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DIFFERENTIAL RECOVERY OF A DEEPWATER SWAMP FOREST ACROSS A GRADIENT OF DISTURBANCE INTENSITY

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Abstract: On the Savannah River Site, South Carolina, USA, large areas of floodplain swamp forest of baldcypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) were destroyed by the cumulative impacts of cooling-water discharges over a 35-year period of nuclear reactor operations. In one floodplain area, four years after thermal discharges ended, we analyzed the pattern of forest recovery across a disturbance gradient spanning from a site of chronic thermal impact and extensive sediment deposition to sites of intermittent thermal impact and little substrate change. Across this spatial gradient, we measured density and size structure of cypress and tupelo and assessed regeneration success in relation to density of surviving canopy trees and to substrate changes. Compared with undisturbed forest, canopy tree density was lower in all disturbed sites and decreased progressively with greater site disturbance. Density of tree regeneration decreased in parallel with declining canopy tree density; however, regeneration was particularly low in the site of chronic impact, where very few canopy trees had survived and where substrates had been modified by sedimentation. Size structures suggested that tree recruitment had occurred synchronously during a 5-year period of regional drought and minimal river flooding. Thus, cypress-tupelo recovery was influenced both by availability of seed sources and by site conditions, but floodplain hydrology also affected regeneration. The pattern of differential recovery across the disturbance gradient has allowed the use of natural regeneration potential in efforts to restore the pre-disturbance forest, and it also illustrates several key factors in wetlands design.

Key Words: deepwater swamp, forest disturbance, forest succession, *Nyssa aquatica, Taxodium distichum,* wetlands restoration

INTRODUCTION

An important concept in plant community ecology is that effects of disturbances to communities vary according to disturbance intensity, frequency, and magnitude (Pickett and White 1985). Less severe disturbance can initiate succession back towards the pre-disturbance community, whereas more severe disturbance may so modify site conditions that the direction of succession is altered and re-development of the pre-disturbance community does not occur. These varying disturbance effects may be value-neutral in an ecological sense, but their outcomes would be quite important for the practical objective of community restoration, where the "recovery" of a specific community-type may be the desired goal. Within this context, we here analyze the consequences of a varying disturbance regime for patterns of succession and community recovery in thermally damaged floodplain forest on the Savannah River in South Carolina, USA.

During 35 years of nuclear reactor operations on the U.S. Department of Energy's (DOE) Savannah River Site, discharges of reactor cooling waters to the river's tributary streams caused severe damage to >1000 hectares of forested wetlands (summarized in Wike et al. 1994). The large volumes of hot water scoured the stream channels and deposited extensive sediment deltas on the river floodplain, where the tributaries enter a deepwater swamp of baldcypress (*Taxodium distichum* (L.) Rich.) and water tupelo (*Nyssa aquatica* L.) (see Figure 1). In the stream corridors and on the floodplain deltas, the original forest cover was destroyed and was replaced by sparse herbaceous vegetation (Sharitz et al. 1974, 1990). Where this severe disturbance has ceased, recovery of the pre-disturbance forest has been slow, especially on the river

