaters interacting with spatial drivers (i.e. riparian landform) also influenced recruitment rates and debris characteristics. This study examines debris recruitment across the same landforms but contrasts two large floods as well as years of average flow. The first flood (1994) was the result of an early summer tropical storm (reported in Palik *et al*., 1998) and the second flood (1998) was the result of above average winter rainfall associated with El Niño conditions in the Pacific Ocean. Specific objectives are (1) to compare debris recruitment rates in average flow years with those with substantial flooding, (2) to compare debris recruitment rates and characteristics across differing riparian landforms and (3) to examine the effects of substantial floods of differing magnitude and antecedent conditions on debris recruitment rates and characteristics.

METHODS

Study area

This study was conducted at the Ichauway Ecological Reserve, an 11 500 ha reserve located in southwestern Georgia, USA, in the Plains and Wiregrass Subsections of the Lower Coastal Plains and Flatwoods Section (ECOMAP, 1993; Keys *et al*., 1995). The reserve is bisected by 23 km of Ichawaynochaway Creek, a 5th-order black-water stream with headwaters that originate in swamp-forest. Mean bank-full width of the stream is about 30 m. Flow in Ichawaynochaway Creek is low and stable in summer and fall. Late winter and early spring storms often result in bank-full discharges, causing flooding of low-lying areas. A long-term USGS stream gaging station is located approximately 18 km upstream from the northern boundary of Ichauway (USGS Milford Gage 02353500). Average annual discharge is $22\,m^3\,s^{-1}$ (Hickey *et al*., 2002).

A series of repeating riparian landforms occur along the stream corridor and include sand ridges, terraces and floodplains (Goebel *et al*., 1996; Palik *et al*., 1998). Floodplains occur along reaches with broad stream valleys and are low in elevation relative to the base-flow channel. Floodplains support a mixed-hardwood forest community. Sand ridges occur within narrower valley segments and, compared to floodplains, are high in elevation above the base-flow channel. Sand ridges support a sparse canopy of longleaf pine (*Pinus palustris* Mill.) and scrub oaks (*Quercus* spp.). Terraces are abandoned floodplains that occur in stream valleys of variable width and elevation. Terraces support longleaf pine forest or mixed-hardwood forest where surface fire has been excluded.

The streamside forest on each of the riparian landforms, that is, the forest growing laterally along stream banks and levees (Palik *et al*., 1998), are mature or climax (Lynch *et al*., 1986). They support a diverse woody community with up to 47 tree species (stems having a dbh $\geq$ 5 cm). Carolina ash (*Fraximus caroliniana*, Mill.), eastern red cedar (*Juniperus virginiana* L.), bald cypress (*Taxodium distichum* (L.) Rich.) and southern live oak (*Quercus*

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virginiana Mill.) are the dominant species (Palik *et al*., 1998). Composition of the streamside community was similar across the riparian landforms at the beginning of the study (Palik *et al*., 1998).

Reach and study site characteristics

Wood debris recruitment was sampled in six reaches. The reaches and adjacent forests had minimal human disturbance and were representative of the range of riparian landforms along the stream. Stream channel morphology has not been altered by human activities, although some removal of coarse woody debris did occur up until the 1980s near boat landings (J. Adkinson, J. W. Jones Ecological Research Center, personal communication). Both sides of each reach were sampled, since riparian geomorphology was not always similar on opposite sides of the reach. Upper and lower reach boundaries were determined from field observations, as well as changes in soils and vegetation apparent on GIS data layers. Average elevation was determined separately for each landform using topographic information. Stream valley width was estimated as the distance from upland terrace to upland terrace at each reach. For this study, riparian landform elevation and stream valley width were used as measures of valley constraint. Reach shape (inside or outside of a meander, straight) was determined from field observations and aerial photography. In all reaches, the stream consisted of a single channel. Physical characteristics of study sites were reported by Goebel *et al*. (1997) and Palik *et al*. (1998). Riparian landforms sampled included three sand ridges, six low terraces and three floodplains.

Hydrological conditions

During 1994, Tropical Storm Alberto and a number of other tropical storms resulted in near record precipitation (192 cm total, 62 cm above average) in Southwest Georgia. Ichawaynochaway Creek and many of the other streams in the Flint River Basin registered the greatest daily discharge on record during July of 1994, which was >500-year recurrence interval (USGS gage 02353500, Table I). Streams in the region remained at or above average discharge during the summer and fall of 1994 and through the spring of 1995 (Figure 1). Maximum discharge during the spring of 1995 had a recurrence interval between 5 and 10 years (Table I). In 1996 and 1997 hydrological conditions were typical of average conditions, with high flows in late winter/spring and lower flows in summer/autumn (Figure 1). Maximum streamflows during 1996 and 1997 had recurrence intervals of less than 2 years. During the winter of 1997 and 1998 above average rainfall resulted from El Niño conditions, the warm phase of El Niño/Southern Oscillation (ENSO). An early spring storm with regional rainfall amounts averaging 20 cm caused extensive flooding and the second highest flows of record in many streams of the lower Flint River basin (Figure 1). Stream discharge was slightly less than the 200-year recurrence interval (Table I).

Table I. Magnitudes and dates of maximum daily flows on Ichawaynochaway Creek in southwest Georgia

Debris recruitment year	Maximum average daily discharge ($m^3 s^{-1}$)	Date of maximum discharge	Recurrence interval (years)
1994	850	7 July 1994	>500
1995	247	13 February 1995	5–10
1996	73	6 February 1996	<2
1997	102	25 February 1997	<2
1998	532	10 March 1998	100–200
1999	62	26 January 1999	<2
2000	71	4 July 1999	<2
2001	76	23 March 2001	<2
2002	39	14 March 2002	<2
2003	111	10 March 2003	<2

Data are from USGS gage 02353500 (http://waterdata.usgs.gov/ga/nwis accessed January 2004). LWD recruitment year is the year a new piece of LWD was first noted and measured. Maximum discharge and when it occurred were determined prior to annual sampling (see Methods).

