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Geomorphic variation in riparian tree mortality and stream coarse woody debris recruitment from record flooding in a coastal plain stream[1]

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Abstract: Large floods are an important process controlling the structure and function of stream ecosystems. One of the ways floods affect streams is through the recruitment of coarse woody debris from stream-side forests. Stream valley geomorphology may mediate this interaction by altering flood velocity, depth, and duration. Little research has examined how floods and geomorphic features interact to control debris recruitment from riparian forests. With this in mind, we examined debris recruitment resulting from tree mortality during a record flood in a Georgia (U.S.A.) stream. We quantified debris characteristics as related to riparian geomorphology, and we examined the influence of floods on the structure of stream-side forests. The flood killed, and recruited into the stream debris pool, an average of 22 trees/km. Variation in recruitment was related to geomorphology; mortality was highest in reaches having narrow valleys and high elevations of riparian landforms, while it was lowest in reaches having wide valleys and low landform elevations. Species differed in probability of mortality; three taxa, out of 47, contributed 75% of new debris to the stream. The structure of stream-side forests reflected the influence of floods on tree mortality; forests along constrained reaches lack small individuals. Our results suggest that constrained reaches are the primary sources of debris during large floods, while unconstrained reaches function as debris sinks. Debris characteristics may be linked to floods through tree demography. Specifically, large floods have the potential to limit future recruitment of larger-sized susceptible species into the stream, by limiting the number of small trees that grow into the canopy.
Keywords: coarse woody debris, riparian forest, coastal plain, flooding, tree mortality.

Résumé: Les crues de forte amplitude contrôlent en grande partie la structure et le fonctionnement des écosystèmes fluviaux. Cette influence est surtout marquée dans l'alimentation du cours d'eau en débris ligneux provenant des ripisylves. La configuration géomorphologique de la vallée est un facteur prépondérant dans cette dynamique fluviale en contrôlant la vitesse d'écoulement, la profondeur de l'eau et la durée des actions riveraines. Peu de travaux ont évalué comment les crues et les processus géomorphologiques qui les accompagnent contrôlent le prélèvement de débris ligneux dans les forêts riveraines. Cette recherche aborde donc la mortalité des arbres en réponse à des crues datées d'un cours d'eau de Georgie (U.S.A.). Les caractéristiques des débris ont été quantifiées selon les unités géomorphologiques riveraines et la structure des ripisylves. Les crues ont provoqué la mortalité et le transport de 22 arbres par km linéaire en moyenne. Les variations dans l'abondance des débris ligneux sont reliées à la configuration géomorphologique, c'est-à-dire que la mortalité des arbres est optimale dans les étranglements du tracé du cours d'eau et là où les formes fluviales atteignent les plus grandes amplitudes. Là où la section fluviale est étalée et où les formes sont basses, il y a généralement peu de débris. La probabilité de mortalité diffère selon les espèces ; trois taxons sur un total de 47 ont fourni 75 % des débris. La structure des ripisylves porte clairement la marque des poussées de mortalité ; les forêts les plus exposées présentent des hiatus dans la strate de régénération. Les sites les plus exposés à l'érosion du cours d'eau constituent la principale source de débris, alors que les sites protégés sont des lieux d'accumulation. L'historique des crues influence aussi la démographie des populations et conséquemment l'abondance des débris. Ainsi, les crues d'amplitude limitent la régénération et influencent indirectement l'abondance des débris disponibles lors de crues ultérieures.
Mots clés: débris ligneux, ripisylve, rive, plaine côtière, crue, mortalité des arbres.

Introduction

The importance of large floods for sustaining the structure and function of stream ecosystems is receiving increased attention (Gore and Shields, 1995; Johnson, Richardson & Naimo, 1995; Décamps, 1996; Stanford *et al.*, 1996; Wootton, Parker & Powers, 1996). One of the mechanisms by which floods may influence streams, at least indirectly, is through mortality of riparian trees and the subsequent input of coarse woody debris into the stream (Harmon *et al.*, 1986). Large floods in particular may kill many stream-side trees, resulting in a pulsed input of debris to the stream and a substantial change in riparian forest structure. Because of the infrequency of record floods, observations of their effects on stream-side forests are limited.

Geomorphology of stream valleys may mediate the interaction that occurs between water and riparian forests during floods (Gregory *et al.*, 1991). For instance, the amount and type of tree death from flooding should differ between constrained and unconstrained reaches. This is because flood characteristics such as flow depths, stream velocities, and bank erosion vary with valley constraint (Malanson, 1993; Nakamura & Swanson, 1994; Rosgen, 1996), potentially influencing rates of tree undercutting and

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stem breakage. Flow velocity also may affect orientation of debris in the channel, as well as movement of debris down stream (Young, 1994). Differences in forest composition among riparian landforms (Goebel *et al.*, 1996; Hupp & Osterkamp, 1996) may have an indirect effect on coarse woody debris recruitment into a stream if certain species are particularly susceptible to mortality from floods.

The importance of woody debris for stream ecosystem function is well established (Harmon *et al.*, 1986; Gregory *et al.*, 1991; Gore & Shields, 1995). Further, input rates and mechanisms, and probabilities of debris recruitment have been studied for some systems (Lienkaemper & Swanson, 1987; Robison & Beschta, 1990; Van Sickle & Gregory, 1990). Additional work is needed that links streams to riparian forests through debris recruitment, specifically during major floods. Further, the role of reach geomorphology in moderating these interactions needs to be examined, in order to provide a landscape perspective to understanding flood effects. With these needs in mind, we assessed the role of riparian geomorphology in controlling tree death and coarse woody debris recruitment into a south Georgia stream during a record flood. Our specific objectives were to: *i*) quantify stream-side tree mortality and characteristics of debris recruitment in several reaches, including amount of mortality, species composition, and location and orientation of debris in the stream channel, *ii*) relate variation in tree mortality and debris characteristics among reaches to geomorphic influences on fluvial processes during the flood, and *iii*) examine the influence of floods on the structure of stream-side forests and the potential feedback to stream coarse woody debris pools.