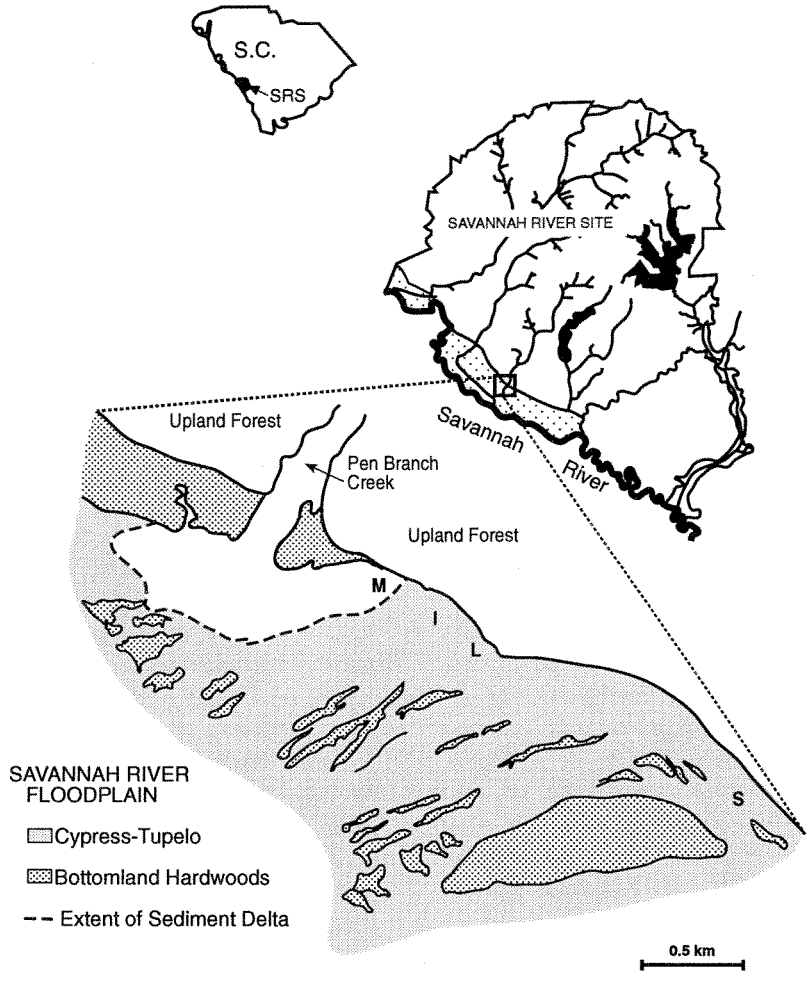

Figure 1. Map of the Savannah River Site, South Carolina, USA. Forest types on the Savannah River floodplain and the location of the Pen Branch Creek sedimentation delta are shown. Study sites representing a gradient of thermal and substrate disturbance are indicated as follows: S = intact swamp, L = least disturbed, I = intermediate disturbed, and M = most disturbed (on sediment delta).

floodplain. Living rootstocks and seed banks of the forest trees were killed by the chronic thermal stress, thus restricting the potential for regeneration from within the deforested delta areas, which range in size from 80 to 350 ha (Wike et al. 1994, Dulohery et al. 1995). In the Steel Creek delta, for example, Dunn and Sharitz (1987) found little evidence of succession towards the original cypress-tupelo forest seventeen years after thermal discharges had ended. They suggested that a combination of limited seed availability, modified substrate conditions, and competition had likely prevented successful regeneration. Given such limited potentials for natural recovery, more active restoration measures would be needed for in-kind mitigation of these historic wetland impacts (U.S. Department of Energy 1991, Dulohery et al. 1995).

In the Pen Branch Creek delta, another impacted floodplain area, we examined more closely the roles of seed availability and of site changes in affecting the natural recovery of the pre-disturbance cypress-tupelo forest. On the Pen Branch delta, thermal flows and Savannah River flooding interacted to create a spatial gradient of decreasing disturbance intensity spanning from the sediment delta area of chronic thermal impact and altered substrates to areas of intermittent thermal impact and no substrate changes. A corresponding gradient of complete-to-partial forest destruction resulted in varying densities of surviving canopy trees across the 150-ha area of impact. Because there were no cypress and tupelo trees in the deforested Pen Branch stream corridor to act as upstream seed sources (surveys in Wike et al. 1994), and because nearby uplands do not support hydrophytic trees, the surviving canopy trees would be a primary source for regeneration apart from any long-distance water dispersal of seeds across the river floodplain (Schneider and Sharitz 1988). In 1992, four years after thermal discharges to Pen Branch had ceased, we measured the extent of cypress-

tupelo regeneration across the spatial disturbance gradient. In this paper, we describe regeneration patterns in relation to the variation in surviving canopy trees and to substrate changes. We also evaluate regeneration patterns in relation to temporal variations in floodplain hydrology. We discuss the practical relevance of the observed recovery pattern for forest restoration efforts in the Pen Branch system (Dulohery et al. 1995), and we note how this pattern illustrates the importance of several key factors in wetland design (Mitsch and Gosselink 1993).