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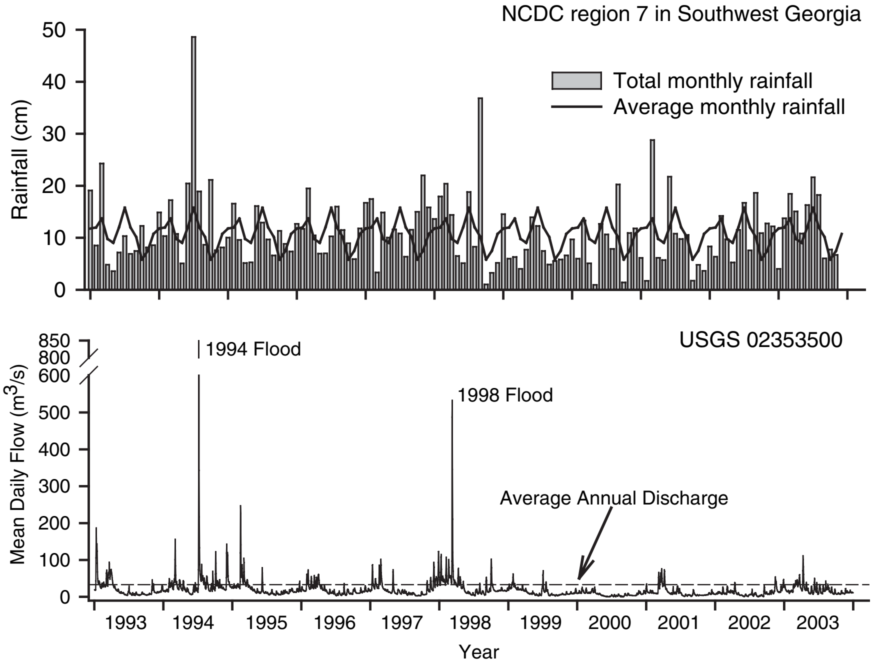

Figure 1. Total monthly rainfall (top panel) and average monthly rainfall for southwestern Georgia. Mean daily flow and average annual discharge (bottom panel) for Ichawaynochaway Creek in southwestern Georgia.

In November 1998, a period of below normal rainfall began. Most of the region was classified as being in a severe to exceptional drought based on drought severity indices (Water Resources of Georgia—http://ga.water.usgs.gov/ accessed January 2004). Total rainfall for 2000, considered the worst year of the drought, was approximately 35 cm below the long-term average, with the lowest flows on record occurring that summer (Figure 1). During 2001–2002 streamflow was generally below long-term averages, with only 5 months recording average or greater amounts of rainfall (Figure 1). The drought abated during the winter of 2002 and spring of 2003 with a return to near normal amounts of rainfall (Figure 1). From 1999 to 2003, the recurrence interval for maximum average daily discharge was <2 years.

LWD sampling

LWD recruitment was sampled initially following the summer 1994 flood and continued annually following large floods or more normal later winter/early spring high-flow periods. On each sampling date only recently recruited trees were sampled. Recent debris was distinguished from older debris by the absence markings from previous surveys and the presence of attached leaves and buds, or intact branches or root-plates. LWD was defined as newly recruited trees that had a dbh ≥ 5 cm and a length of at least 3 m. The lateral area for debris sampling was restricted to the active channel at approximately bank-full width. Measured debris characteristics in each reach included counts of tree mortality (i.e. recruitment into the coarse woody debris pool), species or genera of newly recruited debris, tree dbh, distance of dead trees from base-flow channel (m), contact of trees with the base-flow channel (yes, no), orientation of tree with respect to current flow (expressed as an angle, where parallel to flow with branches downstream was set at $0 \pm 10°$) and tree condition (presence of intact root-plate, presence of branches). Recruitment of trees into the stream was expressed both as a rate (number of newly recruited trees per km reach length) and as frequencies (% of the total pre-flood population of trees in the streamside forests corrected for prior mortality; Palik *et al*., 1998). Each dead tree was labelled with a numbered aluminium tag and its position recorded using a global positioning system. Some trees killed and deposited into the stream, particularly small-diameter individuals may have been transported out of our sample areas and into locations other than the active channel, for

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example floodplains. Although we saw little evidence of this, we could not account for these individuals; consequently, our debris recruitment rates may underestimate actual rates.

Data analysis

Rates of tree mortality across landforms were compared using Friedman Repeated Measures Analysis of Variance and Linear Regression (Sigma Stat Version 3.1, Richmond, CA; SAS version 9.1, Cary, NC). Redundancy analysis (RDA) was used (Davies and Tso, 1982; Ter Braak and Prentice, 1988) to relate characteristics of both recently recruited coarse woody debris (i.e. flood-killed trees) to geomorphic characteristics of stream sites. Characteristics of flood-recruited debris used in RDA included: recruitment rate (number of trees recruited into the stream/km stream length and % of original population of live streamside trees); mean distance of dead tree from base-flow channel (m); contact of dead tree with base-flow channel (% of trees in a reach); crown intact (% of trees in a reach); root-wad present (% of trees in a reach) and orientation of dead tree in the stream (% perpendicular, % parallel). Geomorphic characteristics included average width of the stream valley (m), average elevation of riparian landforms (m), reach length (m) and reach shape (straight, inside meander, outside meander). Reach shape was included as a categorical variable in the analyses. The RDA was run on correlation matrices of untransformed data, and ordination diagrams were constructed using correlation biplot scaling.