Material and methods

STUDY AREA

We conducted our study at the Joseph W. Jones Ecological Research Center, an 11 500 ha reserve located in southwestern Georgia, U.S.A., in the Plains and Wiregrass Plains 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 fifth-order black-water stream with headwaters that originate in a relatively intact Coastal Plain wetland complex. 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 bankfull discharges, causing flooding of low-lying areas. Average annual discharge is 22 m^3 per second (Stokes, McFarlane & Buell, 1992).

The climate of the study area is subtropical (Keys *et al.*, 1995), with annual precipitation averaging 131 cm. Although this precipitation is evenly distributed throughout the year, tropical depressions occasionally modify the weather patterns of the study area and the flow of Ichawaynochaway Creek. One such system, Tropical Storm Alberto (July 3-7, 1994), deposited 71 cm of rain on the upper portions of the Ichawaynochaway Creek Drainage (Hippe *et al.*, 1994). During the storm, peak daily discharge on Ichawaynochaway Creek was estimated at 850 m^3 per second and instantaneous peak discharge was estimated at 1400 m^3 per second (Hippe *et al.*, 1994). Extensive flooding occurred, extending well into the uplands throughout the drainage.

Several repeatable riparian landforms occur along the stream corridor of the study area, including sand ridges, terraces, and floodplains (Figure 1; Goebel *et al.*, 1996). Floodplains occur along reaches with broad stream valleys

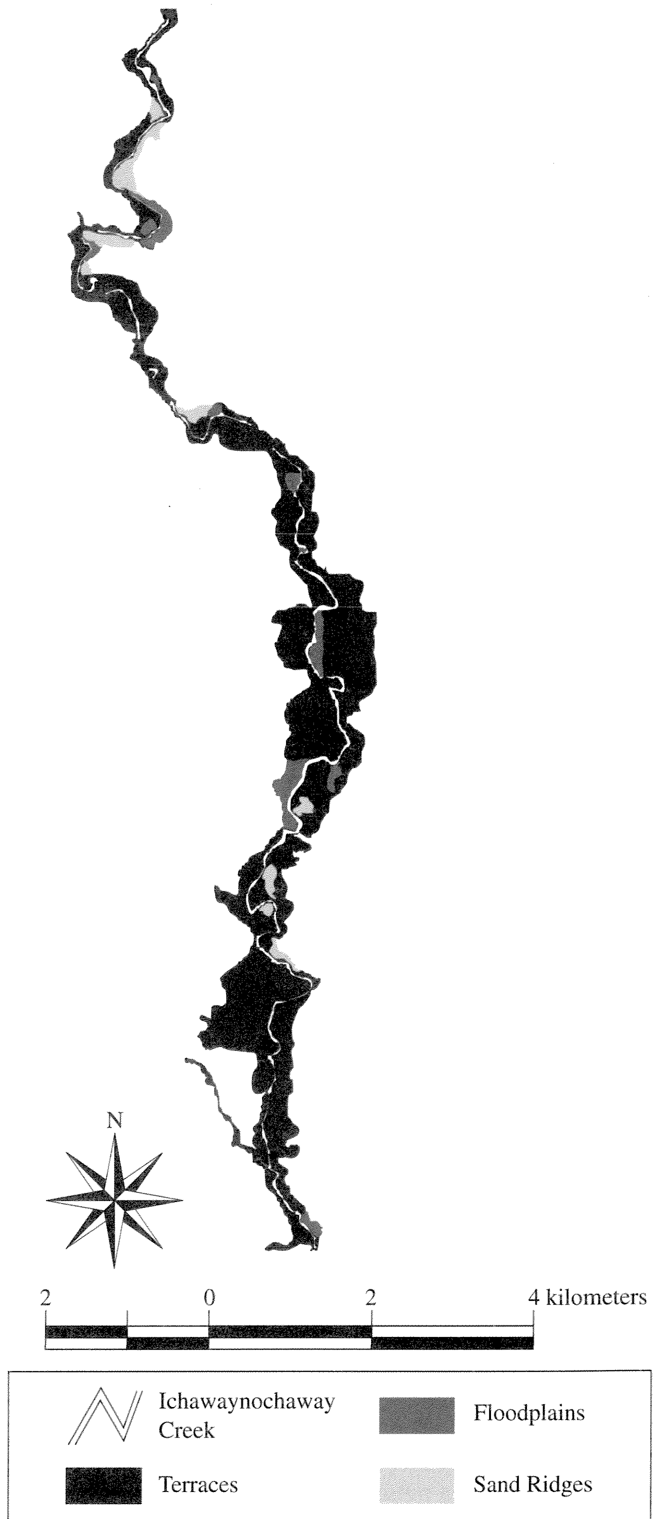

FIGURE 1. The distribution of riparian landforms in the study area.

and are low in elevation relative to the base-flow channel. Floodplain 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 ecosystems, or mixed-hardwoods where surface fire is excluded.