STUDY SITE AND DISTURBANCE HISTORY

Pen Branch Creek is a third-order stream that flows to the Savannah River floodplain at the U.S. DOE Savannah River Site (SRS), South Carolina, USA (33°8′N, 81°42′W) (Figure 1). The principal vegetation of the floodplain is deepwater swamp forest of baldcypress and water tupelo, but elevated natural levees and ridges support bottomland hardwood forest dominated by oaks (e.g. *Quercus laurifolia* Michx., *Q. nigra* L.), sweetgum (*Liquidambar styraciflua* L.), and red maple (*Acer rubrum* L.) (Sharitz et al. 1974, 1990). Thermal effluents from K-reactor were discharged into an upper tributary of Pen Branch Creek over a 34-year operations period (1954–1988). During this period, stream-flow volume was increased more than 30-fold (from a base flow of 0.3 m^3/sec to an average of 11 m^3/sec), and eroded sediments were deposited to a depth >0.5 m in a large alluvial delta where the creek meets the river floodplain (Wike et al. 1994; Figure 1). The high discharge temperatures (averaging 60°C), flooding, and sedimentation caused nearly complete mortality of the closed-canopy forests in the stream corridor and in the delta area of the floodplain (Sharitz et al. 1974).

In addition to the direct effects, interaction between Pen Branch thermal flows and Savannah River flood events caused an expansion of the disturbance regime beyond the direct-impact zone (Shines and Doak 1982, Christensen et al. 1984). Under conditions of river base flow, thermal impact on the floodplain was largely confined to the sedimentation delta area. However, during river flood events, the heated waters were forced eastward and downriver along the border of the adjacent upland terrace, thus introducing pulses of thermal disturbance to parts of the floodplain beyond the delta. As a result, areas of forest damage began spreading downriver; by 1985, the floodplain area either wholly or partially impacted by thermal effluents from the Pen Branch totalled ca. 150 ha (Wike et al. 1994).

In the early 1980s, Scott et al. (1985) surveyed 3 sites representing this gradient of thermal disturbance in the delta and the surrounding floodplain (Figure 1). Their "most disturbed" site was on a peripheral area of the sediment delta and was receiving both chronic thermal discharges and sediment deposition. Their "intermediate" and "least disturbed" sites were located beyond the delta at progressively greater distances downriver, where thermal disturbance was intermittent but where substrates remained unmodified. Across the 3 sites, they found a progressive decline in densities of living tree stems ≥2.5 cm diameter at breast height (dbh), from 908 stems/ha at the least disturbed site to 8 stems/ha at the most disturbed site. Mortality patterns in the two partially disturbed sites indicated that the flooding and thermal pulses killed smaller stems preferentially, leaving mainly larger trees as survivors (Repaske 1981, Scott et al. 1985).

Concurrent studies using multi-spectral scanner imagery (e.g., Jensen et al. 1984) showed that the forest in the sedimentation delta area had been replaced with open water and non-persistent marsh dominated by annual plant species such as water primose (*Ludwigia leptocarpa* (Nutt.) Hara.) and smartweeds (*Polygonum* spp.), whereas the partially-impacted areas developed a scrub-shrub vegetation with willows (*Salix nigra* Marsh., *S. caroliniana* Michx.) and buttonbush (*Cephalanthus occidentalis* L.). After thermal discharges to Pen Branch Creek ended in April 1988, the non-persistent vegetation in the delta began to be replaced by perennial marsh, with a large increase in cover of cattails (*Typha* spp.) in 1991 (Wike et al. 1994).

METHODS

Forest Structure

To study post-disturbance forest structure, we sampled tree and shrub species composition in September–October 1992 in three study areas in the same approximate locations as the "most disturbed" (M), "intermediate" (I), and "least disturbed" (L) sites of Scott et. al. (1985) (Figure 1). As a reference site for assessing forest impact, we also sampled a fourth study area of second growth (80–100 yr old) "intact" swamp forest (S) located ca. 2.5 km downriver of the least disturbed site. Across these four sites, mapped soil types (Rogers 1990) differ as a reflection of the past disturbance gradient. The unconsolidated delta substrate is a Kinston loam (approximately 25% sand, 54% silt, 21% clay), whereas soils in the partially-impacted areas beyond the sedimentation zone are Chastain clay (approximately 11% sand, 46% silt, 43% clay) or Dorovan muck (>60% organic matter). The soil at the intact swamp site is also Chastain clay.

