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The effects of landform and plant size on mortality and recovery of longleaf pine during a 100-year flood[1]

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Abstract: Unlike annual floods, large floods affect plant species outside of bottomland ecosystems. We know little about the effects of catastrophic floods on upland plants because of the rarity of this type of disturbance. Here we report on mortality and vegetative recovery of upland longleaf pines (*Pinus palustris*) after a large flood. The flood top-killed most seedlings and advance regeneration, while most large pines survived. About one-half and one-third of affected seedlings and advance regeneration, respectively, recovered vegetatively through resprouting or reflushing. High rates of initial mortality and vegetative recovery were not population-wide phenomena. Mortality decreased with increasing plant height because tall stems maintain more crown volume above floodwaters. Geomorphology alters patterns of mortality as related to size. Landforms retaining surface water had higher rates of mortality than landforms that shed surface water. Responses of longleaf pine to flooding suggest strong geomorphic control over disturbance regimes and, in turn, over population dynamics. Although infrequent, large floods may be important for regulating age structures of longleaf pine. Understanding the effects of large floods may be important for predicting demography of upland plant populations, and more broadly, for understanding the spatial and temporal boundaries of land-water interactions.
Keywords: coastal plain, flooding geomorphology, riparian, tree mortality.

Résumé: À la différence des crues annuelles, les crues centenaires affectent les plantes occupant le lit majeur. Les effets des crues catastrophiques sur les plantes suprariveraines sont peu connus en raison de leur faible fréquence. Cet article fait état de la mortalité et du rétablissement végétatif de *Pinus palustris* après une crue majeure. L'inondation a tué la majorité des plantules et la majeure partie de la régénération pré-établie, alors que les pins de grande taille ont survécu. Environ la moitié des plantules affectées et le tiers des plantes formant la strate de régénération pré-établie ont réagi au plan végétatif en produisant des rejets. Le taux élevé de mortalité de même que la proportion de plantes ayant répondu au plan végétatif ne sont pas un phénomène répandu à l'échelle de toute la population. En effet, le taux de mortalité décroît en fonction de la hauteur des arbres, car le feuillage non inondé est abondant chez les individus les plus grands. Les conditions géomorphologiques altèrent les patrons de mortalité comme dans le cas de la taille des arbres. La mortalité des pins est maximale sur les terrains mal drainés. La réponse du pin à l'immersion suggère donc un fort contrôle géomorphlogique sur le régime des perturbations et, ultérieurement, sur la dynamique des populations. Bien qu'elles soient peu fréquentes, les crues de grande amplitude peuvent affecter la structure d'âge du pin. L'étude des effets des grandes crues fournit des données essentielles pour comprendre la structure démographique des populations de plantes du lit majeur et, dans une plus large perspective, pour baliser les crues historiques.
Mots-clés: plaine côtière, géomorphologie fluviale, riverain, mortalité des arbres.

Introduction

Periodic floods, particularly large events, are an important process controlling the structure and function of stream ecosystems and riparian areas (Gore & Shields, 1995; Johnson, Richardson & Naimo, 1995; Wootton, Parker & Powers, 1996; Michener *et al.*, 1998). This importance is illustrated by the growing interest in reintroduction of large floods to regulated rivers (Schmidt *et al.*, 1998).

In forest ecosystems, floods may be particularly important for structuring populations of trees. The effects of floods on trees are seen in establishment, for example, through deposition of germination substrates (Johnson, 1992; Viereck, Dyrness & Foote, 1993), in stem growth (Kozlowski, Kramer & Pallardy, 1991), and in mortality (Johnson, 1994; Friedman, Osterkamp & Lewis, 1996; Palik *et al.*, 1998).