REACH AND STUDY SITE CHARACTERISTICS

We selected six reaches to sample recently recruited stream coarse woody debris and adjacent stream-side forests. The reaches and forests had minimal human disturbance and were representative of the range of riparian landforms and conditions along the stream. Stream channel morphology has not been altered by human activities, although some removal of coarse woody debris did occur near boat landings up until the 1980s (J. Adkinson, J.W. Jones Ecological Research Center, pers. comm.). We sampled along both sides of each reach since riparian geomorphology was not always similar on opposite sides of the reach (Table I). Physical characteristics of study sites were determined from GIS data layers of land-cover, topography, and soils. Riparian landforms were delineated by outlining the polygons that extended from the stream channel to the lower boundary of upland landforms, as determined using an existing ecological classification of the study area (Goebel *et al.*, 1997). 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 riparian study area. For this study, we used riparian landform elevation and stream valley width 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.

COARSE WOODY DEBRIS SAMPLING

We sampled coarse woody debris during the autumn of 1994. We only included trees recruited into the stream by the previous summers flood. This debris was distinguished from older debris by the presence of attached leaves or intact branches or root-plates. The lateral area for debris sampling was restricted to the active channel at approximately bank-full width. All dead trees were located near or in contact with the stream bank; none had been moved into the center of the channel. Sampled dead trees had diameters of at least 5 cm at a height of 1.4 m (d.b.h.), and a length of at least 3 m. Sampled characteristics in each study site included counts of tree mortality from the recent flood (*i.e.*, recruitment into the coarse woody debris pool), species or genera of newly recruited debris, tree d.b.h., distance of dead trees from baseflow channel (m), contact of trees with the baseflow 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 from the flood was expressed both as a rate (number of newly killed trees per km reach length) and as a frequencies (% of the total pre-flood population of trees in the stream-side forests; see next section for live-tree sampling methodology). Dead trees were marked with a numbered aluminum tag and their position recorded using a global positioning system so that future movement could be followed. Some trees killed and deposited into the stream by the flood, particularly small diameter individuals (see Results), may have been transported out of our sample areas and into locations other than the active channel, *e.g.*, floodplains. We could not account for these individuals, and consequently our debris recruitment rates may underestimate actual rates.

VEGETATION SAMPLING

Woody vegetation of the stream-side forests was sampled in the fall-winter of 1994 using the point-quarter method (following Brower & Zar, 1984). Sampling was confined to a forest strip growing on the stream-side of natural levees in floodplains, or, in constrained reaches, up to a lateral distance away from the stream that approximated channel width at twice bankfull depth. Initial observations indicated that these areas were the sites of highest tree mortality from flooding and were the primary source areas of wood debris recruited into the active channel. Average (± 1 SD) width of the stream-side forest among all reaches was 5.2 (3.8) m.

TABLE I. Geomorphology of the 12 study sites

Reach	Side of stream[1]	Ecosystem	Landform	Reach shape	Valley width (m)	Reach length (km)	Landform elevation (m)
1	A	Longleaf pine/scrub oak	Sand ridge	Straight	247	0.92	4.8
1	B	Longleaf pine/bluejack oak	Terrace	Straight	247	0.94	3.4
2	A	Bottomland hardwood	Floodplain	Outside meander	379	0.53	5.9
2	B	Bottomland hardwood	Floodplain	Inside meander	379	0.48	2.4
3	A	Longleaf pine/scrub oak	Sand ridge	Straight	255	0.65	4.9
3	B	Longleaf pine/bluejack oak	Terrace	Straight	255	0.64	3.8
4	A	Bottomland hardwood	Floodplain	Inside meander	262	0.44	2.7
4	B	Longleaf pine/bluejack oak	Terrace	Outside meander	262	0.47	2.8
5	A	Longleaf pine/scrub oak	Sand ridge	Straight	227	0.66	10.8
5	B	Longleaf pine/bluejack oak	Terrace	Straight	227	0.73	5.7
6	A	Mesic hardwoods	Terrace	Outside meander	280	0.49	7.8
6	B	Mesic hardwoods	Terrace	Inside meander	280	0.40	8.9

[1]Side of stream: A) east-side of the stream, generally having a westerly aspect; B) west-side of the the stream, generally having an easterly aspect.

In each study site, we located a starting point by pacing a random distance in a direction parallel to the stream, beginning at one end of the reach. Additional points were located at 40 m intervals. The number of points in each study site ranged from eight to 15. At each point, we divided the stream-side area into four quarters, with two quarters located on the down-slope side of the bank and two on the up-slope side. In each quarter, we recorded the species, d.b.h., and distance from the point to the nearest trees in two size classes (5 cm ≤ d.b.h. < 10 cm; d.b.h. ≥ 10 cm). Tree densities are reported as number per unit reach length.

DATA ANALYSIS

We used redundancy analysis (RDA) and canonical correspondence analysis (CCA) (Davies & Tso, 1982; Ter Braak & Prentice, 1988) to relate characteristics of recently recruited coarse woody debris (*i.e.*, flood-killed trees) and stream-side forests 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 percent of original population of live stream-side trees); mean distance of dead tree from baseflow channel (m); contact of dead tree with baseflow channel (percent of trees in a reach); crown intact (percent of trees in a reach); root-plate present (percent of trees in a reach); and orientation of dead tree in the stream (percent). 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. Additionally, we used RDA to examine relationships between riparian forest diameter distributions (all species pooled) and geomorphic features. For this analysis, we were interested in determining if the size class distribution of living trees in the stream-side forests reflected the influence of the recent or previous floods on tree mortality and recruitment of new debris into the stream. Both RDA analyses were run using correlation matrices of untransformed data, and ordination diagrams were constructed using correlation biplot scaling. We used CCA to examine relationships between geomorphic features and species composition of both the riparian forest and the recently recruited coarse woody debris pool. For these analyses, CCA was run using relative abundances of species. In all cases, the ordinations were exploratory, designed to formulate hypotheses rather than test them. Finally, the relative abundance of common tree taxa in stream-side forests and the new debris pool were compared statistically using paired *t*-tests.