At each study site, we established two randomly located strip-transects 50 m long × 10 m wide. Transects

were oriented perpendicular to the direction of river flow and were placed at least 20 m from the adjacent upland (total sample area = 0.1 ha per site). Within each transect, all tree stems with dbh ≥2.5 cm were identified to species, measured for dbh, and classed into three size groups of 2.5–10 cm dbh (poles), 10–20 cm dbh (subcanopy), and ≥20 cm dbh (canopy). In a narrower 50 m × 3 m strip nested within each transect, all tree stems with dbh <2.5 cm were identified and counted according to three size classes: height <30 cm (seedlings), height 30–140 cm (small saplings), and height ≥140 cm (large saplings). Because the tree species showed little evidence of multiple stem-sprouting, stem density represents individual density. All shrubs were also identified and counted within the 50 m × 3 m nested strip. If a shrub was multi-stemmed, it was counted as a single plant and was assigned to a size class according to the height and/or diameter of its largest stem. We used this approach because we wished to assess the regeneration density of shrub individuals relative to the density and size structure of tree regeneration. The method provided realistic estimates of shrub density because multiple stems were seen mainly in the larger individuals and because these individuals were always very distinct from each other. Tree and shrub counts from the two nested transects in each site were combined to give total counts, and all counts were corrected for area sampled to give density estimates per tenth-hectare (0.1 ha). We assessed disturbance impacts on forest structure through comparisons of the canopy layer (stems ≥20 cm dbh) with a "regeneration" layer defined as all stems <10 cm dbh.

Regeneration Patterns

Analysis of the forest structure data suggested to us that most regeneration had occurred as a recruitment pulse. To evaluate this, we combined several datasets. In 1993, we obtained basal tree-ring counts for ten saplings from the most numerous size class (see Results). We also made use of unpublished data collected during an earlier study of seedling dynamics in the floodplain. Between July 1983 and October 1985, seedlings of the dominant forest species, baldcypress and water tupelo, had been monitored to characterize floodplain regeneration processes under the prevailing conditions of thermal disturbance and of permanent changes in river hydrology associated with dam operations (see Sharitz et al. 1990). Germination and survival of cypress and tupelo seedling cohorts were censused in eight 1-m-wide permanent transects (ranging in length from 80 to 150 m) that were spaced equally across the Pen Branch impact area from the least disturbed to the most disturbed site. Seedlings were censused every 2–3 mo during the growing season and after 6 mo over the winter. As reactor shut-down had not been anticipated, the study was terminated after 1985; however, we have incorporated these data here because they provided some insight on seedling establishment processes during an important time interval for forest recovery. For this paper, we analyzed changes in total seedling numbers across all transects.

Concurrent with the seedling study, river water levels were monitored with a continuous water-level recorder placed near the most disturbed site. Although seedling censuses ended after 1985, hydrologic monitoring was maintained through 1992. Absolute values of water levels are not precise because of some recorder drift over the monitoring period (Lide, pers. comm.), but the peaks accurately show the occurrence of Savannah River flood events that could influence seedling establishment.

RESULTS

Post-disturbance Site Conditions

In September–October 1992, all sites were flooded. The most disturbed site had about 50 cm of water over loose sediments, whereas the intermediate and least disturbed sites were covered by about 20 cm of water over more consolidated substrates. Water depth at the intact swamp site was similar to that of the most disturbed site. In the most disturbed site, the dominant vegetation was a persistent emergent marsh with cattail, bulrush (*Scirpus cyperinus* (L.) Kunth.), water primrose (*Ludwigia* spp.), and marsh St. John's-wort (*Triadenum walteri* (Gmel.) Gl.). We observed similar herbaceous species in the ground layers of both partially disturbed sites but at much sparser densities under the established woody shrub and sapling layers. In the intact swamp forest, an herbaceous understory was absent except in canopy gaps.