RESULTS

Comparison of wood recruitment across all years

Total tree mortality varied substantially across years. Generally, tree recruitment rates were greatest in years with substantial floods (1994 and 1998) and debris recruitment during 1994 was significantly greater than other years (Figure 2, repeated measures ANOVA on ranks, $p < 0.001$). Tree mortality also varied across riparian landform. Sand ridges and low terraces generally had greatest mortality during 1994, the year with greatest flooding (Figure 3). However, significant differences were only detectable for low terraces (Figure 3, repeated measures ANOVA on ranks, $p = 0.001$). The pattern of debris recruitment for floodplains was somewhat different with greatest mortality occurring during 1998 (Figure 3), the year with wetter than average conditions during winter and early spring (Figure 1). For each riparian landform type, tree mortality was correlated with the maximum daily flow

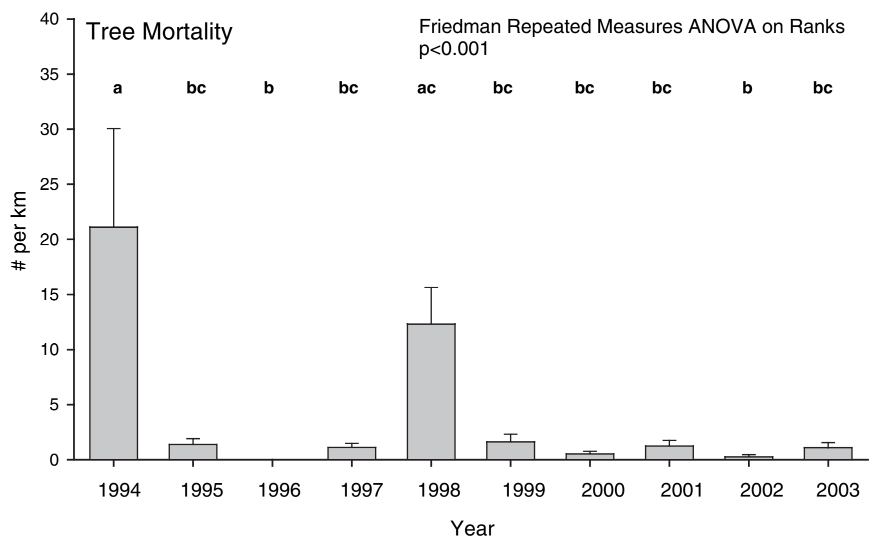

Figure 2. Annual tree mortality (# per km) in Ichawaynochaway Creek in southwestern Georgia. Error bars indicate 1 s.d. Bars with differing letters are significantly different based on Friedman repeated measures ANOVA on rank.

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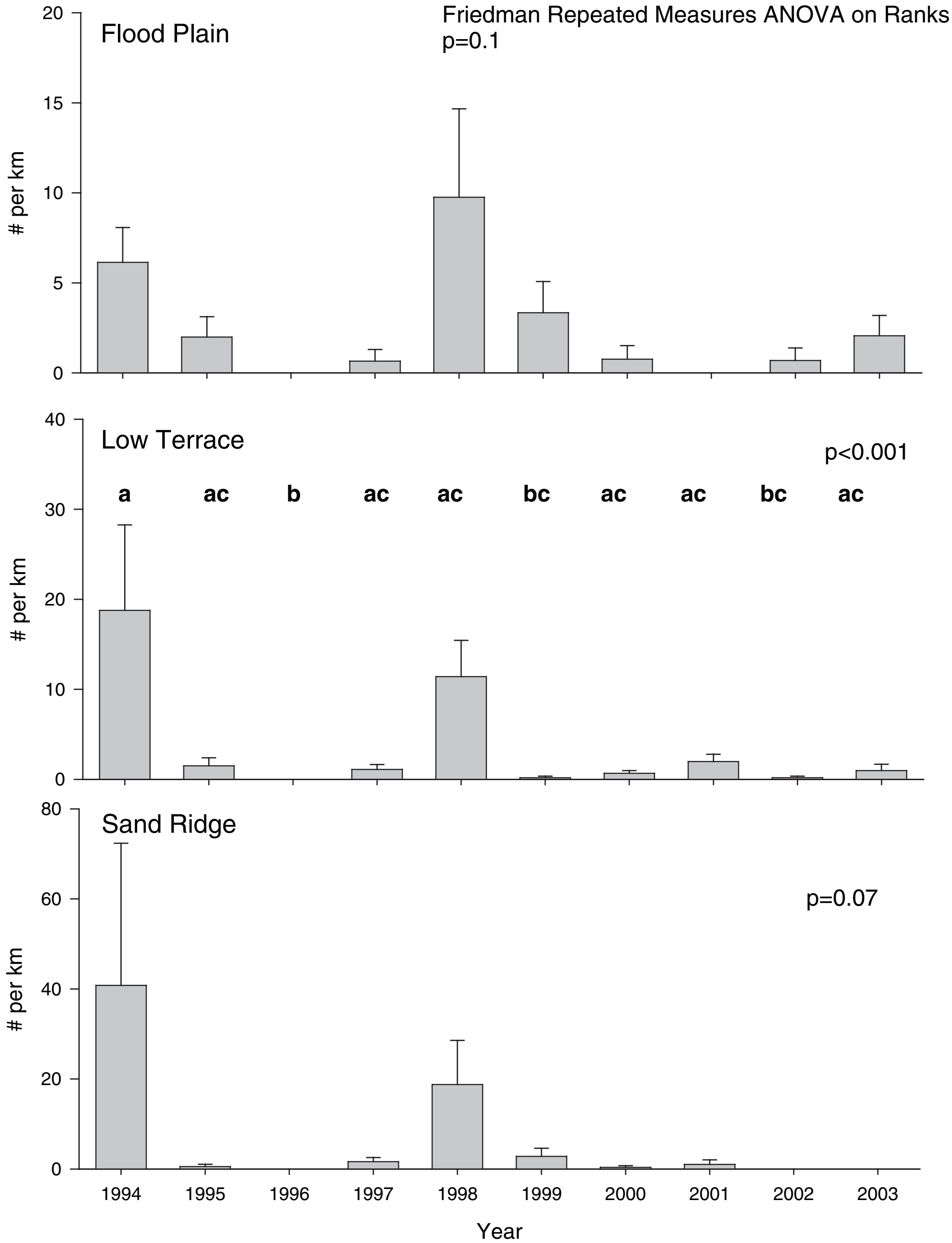