Results

STREAM-SIDE TREE MORTALITY AND DEBRIS PHYSICAL CHARACTERISTICS

We located a total of 175 trees that were killed and added to the stream's coarse woody debris pool during the flood. Pooled over all study sites, mortality averaged 22 stems/km of reach, or 10% of the pre-flood population of trees ≥ 5 cm d.b.h. (Table II). Sixty-seven percent of these trees were in contact with the baseflow channel at the time of sampling, with a mean distance of the root-plate to the baseflow channel of just under 1 m (Table II). Most downed trees had minimal damage to crowns and intact root-plates when sampled (Table II). Orientation of downed trees relative to the stream bank was split similarly between perpendicular and parallel, with only a small percentage of stems oriented between these two extremes (Table II).

TABLE II. Summary statistics for characteristics of downed trees used in the RDA (n = 12 study sites)

	Mean	SD	Range
Average distance from baseflow channel (m)	0.9	1.1	0.0-3.3
Mortality (number per km stream)	22.3	31.5	2.3-103.9
Mortality (% of population)	9.9	15.7	0.9-53.1
Contact with baseflow channel (%)	66.6	30.7	11.6-100.0
Perpendicular to stream (%)	42.4	40.3	0.0-100.0
Parallel to stream (%)	56.2	42.1	0.0-100.0
Root-plate present (%)	85.7	13.4	66.7-100.0
Crown intact (%)	76.3	19.1	50.0-100.0

Values of tree mortality and debris physical characteristics ranged widely among study sites (Table II). Redundancy analysis between stream geomorphic features and characteristics of downed trees accounted for 72% of the total variation with respect to the latter variables. Most of the variation was accounted for by the first (53%) and second (13%) RDA axes (Figure 2; Table III). Correlation coefficients between characteristics of downed trees and geomorphic characteristics of study sites were 0.921 and 0.689 for the first and second RDA axes, respectively.

The RDA axes are related to geomorphic characteristics, with the strength of the relationship proportional to vector length and orientation (Figure 2, dashed lines). Longer vectors have a greater weight in the analysis, and the smaller the vector angle with the axis, the closer the relationship between that characteristic and the axis. The vectors for downed tree characteristics have a similar interpretation (Figure 2, solid lines). The longer the vector and the smaller the angle between geomorphic vector and downed tree vectors, the stronger the relationship between the two sets of variables. Finally, centroid locations for categorical variables (reach shape; Figure 2, solid squares), reflected associations between downed tree characteristics and classes of the categorical variable.

Several relationships between characteristics of downed trees and geomorphology of the study sites are suggested by the analysis. Stream valley width is strongly correlated with RDA axis 1 (r = 0.83), and the orientation of downed trees is also strongly associated with this axis. Downed trees in reaches with broad stream valleys were often oriented perpendicular to the channel, while those in narrow valleys tended to be oriented parallel to the channel. Further, perpendicular orientation was more likely on the outside of a meander, whereas parallel orientation occurred more frequently on straight reaches. Landform elevation is negatively correlated with RDA axis 2 (r = -0.77). Greatest tree mortality (percent of original stream-side tree population and number of trees killed by the flood/km) occurred in sites whose adjacent riparian landforms are higher in elevation above the channel (*i.e.*, greater constraint). Further, the average distance between downed trees and the baseflow channel was greater in these sites as well,