Post-disturbance Forest Structure

The past disturbance gradient resulted in varying densities of surviving canopy trees that could supply seeds for regeneration within each site (Table 1). In the undisturbed swamp, which was a second-growth forest, there were 106 canopy trees/0.1 ha (= 1060/ha), the majority of which were water tupelo (*Nyssa aquatica*). In all disturbed sites, canopy tree density was substantially lower. Tree density decreased progressively with greater disturbance, from an equivalent of 80 trees/ha at the least disturbed site to 20 trees/ha at the most disturbed (delta) site, and relative representation of water tupelo also declined (Table 1). The data from the most disturbed site probably over-esti-

Table 1. Densities (per 0.1 ha) of canopy trees (dbh ≥20 cm), subcanopy trees (dbh 10–20 cm), and of tree stems and shrubs in the regeneration layer (dbh <10 cm) across a disturbance gradient of intact swamp, least disturbed, intermediate, and most disturbed sites. * denotes a double-stemmed tree.

Stratum and Species	Intact Swamp	Least Disturbed	Intermediate Disturbed	Most Disturbed
Canopy stratum				
Nyssa aquatica	91	7	1*	0
Taxodium distichum	15	1	4	2
Canopy total	106	8	5	2
Subcanopy stratum				
Nyssa aquatica	17	0	0	0
Taxodium distichum	5	0	0	0
Subcanopy total	22	0	0	0
Regeneration stratum				
Tree species:				
Nyssa spp.[1]	1083	954	366	0
Taxodium distichum	247	216	432	95
Salix spp.[2]	67	92	180	104
Other[3]	50	14	56	7
Tree total	1447	1276	1034	206
Shrub species:				
Cephalanthus occidentalis	23	543	110	170
Myrica cerifera	0	327	150	80
Other[4]	7	3	0	0
Shrub total	30	873	260	250

[1] *Nyssa aquatica* plus a few *N. sylvatica* var. *biflora* (Walt.) Sarg.
[2] *Salix nigra* and/or *S. caroliniana.*
[3] *Acer rubrum, Fraxinus* spp., *Liquidambar styraciflua,* and *Pinus* spp.
[4] *Itea virginica* L. and *Rubus* spp.

mate tree density across the entire sediment delta because so few trees survived in this area and their occurrence is scattered.

In the regeneration stratum (all stems with dbh <10 cm), total density of tree species was highest in the intact swamp and declined inversely with greater disturbance (Table 1). The decline was substantial in the most disturbed site, where regeneration density was an order of magnitude lower than in the other disturbed sites. The combined totals of cypress and tupelo stems decreased from 1170 stems/0.1 ha in the least disturbed site to 95 stems/0.1 ha in the most disturbed site, in parallel with the disturbance gradient of declining canopy tree density. Relative representation of tupelo also decreased with greater disturbance, with no tupelo stems found in the most disturbed site. In the most disturbed site, regeneration of cypress was patchy as well as sparse: stems were typically seen on or near elevated and stable spots such as fallen logs (see also Huenneke and Sharitz 1986), and 73% of stems were found within 10 m of the locations of the canopy trees within the transects.

Shrubs and early-successional willows (*Salix*) were minor components in the regeneration layer of the intact swamp but were more common in the disturbed sites (Table 1). More than 98% of the shrubs were either buttonbush or wax myrtle (*Myrica cerifera* L.). In the least disturbed and intermediate sites, shrub densities were lower than the densities of tree regeneration at each site, whereas in the most disturbed site, the low shrub and tree densities were of similar magnitude to each other (ca. 200 plants/0.1 ha) (Table 1).

Temporal Patterns of Regeneration

The intact swamp site had a size-class structure typical of closed-canopy forest: 89% of cypress and tupelo stems in the regeneration layer were seedlings or small saplings, and there were low densities of all larger size-classes relative to the high density of canopy trees (large saplings: 37 stems/0.1 ha; poles: 10 stems/0.1 ha; subcanopy trees: 22 stems/0.1 ha) (Figure 2 and Table 1). However, a different size structure was found in the disturbed sites, and it suggested that most regeneration in these sites had been synchronous. In all three disturbed sites, subcanopy trees were absent (Table 1), there were few seedlings or poles, and the most abundant size-class (65–71% of the regeneration) consisted of large saplings (Figure 2). Within the pole size-class (2.5–10 cm dbh), no stems were actually larger than 5 cm dbh.