Figure 3. Annual mortality rates (# per km) across differing riparian landforms in Ichawaynochaway Creek in southwestern Georgia. Error bars indicate 1 s.d. Within a panel bars with differing letters are significantly different based on Friedman repeated measures ANOVA on rank.

during the period preceding annual debris surveys. This relationship was particularly strong for sand ridges ($r^2 = 0.942$) and low terraces ($r^2 = 0.915$), but was significant for floodplains as well ($r^2 = 0.413$) (Figure 4). Slopes of regression lines were significantly different for the different riparian landforms (ANCOVA; $p < 0.0001$). Greatest rates of debris recruitment per maximum daily flow were observed for sand ridges followed by low terraces. Flood plains had the lowest rates of debris recruitment. Tree mortality was also related to the maximum monthly flow for the period preceding debris surveys although the strength of the relationship tended to be weaker

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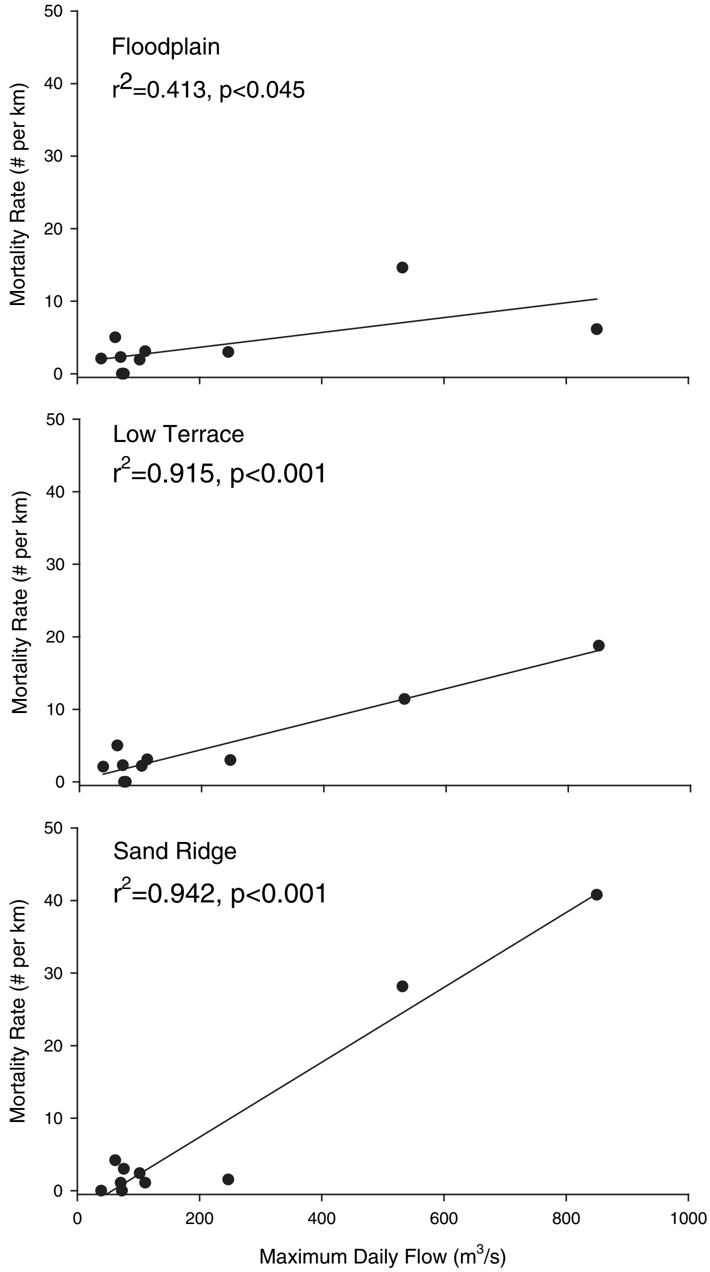

Figure 4. Linear regressions of tree mortality rate versus annual maximum daily flow by landform for Ichawaynochaway Creek in southwestern Georgia.

than for maximum daily flow ($r^2 = 0.86$, 0.80, 0.40 for sand ridges, low terraces and flood plains, respectively, regressions not shown).

Comparison of debris characteristics during 1994 and 1998 floods

Only during substantial floods (i.e. 1994 and 1998) was debris recruitment sufficiently abundant to permit comparison of debris characteristics. During the 1998 flood, debris was recruited over a slightly longer average distance from the base-flow channel than in 1994 (Table II). Mortality frequency (% of pre-flood forest corrected

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Table II. Characteristics of large wood debris recruited during large floods in 1994 and 1998

	1994 Flood mean (s.d.)	1998 Flood mean (s.d.)
Average distance from base-flow channel (m)	0.9 (1.1)	1.8 (0.9)
Mortality (# per km)	22.3 (31.5)	12.3 (11.6)
Mortality (% of population)	9.9 (15.7)	7.2 (10.4)
Contact with base-flow channel (%)	66.6 (30.7)	42.0 (29.3)
Perpendicular to base-flow channel (%)	42.4 (40.3)	45.0 (22.2)
Parallel to base-flow channel (%)	56.2 (42.1)	32.9 (21.2)
Root-plate present (%)	85.7 (13.4)	87.5 (22.5)
Crown intact (%)	76.3 (19.1)	85.5 (16.5)

for annual mortality) and percentage of downed trees perpendicular to the base-flow channel were similar among floods. The 1994 flood had a greater frequency of wood in contact with the base-flow channel and a greater frequency of wood parallel to the base-flow channel (Table II). During both floods comparable numbers of downed trees had intact root-plates; however, a greater percentage of downed trees had intact crowns following the 1998 flood.