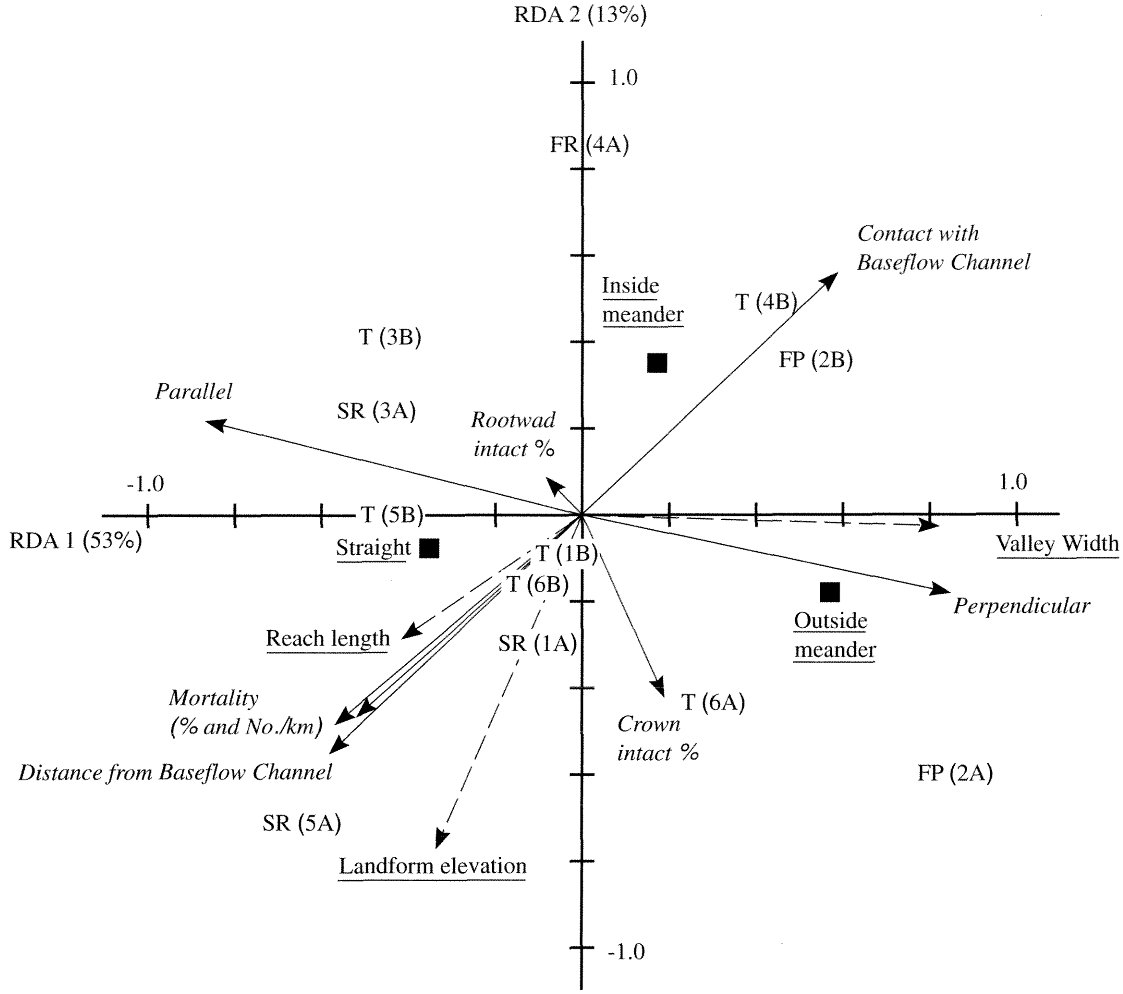

FIGURE 2. Redundancy analysis triplot of stream coarse woody debris characteristics (solid vectors) and riparian geomorphic variables (dashed vectors; solid squares). RDA axis 1 is related to debris orientation (parallel, perpendicular), while RDA axis 2 is related to amount of debris recruitment from flooding (mortality as percent of original population and number of stems per km of stream reach), distance of debris from the baseflow channel, and contact of debris with the baseflow channel. Debris characteristics are correlated to the geomorphic variables that they most closely parallel. Symbols for study sites designate landform (*e.g.*, SR = Sand ridge), reach number (1-6), and side of stream (A or B), as in Table I.

TABLE III. Summary statistics for redundancy analysis of downed-tree characteristics with stream reach geomorphic characteristics

	RDA1	RDA2	RDA3
Eigenvalue[1]	0.526	0.126	0.052
Downed-tree/segment correlation	0.921	0.689	0.894
Cumulative variation of downed-tree characteristics (%)	52.6	65.2	70.4
Cumulative variation of downed-tree/segment relation (%)	73.5	91.2	98.4

[1]Sum of all canonical eigenvalues = 0.720

suggesting that flood-induced mortality and recruitment of trees into the stream occurred laterally over a wider area in these locations.

STREAM-SIDE FOREST AND FLOOD-RECRUITED DEBRIS COMPOSITION

The stream-side forests of the study sites support a diverse tree community. We identified forty-seven woody species having a d.b.h. ≥ 5 cm (data not shown). Pooled across all sites, four of the species, Carolina ash (*Fraxinus caroliniana* Mill.), eastern red cedar (*Juniperus virginiana* L.), baldcypress (*Taxodium distichum* (L.) Rich.), and southern live oak (*Quercus virginiana* Mill.) accounted for over 50% of relative density. All oak species combined had a relative density of 23%. Each of the remaining species had mean relative densities below 6%. Stream-side forest composition was similar among study sites. Little variation was related to riparian geomorphic characteristics. The CCA ordination between stream-side forest composition and geomorphology accounted for only 10% of species variation on all axes, and only 5% on the first axis (results not shown).

Three taxa, eastern red cedar, river birch (*Betula nigra* L.), and oak, accounted for over 75% of all trees killed by the flood (Figure 3). Unidentified taxa accounted for only 2.3% of killed trees. As with live trees, the species composition of newly killed trees was poorly related to geomorphology. The CCA ordination between new debris composition and geomorphology accounted for only 43% of total variation and only 25% on the first axis (data not shown).

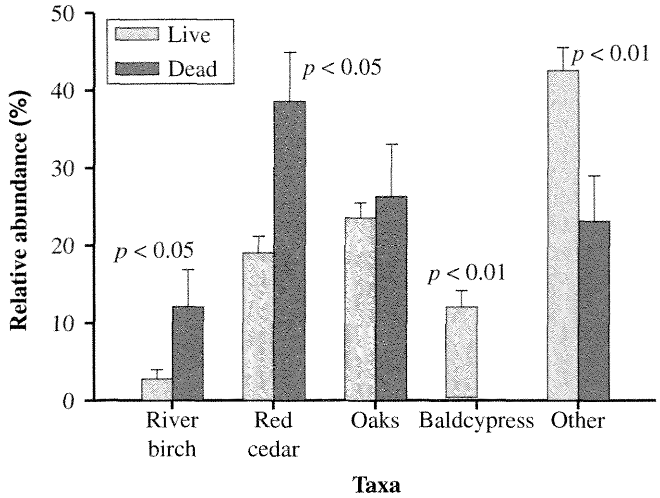

FIGURE 3. Relative abundance of different taxa in stream-side forests and recently recruited coarse woody debris. Probabilities indicate significant differences within taxa based on paired t-tests. Values are means ± 1 SE. $N = 12$.

Dominant taxa did differ in their susceptibility to mortality from flooding (Figure 3). Relative density in the debris pool (percent of total trees killed by the flood) for both river birch and eastern red cedar were significantly greater than pre-flood live relative densities in the stream-side forests (paired t-test by taxa, Figure 3), while there was no significant difference for oaks. Baldcypress, a common taxa in the stream-side forests, were highly resistant to flooding; no downed baldcypress were found in any of our riparian study areas. When pooled, all other taxa also appeared to be resistant to flooding (Figure 3).