Because the similar size distributions suggested a defined episode of recruitment, we estimated the ages of establishment of stems from the most abundant sapling size class. Of 10 large saplings of *Nyssa* and *Taxodium* ranging from 0.5 to 2.8 cm dbh, eight had established in 1985 or 1986, and two had established in 1987. Although ages were determined for only a small number of stems, the data show that recruitment had occurred *prior* to the end of thermal discharges in 1988.

The seedling dynamics of cypress and tupelo from 1983–85 (Table 2) and the water-level record from 1983–1992 (Figure 3) are consistent with the occurrence of a regeneration pulse. New seedling cohorts emerged each year (Table 2). However, in 1983 and 1984, survivorship of seedlings over the growing season was essentially zero, a pattern that has been attributed not only to thermal impacts but also to elevated floodplain water levels and summer floods (e.g., in 1984; Figure 3) associated with water-management activities on the Savannah River. By April 1985, no

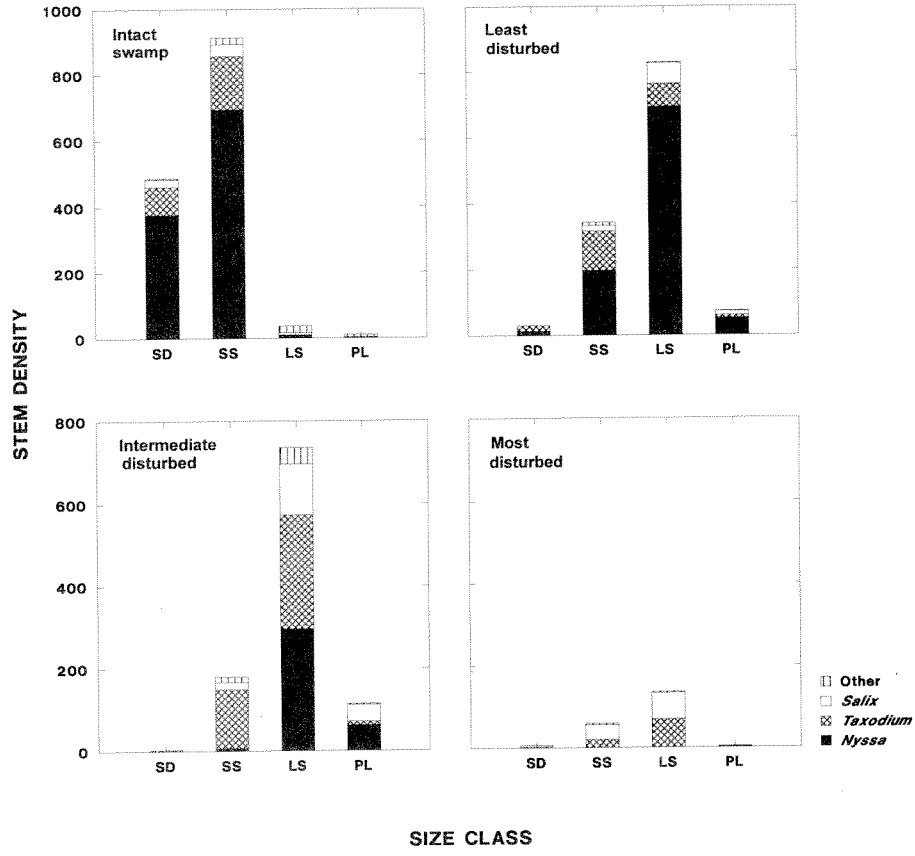

Figure 2. Size-class densities (per 0.1 ha) of regeneration by tree species across a disturbance gradient of intact swamp, least disturbed, intermediate, and most disturbed sites. Size classes of the regeneration layer are as follows (see Methods): SD = seedling, SS = small sapling, LS = large sapling, PL = pole. '*Nyssa*' includes *N. aquatica* plus a few *N. sylvatica* var. *biflora*; '*Salix*' includes *S. nigra* and *S. caroliniana*; 'Other' includes *Acer rubrum, Fraxinus* spp., *Liquidambar styraciflua,* and *Pinus* spp.

Table 2. Changes in total seedling numbers from 1983 to 1985 in 8 census transects spaced across the disturbed floodplain area from the least disturbed to most disturbed sites. 'Number alive at census date' is the sum of all survivors from the previous date plus new germinants.