Studies on the effects of floods (or flow regimes) on trees and forests are concentrated in bottomland and streamside ecosystems (Johnson, Burgess & Keammerer, 1976; Johnson, 1994; Friedman *et al.*, 1996; Palik *et al.*, 1998; Yin, 1998). Major floods (*e.g.*, 100-500 year events), however, extend beyond active floodplains and low terraces in stream valleys. Under extreme conditions, floodwaters can extend into upland ecosystems that are rarely subject to inundation. We have only limited understanding of the effects of rare floods on tree populations outside floodplains and riparian areas. Individuals of long-lived taxa in uplands may experience multiple floods during a lifetime, perhaps effecting their growth or fecundity. Additionally, population

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age structures may carry the imprint of past floods, as a result of either increased mortality or establishment.

A 100-year flood occurring in the southeastern U.S.A. during 1994 provided us with an opportunity to document the effects of flooding on tree populations in an upland landscape. Specifically, we examined the influence of the flood on mortality of longleaf pine (*Pinus palustris* Mill.) in the southwestern Georgia Coastal Plain. Longleaf pine is a long-lived species (> 400 years) that grows across a wide hydrologic gradient, ranging from xeric sand deposits to wet-mesic fine-textured soils adjacent to wetlands (Ware, Frost & Doerr, 1993). While not strictly an upland species, longleaf pine is uncommon in bottomland and wetland ecosystems (Goebel *et al.*, 1996) and apparently is intolerant of flooding (Wahlenberg, 1946). Because of longleaf pine's rarity in bottomlands, studies of natural disturbance regimes for this ecosystem have ignored flooding, instead focusing on fire, lightning, and wind (Platt, Evans & Rathbun, 1988; Palik & Pederson, 1996).

We are not aware of any studies that have examined flood mortality of a single upland tree species across a wide ecological gradient. We speculated that flood mortality of longleaf pine would differ across an elevation gradient in the flood zone, and among different landforms, because of variation in soil drainage properties, water holding capabilities of landforms, duration of inundation, and current velocities. Our intent here is to assess the ability of landforms and landscape positions to mediate the effects of flooding on longleaf pine populations. The conceptual framework for examining the interaction of disturbance and geomorphology on ecological processes comes mainly from observations in steep gradient systems of the Pacific Northwest (Swanson *et al.*, 1988; Swanson *et al.*, 1998). We know comparatively little about how similar interactions affect species and ecosystems in the low gradient Coastal Plain. We also examine how plant size influences flood mortality, particularly as it interacts with landscape position to determine extent and duration of inundation. Specific objectives of our study are to: *i*) quantify longleaf pine mortality among populations distributed across a Coastal Plain landscape; and *ii*) relate mortality and vegetative recovery of individuals to elevation above flood waters, landform shape, soil texture within landforms, and plant height.

Material and methods

STUDY AREA

We conducted our study at Ichauway, a 115 km^2 ecological reserve located at the J. W. Jones Ecological Research Center in southwestern Georgia (Figure 1). The location of the site is along the Flint River at its confluence with Ichawaynochaway Creek. Approximately 22 km of Ichawaynochaway Creek bisects the study area, while an additional 19 km of the Flint River delineates the southeastern border. Average annual discharges range from 236 m^3 sec^{-1} for Ichawaynochaway Creek, to approximately 2060 m^3 sec^{-1} for the Flint River (Stokes, McFarlane & Buell, 1992). Flows are generally low and stable from early summer through autumn. Winter and early spring storms frequently result in bankfull discharges and seasonal inundation of low-lying areas. The Jones Center contains 7 500 ha of 70 to 90 year-old second-growth longleaf pine forests (Palik & Pederson, 1996; Palik *et al.*, 1997). These forests span a xeric to wet-mesic hydrologic gradient across the upland landscape (Goebel *et al.*, 1997).