FLOOD-KILLED TREES AND STREAM-SIDE FOREST DIAMETER DISTRIBUTIONS

The flood killed trees had a wide range of diameters (5-80 cm), although the majority came from the 15-40 cm d.b.h. range (data not shown). Mortality and stream recruitment was highest for 20-25 cm d.b.h. stems. The possibility exists that some stems smaller than 20 cm d.b.h. may have been killed by the flood and transported to areas outside of our sample sites, perhaps being deposited in floodplains. Consequently, our estimates of tree death and debris recruitment for smaller size classes should be considered conservative. In contrast, we observed little movement of larger trees during or soon after the flood.

The diameter distributions of live trees in the stream-side forests appear to have been shaped by the variable influence of flooding on tree mortality (Figure 4). The shape of distributions range from a reverse J to nearly flat. RDA ordination between frequency of stems in each diameter class and geomorphic characteristics of study sites accounted for 77% of total variation with respect to diameter distributions (Table IV). The first axis alone accounted for 66% of total variation and reflected a negative correlation ($r = 0.93$) between frequency of the three smallest diameter classes (5-10, 10-15,15-20 cm) and stream constraint, as measured by riparian landform elevation and valley width (Figure 5). Stream-side forests along highly constrained reaches, *i.e.*, narrow valleys and high riparian landforms, had flat diameter distributions because they were lacking live trees in the smallest diameter classes.

Discussion

FLOODING, COARSE WOODY DEBRIS RECRUITMENT, AND RIPARIAN GEOMORPHOLOGY

Our study supports the concept that natural hydrologic regimes, including large floods, are important processes controlling the structure and function of stream and river ecosystems (Gore & Shields, 1995; Décamps, 1996; Stanford *et al.*, 1996; Wootton, Parker & Powers, 1996). Record flooding killed a large number of stream-side trees and, consequently, added large amounts of coarse woody debris into the system.

Along some reaches, mortality from flooding exceeded 50% of trees ≥ 5 cm d.b.h.. We began monitoring debris recruitment in response to the 1994 flood; however, our observations since that time suggest that tree death and debris recruitment into the stream is low during annual flooding. This temporal trend is consistent with debris recruitment in many terrestrial and stream ecosystems, where low background rates of debris input are punctuated by increased recruitment during infrequent disturbances (Harmon *et al.*, 1986; Fetherston, Maiman & Bilby, 1995). Harmon and Hua (1991) do point out that background mortality (*i.e.*, outside of major disturbances) may often result in more tree death over longer-time periods than infrequent large disturbances. However, the pulsed input of large amounts of debris into a system, such as the stream we studied, may be as important as cumulative abundance. It is this kind of punctuated ecological input that is often lacking in regulated rivers (Malanson, 1993; Gore & Shields,1995; Johnson, Richardson & Naimo, 1995).

Geomorphic differences among reaches resulted in distinctly different 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 ecosystem patterns and processes (Swanson *et al.*, 1988). Constrained reaches, *i.e.*, 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 low mortality and recruitment. We attribute higher mortality with increasing constraint to greater current velocities during floods (Malanson, 1993).

Constrained reaches also had more debris pieces oriented parallel to stream flow, presumably because of greater stream velocity during flooding. Differences in orientation suggest different mechanisms of mortality and debris recruitment are important among different riparian landforms. In floodplains, trees appear to have been undermined through bank cutting, followed by collapse into the active channel. Along sand ridges, trees were pushed over by the force of the current and deposited near the bank. Variations in debris location associated with flow regime have been reported in other studies. For example, lateral cutting and