Wood debris recruited during floods was generally small. Median diameter of downed trees ranged from 16.5 to 25 cm dbh (Figure 5). There were no consistent differences in the size of debris recruited across landforms for either flood (ANOVA on ranks, $p > 0.05$). Riparian landform types differed in the size of debris recruited across floods. For both floodplains (Mann Whitney Rank Sum Test, $p = 0.08$) and sand ridges ($p = 0.05$) downed trees recruited during the 1994 flood were slightly larger in diameter than those recruited in 1998.

During the floods, three taxa, eastern red cedar, river birch (*Betula nigra* L.) and oak accounted for 75% of all downed trees. Dominant taxa differed in their susceptibility to flood-induced mortality. Percent mortality of river birch and eastern red cedar was significantly greater than their percent composition during the 1994 flood, while percent mortality of bald cypress and other species combined was significantly less than their percent composition (paired *t*-tests, $p < 0.05$, Figure 6). During the 1998 flood, river birch again had greater percent mortality than percent composition. Oaks and bald cypress were under-represented in the debris pool compared to their percent composition in 1998 (paired *t*-tests, $p < 0.05$, Figure 6).

RDA of debris characteristics

RDA between debris characteristics and reach geomorphology accounted for 70.6% of total variation for the 1994 flood and 78.6% for the 1998 flood (Table III). During both floods, the first two axes of the analysis accounted for most of the variation (Table III, Figures 7 and 8). Correlation coefficients between debris characteristics and reach geomorphology were 0.929 and 0.732 for the 1994 flood and 0.963 and 0.973 for the 1998 flood for axes 1 and 2, respectively.

In interpreting the RDA the axes are related to reach geomorphology, with the strength of the relationship proportional to vector length and orientation (Figures 7 and 8, dashed lines). Longer vectors have a greater weight in the analysis and proximity to an axis is an indication of the strength of the relationship between that factor and the axis. Vectors for debris characteristics are interpreted in a similar manner (Figures 7 and 8, solid lines). Centroid locations for categorical variables (reach shape, Figures 7 and 8, solid squares) reflect associations between debris characteristics and reach shape.

The RDA analyses suggest both similarities and differences in the characteristics of wood debris and reach geomorphology during the floods. For both floods, landform elevation was strongly correlated with an RDA axis (axis 2 in 1994, $r = -0.86$; axis 1 in 1998, $r = 0.85$). During both floods greatest tree mortality (frequency and # per km) was associated with higher elevation landforms (Figures 7 and 8). The average distance of downed trees from the base-flow channel was also greater for higher elevation landforms. Downed trees on low elevation landforms or those with broad stream valleys were more likely to be in contact with the base-flow channel for both floods. Debris orientation during the 1994 flood was strongly associated with stream valley width and reach shape. Downed trees

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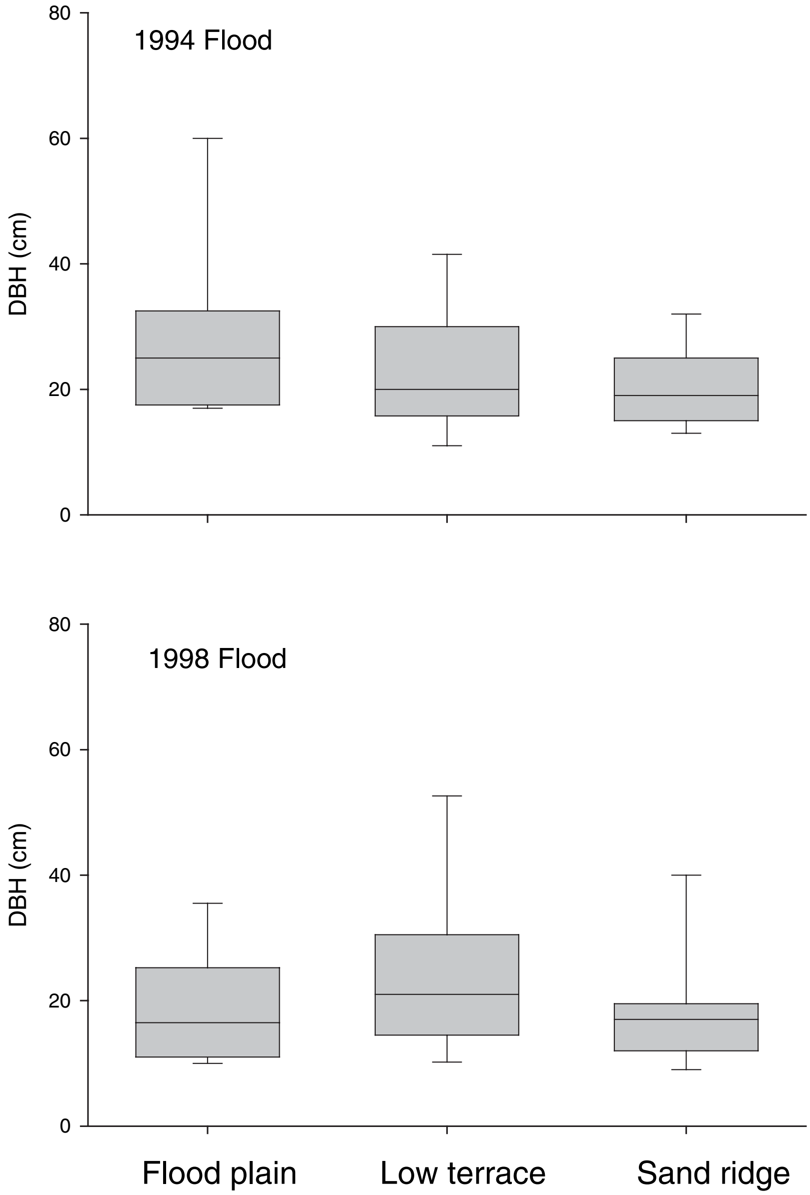

Figure 5. Diameters of downed trees by landform for two large floods in Ichawaynochaway Creek in southwestern Georgia.

in broad stream valleys tended to be oriented perpendicular to the stream channel while those in more constrained reaches tended to be parallel (Figure 7). Perpendicular orientation was more likely to occur on the outside of a meander while parallel orientation tended to occur on straight reaches. In contrast, debris orientation was not strongly associated with reach characteristics during the 1998 flood.