CHARACTERISTICS OF TROPICAL STORM ALBERTO

Tropical Storm Alberto made landfall on the Florida panhandle near Fort Walton Beach on July 3, 1994, and traveled inland. Because of weak steering currents, the storm remained relatively stationary over southwestern Georgia and southeastern Alabama. Over a period of six days (July 2-7, 1994), one-third of Georgia and one-sixth of Alabama recorded over 17 cm of precipitation (Garza, 1995). Rainfall was especially heavy (up to 53 cm) in the Flint and Ocmulgee River basins in southwestern Georgia. Flow on tributaries and mainstems of the two rivers (including our study area) exceeded 100-year flood discharges along most reaches (Stamey, 1995; Michener *et al.*, 1998).

FLOOD EXTENT AND ELEVATION CONTOURS

We monitored the progression of the floodwaters on site using a global positioning system (GPS) having submeter accuracy. Using the GPS, we recorded the maximum elevation of floodwaters at approximately 350 locations along Ichawaynochaway Creek and the Flint River. We used ARC/INFO to digitize elevation spot heights and 1.5 m (5 ft.) contours, from United States Geological Survey quadrangles. We developed a flood boundary map by overlaying maximum water levels on topography, and extrapolating along contour lines between the points to form a flood polygon (Figure 1). Within this polygon, we used the 1.5 m contours to delineate a series of flood zones that occur between stream bank-full (baseline) and maximum

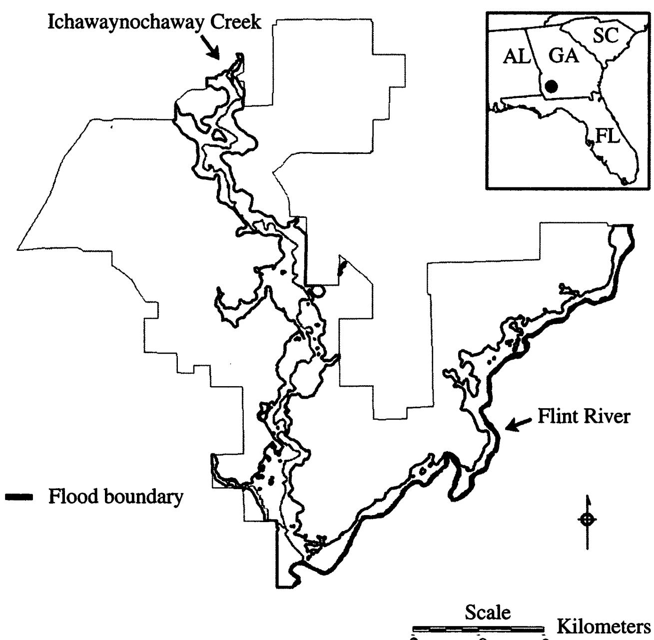

FIGURE 1. Location of the study area showing extent of flooding associated with Tropical Storm Alberto. Note that only one side of the Flint River is included within the study area.

flood elevations. Flood zones characterize the magnitude of flooding. For example, the first flood elevation contour is that area within 1.5 m (± 0.75 m) vertical elevation of the stream at bankfull conditions. This zone experienced the longest period of inundation and deepest floodwaters. Details of the processing steps for developing flood contours are in Michener & Houhoulis (1997).

FIELD SAMPLING AND LABORATORY PROCESSING

We characterized the general effects of flooding on longleaf pine populations during an initial reconnaissance of the study area in mid-July, 1994. We determined that flooding did not kill pines larger than about 10 m in height, apparently because total submergence of larger trees was rare. Because of this, we restricted sampling to populations that contained some individuals < 10 m tall, whether they were alive or dead. Longleaf pine in these populations occur in patches that range in size from 0.1 to several hectares, with the patches themselves dissociated from large overstory trees. We located populations by walking transects running perpendicular to Ichawaynochaway Creek and the Flint River. Sampled populations contained at least 50 individuals that were < 10 m tall. We located and sampled 138 populations meeting the minimum size requirements. This represented a near total enumeration of the entire population of regeneration patches within the zone of flooding. Sampling occurred once during January-February 1995, six months after the flood.