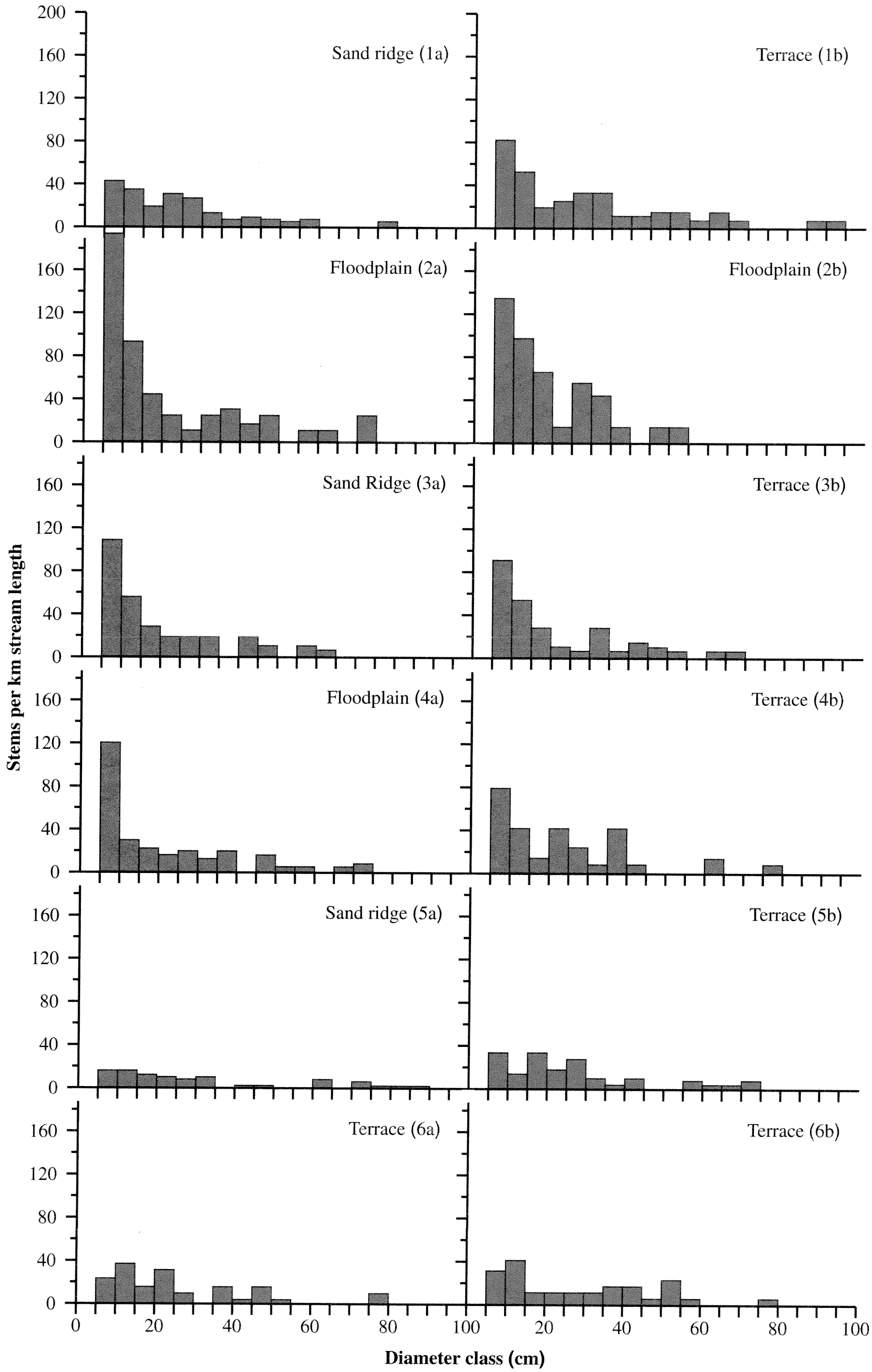

FIGURE 4. Diameter (d.b.h.) distributions of live trees (all species combined) in 12 stream-side forests. Symbols for study sites, *e.g.*, Sand ridge (1a), designate landform, reach number, and side of stream, as in Table I.

TABLE IV. Summary statistics for redundancy analysis of live-tree diameter distributions with stream reach geomorphic characteristics

	RDA1	RDA2	RDA3
Eigenvalue[1]	0.661	0.059	0.022
Downed-tree/segment correlation	0.931	0.905	0.831
Cumulative variation of downed-tree characteristics (%)	66.1	71.9	74.1
Cumulative variation of downed-tree/segment relation (%)	86.0	93.7	96.5

[1]Sum of all canonical eigenvalues = 0.768

bank collapse appear to be uncommon in higher gradient streams (Lienkaemper & Swanson, 1987), where high current velocities during floods deposit wood on stream banks. Differences in mechanisms of tree mortality among reach-types may have important consequences for stream processes that depend on debris, since a higher percentage of downed trees in unconstrained reaches are immediately available for aquatic habitat (because of deposition into the active channel), relative to constrained reaches.

FLOODING AND RIPARIAN TREES

In other studies, variation in debris abundance and its physical characteristics among streams has been linked to compositional differences of riparian forests (Silsbee & Larson, 1983). However, in our study, composition of the stream-side forests, *i.e.*, the source area for debris entering the channel, was similar among study sites. Consequently, differences in debris recruitment rates and physical characteristics were not the result of variation in abundances of susceptible species among riparian landforms.

Individual taxa, however, did vary in their susceptibility to floods. Eastern red cedar and river birch were prone to flood mortality. Both species have dense branch networks (pers. observ.), a growth-form that may expose them to greater current force during floods. Baldcypress, in contrast, was resistant to flood damage even though it grows near