DISCUSSION

Factors influencing debris recruitment and characteristics

Our study indicates that large floods, that is those with much greater than bank-full discharge, are a significant source of wood debris recruitment to coastal plain streams. In addition to debris recruitment, large floods probably

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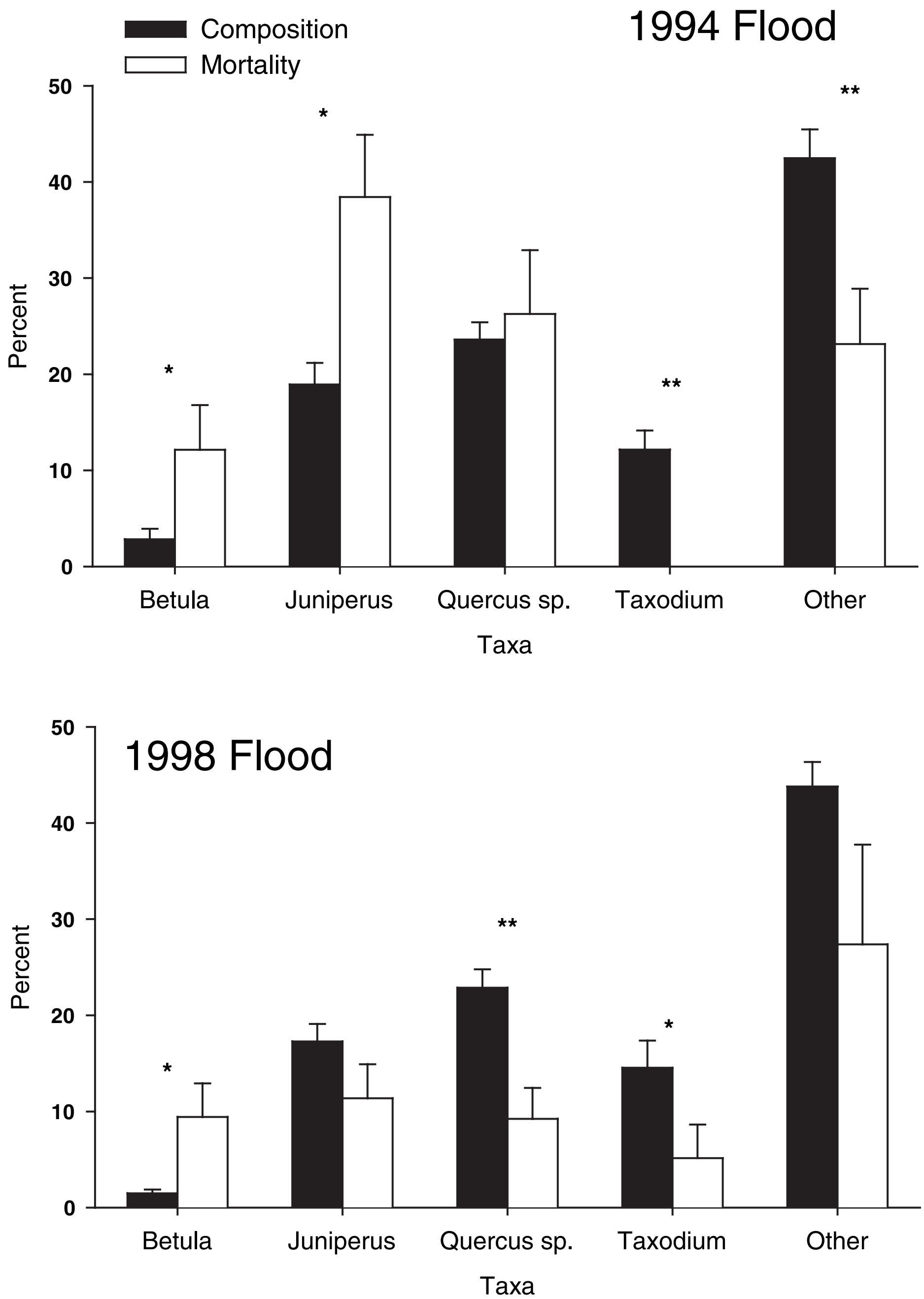

Figure 6. Frequency of tree species in riparian forests and their contribution to the debris recruitment in Ichawaynochaway Creek in southwestern Georgia. Error bars indicate 1 s.d. Bars with stars indicate a significant difference between composition and mortality ($^{*}p < 0.05$, $^{**}p < 0.01$).

provide a number of additional ecological benefits to streams and riparian areas, including stimulating recruitment of aquatic fauna, maintenance of habitat heterogeneity and providing pulses of biologically important material that stimulate productivity (Michener and Haeuber, 1998). This is consistent with the growing recognition that diverse natural hydrological regimes are important in controlling the structure and function of stream ecosystems (Decamps *et al.*, 1995; Gore and Shields, 1995; Stanford *et al.*, 1996; Wootton *et al.*, 1996; Richter *et al.*, 1997).

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Table III. Summary statistics for redundancy analysis of downed-tree characteristics with stream reach geomorphic characteristics for 1994 and 1998 floods

	RDA1	RDA2	RDA3
1994 Flood			
Eigenvalue[†]	0.534	0.124	0.004
Downed tree/reach or geomorphic correlation	0.929	0.732	0.733
Cumulative variation of downed tree characteristics (%)	53.4	65.8	70.2
Cumulative variation of downed tree/segment relation (%)	75.6	93.2	99.4
1998 Flood			
Eigenvalue[‡]	0.332	0.322	0.080
Downed tree/reach or geomorphic correlation	0.963	0.973	0.672
Cumulative variation of downed tree characteristics (%)	33.2	65.4	73.4
Cumulative variation of downed tree/segment relation (%)	42.2	83.2	93.4

[†]Sum of all canonical eigenvalues = 0.706.
[‡]Sum of all canonical eigenvalues = 0.786.