	Taxodium distichum		*Nyssa aquatica*	
Seedling Census Date	Number Alive at Start of Census Date	% Surviving to Next Census date	Number Alive at Start of Census Date	% Surviving to Next Census Date
Jul 1983	978	6.2	240	0.0
Sep 1983	1100	86.7*	297	68.7*
Apr 1984	1183*	10.6	352*	0.3
Jul 1984	878	0.0	144	0.0
Oct 1984	12	0.0	6	0.0
Apr 1985	232	70.1	267	56.6
Jul 1985	598	80.8	546	65.6
Oct 1985	574	—	750	—

* Values were extrapolated from 4 of 8 transects because severe river flooding prevented access to some transects.

seedlings of the 1983 and 1984 cohorts remained alive (Table 2). In contrast, growing-season survivorship of the 1985 seedling cohorts was relatively high. The water-level record (Figure 3) shows an absence of river

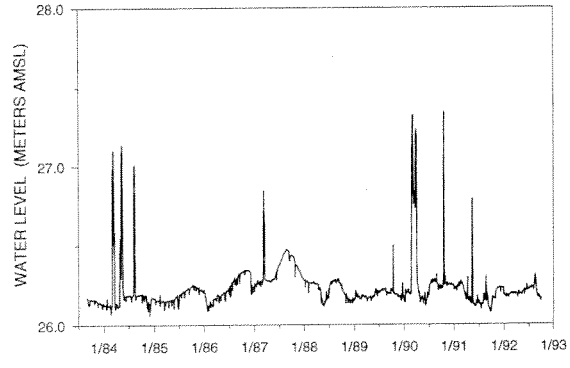

Figure 3. Floodplain water-level record (meters above mean sea level) from a continuously-recording hydrograph placed near the most disturbed site (see Figure 1) from September 1983 to September 1992. The peaks indicate Savannah River flooding events.

flooding in 1985 that continued through 1989 (apart from a winter flood in early 1987); these five years include the estimated establishment dates (1985–1987) of the dominant sapling size-class (large saplings) in the disturbed sites. This period of minimal river flooding coincided with a ten-year period of below-normal rainfalls and progressive drought in South Carolina between 1980 and 1990 (data from NOAA Climatological Data Annual Summaries). Noticeable flooding resumed in 1990 and 1991 (Figure 3) and may have reduced subsequent establishment, as reflected in relatively low seedling densities in all disturbed sites (cf. Figure 2).

DISCUSSION

Effect of Disturbance Intensity on Forest Succession

It seems that chronic thermal disturbance to the sediment deltas on the Savannah River floodplain has changed the course of succession away from recovery of the pre-disturbance cypress-tupelo forest. Instead, recent field surveys (in Wike et al. 1994), plus the longer-term record from Steel Creek delta (Dunn and Sharitz 1987), suggest that vegetation dynamics on the impacted deltas will follow a more prolonged succession from marsh to scrub-shrub to (perhaps) bottomland hardwoods forest, similar to the pattern for large-river deltaic plains (Rejmánek et al. 1987). Dunn and Sharitz (1987) had hypothesized that seed source limitation, permanent substrate modifications, and competition with successional vegetation were responsible for failure of cypress-tupelo recovery. In the Pen Branch system, the pattern of tree regeneration across the spatial gradient from partial to severe disturbance supports the conclusion that both insufficient seed sources and changes in site conditions have affected the potential for forest recovery.

The positive correlation between the density of surviving canopy trees and the density of cypress-tupelo regeneration was evidence that surviving trees were the principal seed sources for regeneration. More equivalent densities of regeneration across sites might have been expected if long-distance transport across the floodplain had contributed significant seed inputs. In the absence of floods, cypress and tupelo seeds do not disperse far from parent trees and may be incorporated into the short-lived seed bank (Schneider and Sharitz 1986), whereas high flooding may reduce seed trapping against emergent substrates and result in the net transport of seeds downriver and out of the swamp (Schneider and Sharitz 1988). Thus, in the partially-disturbed floodplain sites where substrate changes were minimal, regeneration was successful given that canopy trees were present to provide seeds. Competition with the scrub-shrub cover that had developed in these two sites was probably not a major factor limiting initial tree establishment since measured shrub densities were lower than the densities of tree regeneration in both the sites. However, future recruitment may now be limited by the established canopy of regenerating trees and shrubs.