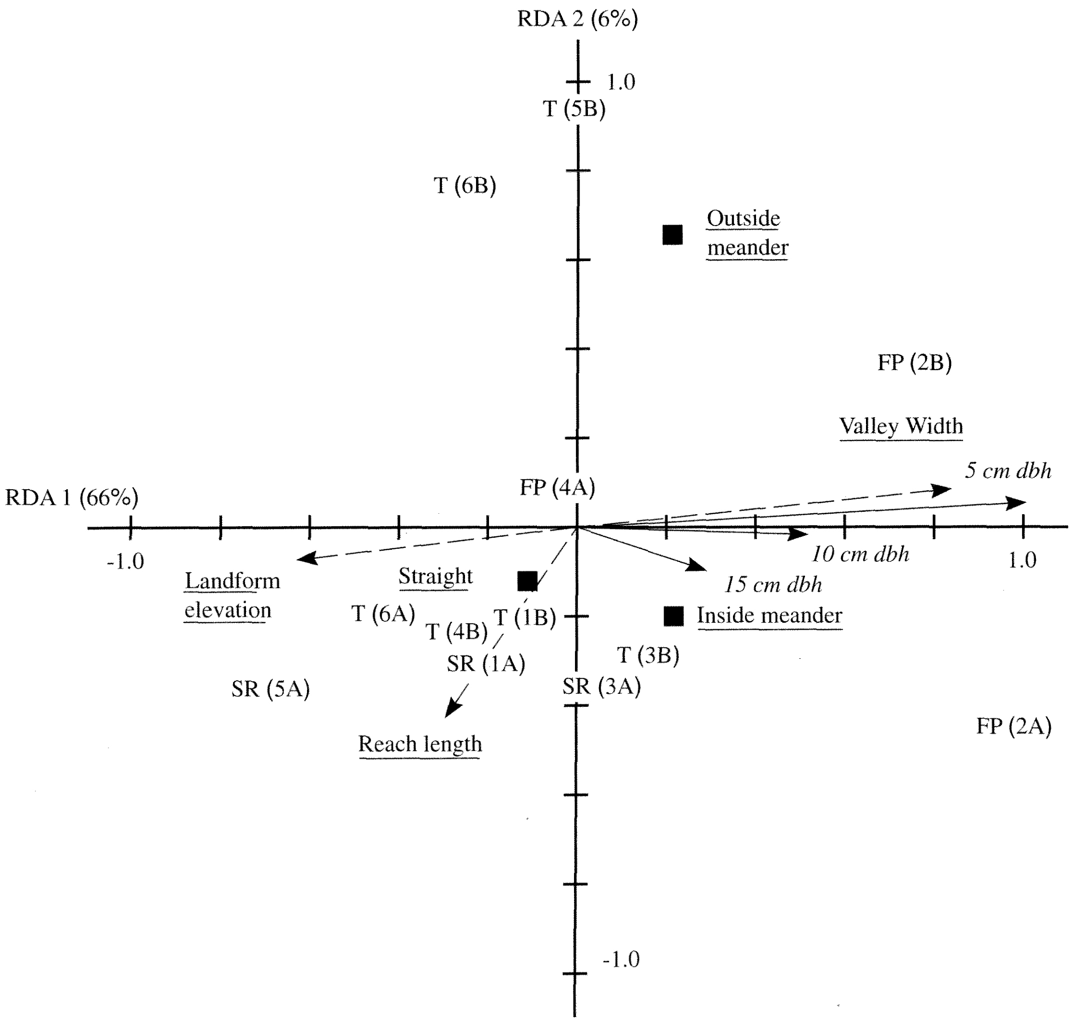

FIGURE 5. Redundancy analysis triplot of diameter distributions in stream-side forests (number of stems in 5 cm diameter classes) (solid vectors) and riparian geomorphic variables (dashed vectors; solid squares). RDA axis 1 is related to the number of stems in the 5, 10, and 15 cm d.b.h. classes. Diameter classes are correlated to the geomorphic variables that they most closely parallel. For clarity, only diameter classes are shown that were important for defining an axis. Symbols for study sites designate landform (*e.g.*, SR = Sand ridge), reach number (1-6), and side of stream (A or B), as in Table I.

and within the baseflow channel. Baldcypress have few low branches which, along with root buttressing, may provide resistance to uprooting (Wilhite & Toliver, 1990). Perhaps additional differences in root systems among species result in differential mortality from flooding.

High flood mortality of eastern red cedar and river birch in constrained valleys, along with the low density of small diameter individuals in the corresponding stream-side forests (Figure 4), suggests a potential interaction among flood frequency, tree demography, and recruitment of debris into the stream. Continued high mortality of cedar and birch in smaller diameter classes, from floods of the magnitude we examined, may lead to reduced recruitment of these species into the overstory. Ultimately, cedar and birch could be eliminated from the stream-side forests of constrained reaches. Accordingly, the composition and size distribution of debris in the stream will change over time, as populations of susceptible species, as well as larger diameter stems, decline in the stream-side forests. However, if cedar and birch have persisted for extended periods of time in these forests, and if overstory densities have remained relatively stable over longer time-scales, then the frequency of large floods must be sufficiently low as to allow establishment and periodic growth of advance regeneration into the overstory. In this case, composition, abundance, and the size distribution of debris in the stream will remain relatively stable over longer time-periods.

Riverine landscape considerations

The importance of floodplains for the functioning of larger streams is well established (Junk, Bayley & Sparks, 1989; Décamps, 1996). However, our data suggests that floodplains are not the only geomorphic feature of a stream valley that is important for stream ecosystems, if, as we observed, constrained reaches are the primary location for coarse woody debris input into the system. In this case, it is the diversity of geomorphic features within the system that are required to support all of the processes important for stream functioning (Gregory *et al.*, 1991; Johnson, Richardson & Naimo, 1995).

The spatial pattern of tree mortality and debris input we observed suggests that constrained reaches may function as source areas of debris for the larger stream system. Downstream transport of debris is characteristic of higher order streams such as the one we examined (Keller & Swanson, 1979; Lienkaemper & Swanson, 1987). Consequently, unconstrained reaches may be sinks for debris, with loadings becoming more evenly distributed among reaches during periods between large floods. Under this scenario, approximately 12% of total stream length of the study area may be a source of debris during floods, because of adjacency to sand ridges on at least one side, while 6% of stream length may be a debris sink because of adjacency to floodplains (Figure 1). The remaining 82% of the stream corridor borders terraces, and may be a mixture of debris source and sink areas, depending on terrace elevation and stream-channel shape.

The debris source-sink relationship has some application to restoration efforts for riverine systems. Rehabilitation strategies for streams often include selective placement of coarse woody debris in the channel (Gore & Shields, 1995). This is a short-term solution to a debris depletion problem. A longer-term solution is to ensure that sources of dead trees are always available, *i.e.*, stream-side forests. In developed landscapes, long stretches of stream-side forest are not likely to be completely conserved or restored. However, conservation and restoration efforts could begin by focusing on select locations that function as "biological hot spots" for the larger system (*sensu* Doppelt *et al.*, 1993); *i.e.*, small, less-disturbed areas within a degraded systems that provide important ecological inputs. For streams like the one we studied, hot spots should include reaches that have high rates of stream-side tree mortality during flooding and, consequently, contribute large amounts of coarse woody debris to the system.

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