While large floods are infrequent, and thus unpredictable events, their occurrence can be linked to long-term variations in climate. Two primary factors, the ENSO and tropical storm frequency, influence the seasonal timing and annual variation in rainfall in the Southeastern US. ENSO is a cyclical variation in the sea surface temperature of the eastern Pacific Ocean. Warmer than average temperatures, termed El Niño, cause greater than average winter rainfalls (Green *et al*., 1997). The early spring flood we observed in 1998 was a result of El Niño conditions. Since 1945, El Niño conditions have occurred during 11 years.

Tropical storm frequency also strongly influences patterns of rainfall and streamflow, particularly late summer and early autumn (Golladay *et al*., 2000). From 1899 to 1992, 219 hurricanes including 89 major hurricanes ($\geq$category 3; Gray, 1990) affected the southeastern US (Michener *et al*., 1997). Tropical storm frequency, and in particular major hurricane frequency, is associated with cyclical variations in sea surface temperatures and patterns

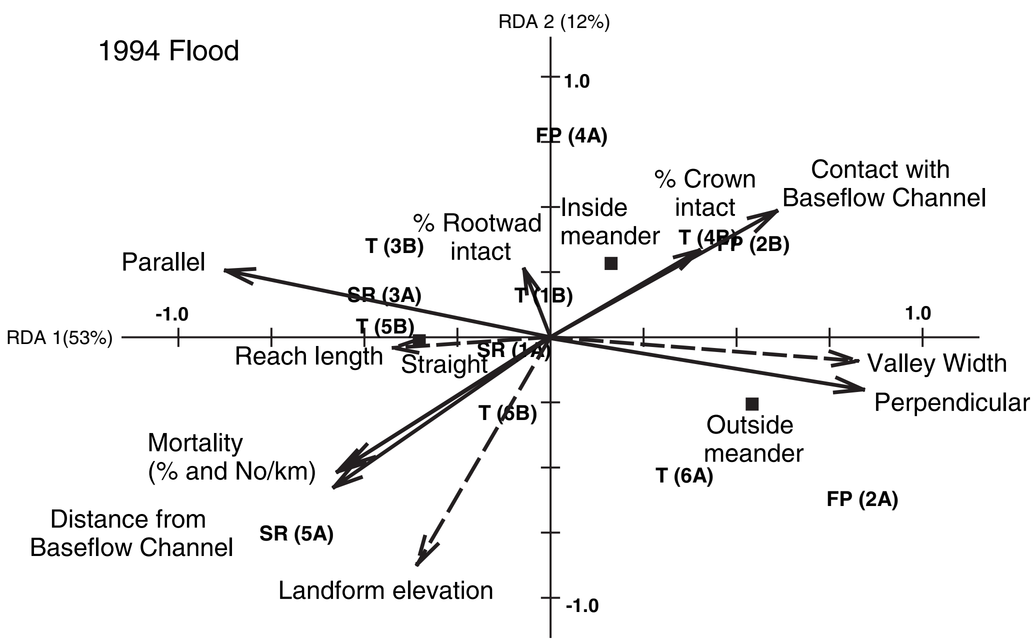

Figure 7. Redundancy analysis triplot of stream coarse woody debris characteristics (solid vectors) and riparian geomorphic variables (dashed vectors; solid squares) for a 1994 flood in Ichawaynochaway Creek in southwestern Georgia.

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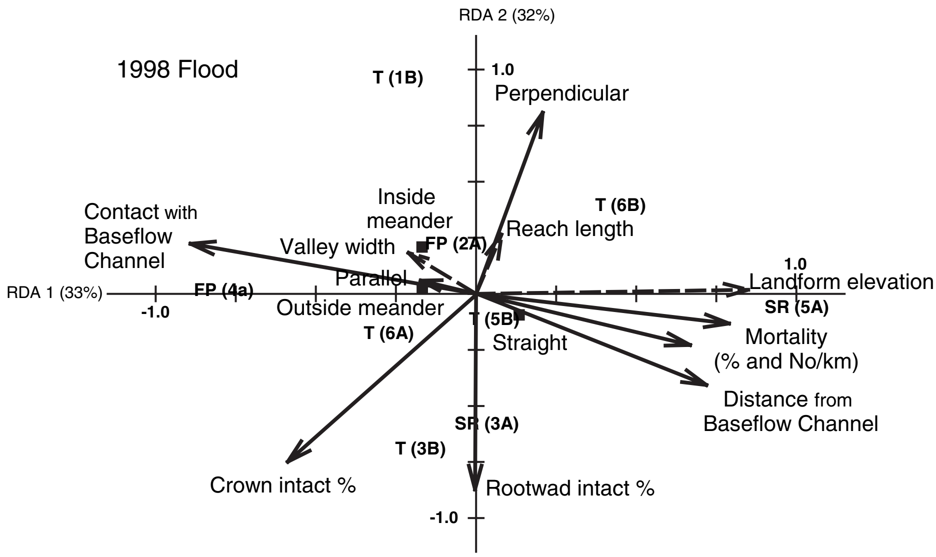

Figure 8. Redundancy analysis triplot of stream coarse woody debris characteristics (solid vectors) and riparian geomorphic variables (dashed vectors; solid squares) for a 1998 flood in Ichawaynochaway Creek in southwestern Georgia.

of precipitation in western Africa (Gray, 1990). For example, the period from 1947 to 1969 was warmer and wetter than average, resulting in greater frequencies of hurricanes than the period from 1970 to 1987 (Gray, 1990). Thus, while large floods are not predictable, their occurrence in the southeast is linked to cyclical climatic fluctuations and associated periods of greater than average rainfall. In turn, cyclical variations in rainfall cause periodic pulses of wood debris to enter streams and rivers.