In the most-disturbed delta site, scattered canopy trees had survived and some seedling establishment occurred near the surviving trees. However, the density of regeneration on the delta was an order of magnitude lower than in the partially-disturbed sites, which suggested that altered site conditions were also a factor limiting recovery. Several site changes may be responsible. First, the silty, unconsolidated sediments may be too unstable for successful seedling establishment (cf. Dunn and Sharitz 1987). Second, the delta area seems to be somewhat more flooded than the partially-disturbed sites, perhaps owing to small differences in relative elevation (see also Dulohery et al. 1995). The limited cypress regeneration that had occurred on the delta site was generally found on more elevated microsites. Finally, whether competition was a contributing site factor is unclear. The dense cattail marsh vegetation, which may now inhibit successful seedling establishment (cf. Dunn and Sharitz 1987), did not show large increases in the delta area until 1991. Prior to 1991, more than two-thirds of the delta consisted of open areas and non-persistent vegetation (Wike et al. 1994).

Apart from spatial differences in regeneration, a clearly important factor across all sites was the fortuitous timing of hydrologic conditions that favored successful tree establishment. Many trees of swamp and bottomland forests require wet but unflooded soils for germination and seedling establishment (Burns and Honkala 1990), and their regeneration is inhibited by growing-season floods (e.g., Streng et al. 1989, Sharitz et al. 1990). Typically, natural seasonal drawdowns in river water levels would provide suitable germination conditions. However, on many rivers, dam construction and other flood-control measures have caused permanent hydrologic changes that, in turn, have impaired natural regeneration processes in riparian wetlands (e.g., Conner and Day 1988, Busch and Smith 1995). Water management on the Savannah River has reduced the seasonal variance in hydrology and has increased the occurrence of growing-season floods that cause high seedling mortality (Schneider et al. 1989). It appears that a period of minimal river flooding between 1985–1989 provided a temporal "window" of regeneration opportunity in the Pen Branch system, as reflected in the size and age structure of cypress and tupelo in the disturbed sites.

Restoration Issues

Restoration of riparian forested wetlands presents challenging problems (Clewell and Lea 1990, Mitsch and Gosselink 1993). Recent discussions of wetlands design (Brinson and Lee 1989, Mitsch and Gosselink 1993) have emphasized that the most critical factor for any successful restoration or creation is establishing proper hydrology, followed in importance by the presence of appropriate soils and by availability of suitably-adapted biotic components. In riverine systems, human activities have extensively altered hydrology, substrates, and regeneration processes in riparian forests. Forest restorations require long development times, and the success of planting techniques is inadequately proven (Clewell and Lea 1990). Thus, where the site conditions are suitable, use of natural regeneration potential in forest restorations may be an important supplement to more expensive, labor-intensive seeding and planting measures (Clewell and Lea 1990).

In the Pen Branch system, the critical design factors are well-illustrated by the variation in cypress-tupelo regeneration across the spatial disturbance gradient, and this differential recovery pattern has been incorporated into forest restoration plans for the impacted floodplain (Dulohery et al. 1995). In the partially-disturbed sites, where substrates had not been altered and surviving canopy trees provided adequate seed input, only a critical occurrence of favorable hydrology was needed to promote successful germination and establishment by cypress and tupelo. The resulting density of advanced regeneration in these sites exceeds the threshold recommended as a 'success criterion' for forested wetlands restorations (Clewell and Lea 1990), and it has been deemed sufficient to meet restoration goals (Dulohery et al. 1995). However, where the forest cover was eliminated and extensive sediments were deposited, the shortage of in-site seed sources and the changed site conditions greatly reduced successful recruitment despite a period of favorable hydrology. Restoration of the pre-disturbance cypress-tupelo forest in the sedimentation delta has thus required direct planting of seedlings (Dulohery et al. 1995). By directly planting the desired species, the problem of insufficient regeneration sources is by-passed. However, monitoring will be required to determine if the current hydrologic, substrate, and other site conditions will favor successful long-term recovery of the planted areas.

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