For each patch, we recorded the total number of longleaf pines and assigned each to one of two size classes; grass-stage seedlings and advance regeneration. The grass-stage is a life-history stage characterized by short stature (< 0.1 m), little height growth, and a dense tuft of needles protecting the apical meristem of the seedling (Wahlenberg, 1946). We measured the height of advance regeneration (*i.e.*, individuals that had begun height growth) to the tip of the dominant leader. We assigned stems to one of three physiological conditions: live, dead, or resprouting/reflushing. An individual was resprouting if a new shoot had initiated from a living root system (restricted to grass-stage seedlings), and reflushing if any new needles had developed on the dead crown (usually restricted to advance regeneration).

We determined flood zone (1.5 m elevation contour) and local landform for each population. Landforms ranged in size from several hundred to several thousand m^2. We coded landform shape into the following classes: depressions (deep concave landforms, slopes > 5%); hollows (shallow concave landforms, slopes < 5%); flats (no identifiable depression, slopes < 5%); slopes (linear features, slopes > 5%); hills (convex features, slopes < 5% on most sides); and ridges (linear convex features, slopes > 5% on two sides). These landform classes represent an categorization from those most likely to retain surface water to those most likely to shed surface water.

We collected soil samples for texture determination from a depth of 100 cm at a central location within each landform. While not diagnostic of the entire soil profile, texture at 100 cm does reveal the presence or absence of clay horizon that is reflective of drainage conditions in longleaf pine ecosystems of the study area (Goebel *et al.*, 1997). Soil textures are generally homogeneous within the small landforms of our study. We passed air-dried samples through a 2 mm mesh sieve to remove coarse fragments (2-75 mm; a small percentage of total soil weight in all samples) and determined silt + clay (< 0.05 mm) and sand contents by wet sieving after dispersion in a Calgon solution. We separated sand size fractions at the 100-cm depth, including very coarse + coarse sand (0.5-2.0 mm), medium sand (0.25-0.5 mm), and fine + very fine sand (0.05-0.25 mm), by dry sieving.

STATISTICAL ANALYSIS

We used logistic multiple regression (Hosmer & Lemeshow, 1989) to model mortality and resprouting/reflushing ability of seedlings and advance regeneration. We fit regression models to a single binary (0-1) dependent variable using the SAS LOGISTIC procedure (SAS Institute Inc., 1990). The logistic model has the form:

$$\text{logit}(\psi) = \log(\psi(1-\psi)^{-1}) = \text{I} + \vartheta' x, \qquad [1]$$

where I is the intercept, ϑ is the set of slope parameters associated with the predictor variables x, and ψ is the probability that the response (Y) equals 1 given its vector (x) of predictor variables (*i.e.* $\psi = \Pr(Y=1 \mid x)$. We modeled mortality by assigning 0 for both "crown dead" at the time of sampling and "crown resprouting/reflushing" at the time of sampling (*i.e.*, top-killed, but recovering) and 1 for "crown live" at the time of sampling. Similarly, we modeled resprouting/reflushing ability by assigning 0 for "crown dead" at the time of sampling and 1 for "crown resprouting/reflushing." We chose to model mortality as dead plus resprouting/reflushing individuals, rather than strictly dead individuals, so as to increase sample sizes for the logistic regressions. Further, it is common to assess mortality of trees in this way, despite the fact that many species may recover from living root systems. Predictor variables in the models include:

i) stem height (cm; advance regeneration models only) expressed in log10 transformed values (transformed to meet normality assumption), together with the square of the transformed values [(log10(height))2];

ii) elevation contour indicators (height interval in meters above bankfull conditions: 0-1.5, 1.6-3.0, 3.1-4.6, 4.7-6.0, 6.1-7.6, 7.7-9.1, 9.2-10.7);

iii) interactions between height and elevation contour indicators; and

iv) soil texture expressed as percentages of very coarse + coarse sand, medium sand, very fine + fine sand, and silt + clay.