Geomorphic differences among reaches resulted in differential patterns of tree death and coarse woody debris recruitment into the stream, a result that is consistent with the view that landforms control a variety of stream ecosystem patterns and processes (Swanson *et al*., 1988; Swanson, 2003). Differences in debris recruitment among landforms were consistent across floods. Constrained reaches, that is, those with higher riparian landform elevations (sand ridges and some terraces) had the highest tree mortality and subsequent recruitment of new debris into the stream. In contrast, unconstrained reaches, having lower riparian landform elevations (floodplains and some terraces), had lower rates of recruitment. We attribute higher mortality with increasing constraint to greater current velocities during floods (e.g. Malanson, 1993). Over the long term, debris inputs to coastal plain streams appear to be both spatially and temporally variable and largely controlled by the interaction of climate cycles and riparian geomorphology.

Characteristics of recently recruited wood debris varied across riparian landforms, but this effect was not consistent across floods. In the 1994 flood, constrained reaches had more debris pieces oriented parallel to streamflow than unconstrained reaches and this was attributed to differential mechanisms of mortality (Palik *et al*., 1998). Along sand ridges (relatively constrained), trees were uprooted by force of the current and deposited near the bank. In floodplains (relatively unconstrained), trees were undermined through bank cutting, followed by collapse into the active channel. In contrast, there was little relationship between wood debris characteristics and riparian landform during the 1998 flood. The lack of relationship may have been caused by antecedent conditions. The extended wet period preceding the flood may have reduced the differential impacts of current across landforms because riparian soils were all saturated. Saturated soils would tend to reduce anchoring, making trees on all landforms susceptible to flooding. The absence of a riparian landform effect on orientation might also be due to the depletion of particularly susceptible trees caused by the preceding (1994) flood.

Variation in debris abundance and physical characteristics among streams has been linked to compositional differences of riparian forests (e.g. Silsbee and Larson, 1983). However, the initial (i.e. pre-1994) composition of the streamside forests in our study was similar across riparian landforms. Consequently, differences in debris

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recruitment rates and physical characteristics of downed trees did not appear to be the result of variation in abundances of susceptible species among riparian landforms.

Individual taxa, however, did vary in their susceptibility to floods and this varied across floods. In the 1994 flood, eastern red cedar and river birch were prone to flood mortality (Palik *et al*., 1998). Both species have dense branch networks (personal observations); and it was assumed that their growth-form exposed them to greater current force during floods. In the 1998 flood, only river birch was prone to flood mortality. The reduced relative mortality of eastern red cedar during the 1998 flood may have been due to the loss of susceptible trees in 1994. Bald cypress, in contrast, was resistant to flood damage during both floods even though it grows near and within the base-flow channel. Bald cypress has few low branches which, along with root buttressing, may provide resistance to uprooting (Wilhite and Toliver, 1990). Thus, long-term patterns of streamside forest composition may not be determined solely by interactions of flooding and riparian geomorphology. However, forest composition immediately following large floods may be altered as particularly susceptible species are reduced in abundance. In particular, constrained landforms, with relatively high mortality rates, may be characterized by a depletion of susceptible species. Presumably, inter-flood periods are essential to the reestablishment of those species.

Implications for conservation and management of Coastal Plain streams

The temporal trends in debris recruitment we observed are consistent with debris recruitment in many terrestrial and aquatic systems, where low rates of recruitment are punctuated by occasional pulses during infrequent disturbances (Harmon *et al*., 1986; Fetherston *et al*., 1995). Over longer periods of time background mortality may often result in greater tree death than infrequent disturbances (Harmon and Hua, 1991). Pulsed input of debris, as we observed may be as important as cumulative abundance.

Larger floods and pulsed debris inputs are often lacking in regulated rivers (Malanson, 1993; Gore and Shields, 1995; Johnson *et al*., 1995). In a regulated river system it may be desirable to stimulate debris recruitment in order to provide the associated ecological benefits. It may also be unrealistic or undesirable to wait for a large-magnitude flood necessary for a significant pulse of debris. The relationship we observed between maximum average daily flow and debris input has important implications for river management and can provide some guidance in this area. For example, in our study, a discharge equal to two times greater than average annual maximum flow would hypothetically result in the recruitment of 42%, 45% and 89% of the debris recruited during the 1994 flood for sand ridges, low terraces and floodplains, respectively (determined from Figure 3). A flood pulse equal to the long-term average annual maximum flow would recruit about half that amount. This relationship could be established for unregulated reference rivers and then tested in regulated rivers in the same region by the release of artificial flood pulses. If a river has been regulated for an extended period, the amount of recruitment may even be higher than predicted due to an extended period without flooding. The timing and duration of flood pulses could be varied under differing climatic regimes (i.e. wetter versus drier) to provide additional heterogeneity in the characteristics of debris inputs.

Our results are also consistent with the observation that some river systems are composed of a mosaic of functional units rather than a gradient of gradually changing conditions from small to larger streams (Frissell *et al*., 1986; Pringle *et al*., 1988). This also has important consequences for river management and conservation. In our case, constrained reaches, the primary source of debris recruitment, represent about 12% of total stream length (Palik *et al*., 1998). Therefore, protection or restoration of constrained reaches would therefore be a critical priority in the development of stream conservation or management plans because they are the primary source of wood recruitment. Additionally, as trees have begun to break down and enter the mobile debris pool, we have observed that many unconstrained or floodplain reaches act as depositional areas for debris (Golladay, personal observation). These reaches represent an additional 6% of stream length (Palik *et al*., 1998). While debris recruitment is only one aspect of stream structure, it is recognized as a critical element of coastal plain streams (Benke, 2001). Our results indicate that this element of stream structure might be preserved by targeting a modest amount of stream length (approximately 18%). We acknowledge that complete and intact stream buffers (i.e. mature forests in the southeast) covering entire floodplains are a desirable goal. However, this goal is seldom attained in a developed watershed. If conservation priorities need to be established then the wood source and depositional areas would be strong candidates in efforts to preserve stream structure and function.

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