The potential for model over-specification and observed statistically significant interactions among height, landform, and elevation contour in preliminary analyses required development of individual models for each landform. We used stepwise backward elimination to select statistically significant ($p < 0.05$) predictors. For the elevation contours, we choose the 4.7-6 m interval as a reference zone since this elevation was most consistently represented among all landforms. Thus, indicator regressors and predictors for the other zones model the differences between these zones and the 4.7-6 m contour.

Indices used for evaluating the quality and predictive ability of the individual logistic multiple regression models include: (*i*) likelihood ratio tests; (*ii*) fraction of concordant and discordant pairs; and (*iii*) Somer's D. The Likelihood ratio statistic provides a test for the statistical significance of the regressors based on -2 log likelihood and has an asymptotic chi-square distribution under the null hypothesis that coefficients of explanatory variables in the model are zero. A large value for -2 log likelihood is analogous to a regression sum of squares, reflecting greater variance explained by the model. For all live *versus* dead (or dead *versus* resprouting/reflushing) pairwise combinations, concordance (discordance) is the percentage of pairs in which the dead observation has a higher (lower) predicted probability of mortality than the live observation. Ties result when the pair is neither concordant nor discordant. Somer's D is an index of rank correlation between predicted probabilities and observed responses (Hosmer & Lemeshow, 1989; SAS Institute Inc., 1990).

Results

GRASS-STAGE SEEDLINGS

Two-thirds (66.4%; 4808 of 7244) of the grass-stage seedlings in the flooded area were top-killed by the flood (Table I). However, over half of these seedlings (2585) resprouted (or reflushed) by the time of sampling. One-third of all seedlings were unaffected by flood waters (33.6%). Ultimately, nearly 70% of all seedlings (living plus resprouts) survived the flood to the time of sampling.

Mortality rates of grass-stage seedlings varied among landforms. Pooled across flood elevation zones, mortality (percent top-killed; percent dead) was highest in hollows (92.3%; 65.3%) and depressions (85.2%; 46.8%), intermediate in flats (69.3%; 34.8%) and slopes (63.6%; 24.7%), and lowest on hills (58.6%; 18.8%) and ridges (24.0%; 0.7%; Table I). There were no obvious trends related to landform in resprouting ability of grass-stage seedlings (Table I).

Logistic regression models for the probability of grass-stage seedling mortality (includes percent dead plus percent top-killed, but resprouting) and resprouting/reflushing (Table II) retained one or more elevation contours and one or more soil texture parameters (Table III). The various measures of model performance (Table II) indicated high statistical significance and good predictive capabilities in most landforms (somewhat better for modeling mortality than resprouting ability). Although grass-stage seedling responses to flooding were complex, some general trends are evident. First, mortality was consistently high across all flood zones for both depressions and flats (Table I). Second, mortality declined with flood elevation for slopes (except for the lowest flood zone), and was consistently low for ridges (Table I). Hollows and hills did not occur on enough elevation contours to suggest any clear trends. Further, no clear trends were evident for the probability of resprouting across elevation contours (Table I).

Many soil texture parameters in the models were significant (Table III). However, there were inconsistencies in relationships between percentages of sands and fines and the probability of mortality and resprouting/reflushing. This suggests high inter-landform variability in soil properties, rather than any specific relationship between dependent and independent variables.

ADVANCE REGENERATION

Mortality of advance regeneration in the flooded area approached 70% (Table I). Less than one-third of all stems (21.3%) had reflushed by the time of sampling. Approximately one-third (30.9%) were unaffected by flood waters. Taken together, live stems and those that reflushed accounted for 52% of all advance regeneration. Overall, advance regeneration had higher rates of mortality and lower probability of vegetative recovery than did grass-stage seedlings (Table I).

Mortality (percent top-killed; percent dead) of advance regeneration was highest in depressions (91.0%; 70.2%) and hollows (82.5%; 62.8%), intermediate in flats (74.4%; 52.4%) and slopes (69.6%; 45.4%), and lowest on hills (42.5%; 25.5%) and ridges (20.0%; 3.7%) (Table I). The proportion of advance regeneration that reflushed following death was relatively consistent across all landforms, ranging from 16.3 to 24.2% (Table I).

Advance regeneration exhibited complex responses to flooding within individual landforms. The best logistic regression models of mortality (in terms of predictability and interpretability) for depressions, flats, and slopes include plant height (and/or height^2), one or more elevation contours, all soil texture parameters, and numerous two-way interaction terms between height (or height^2) and elevation contour (Tables IV and V). Model performance was good in most cases (Table IV), but was somewhat better for predicting mortality than reflushing ability. (Sample sizes were insufficient on hollows, ridges, and hills for logistic regression models to statistically discriminate differences in ecological responses among elevation contours [$p > 0.05$]; see Table I)

The models suggest several general patterns in mortality as related to stem heights and flood elevation zones. First, the probability of mortality decreased with increasing plant height (Figures 2a-c). The exception to this general trend occurred at the 7.7-9.1 m elevation contour on slopes (Figure 2c), probably because of the presence of a single 8.0-m stem that died. Second, the probability of mortality often increased once regeneration reached a height of 20 cm. The bell-shaped curves for several of the elevation contours show this trend (Figures 2a-c), as does the statistically significant ($P < 0.05$) height^2 parameters and height^2-elevation contour interactions in the logistic regression models (Table V). Third, mortality on depressions and slopes was negatively related to flood zone elevation (Figure 2; Table V), *i.e.*, highest at sites closest to the active channels. Finally, the probability of mortality increased with increasing amounts of coarse sands and decreasing amounts of medium sands and silt + clay (Table V). However, the biological significance of these soil relationships is not apparent.

TABLE I. Percent mortality and vegetative recovery of longleaf pine grass-stage seedlings and advance regeneration by landform and flood elevation zone

Landform[6]	Elevation zone (m)	Grass-stage seedlings[1]				Advance regeneration[2]			
			Top-killed[3]				Top-killed		
		Live	Dead	Resprout[4]	Total	Live	Dead	Reflush[5]	Total
		%	%	%	n	%	%	%	n
Depression	0.1 - 1.5	0.0	76.5	23.5	17	5.7	87.1	7.1	70
(n = 27)	1.6 - 3.0	0.6	73.5	25.9	162	12.9	64.7	22.4	85
	3.1 - 4.6	16.0	38.9	45.1	736	4.3	73.4	22.2	899
	4.7 - 6.0	24.0	45.1	30.9	275	24.6	49.3	26.1	211
	6.1 - 7.6	7.2	58.4	34.4	125	15.7	76.9	7.4	121
	Subtotal	14.8	46.8	38.4	1315	9.0	70.2	20.8	1386
Hollow	3.1 - 4.6	9.9	55.8	34.3	233	7.9	57.9	34.2	76
(n = 6)	4.7 - 6.0	5.2	75.8	19.0	211	29.5	68.9	1.6	61
	Subtotal	7.7	65.3	27.0	444	17.5	62.8	19.7	137
Flat	1.6 - 3.0	13.4	33.6	53.0	336	32.0	52.3	15.7	153
(n = 33)	3.1 - 4.6	14.2	64.4	21.3	506	16.4	72.3	11.4	483
	4.7 - 6.0	57.9	14.5	27.6	359	35.7	44.3	20.0	255
	6.1 - 7.6	46.8	18.1	35.1	365	25.3	27.0	47.7	237
	7.7 - 9.1	5.5	18.2	76.4	55	4.2	16.7	79.2	24
	9.2 - 10.7	22.2	11.1	66.7	9	54.7	39.6	5.7	53
	Subtotal	30.7	34.8	34.5	1630	25.6	52.4	22.0	1205
Slope	0.1 - 1.5	47.2	29.8	23.0	161	27.4	46.8	25.8	62
(n = 44)	1.6 - 3.0	5.1	59.0	36.0	178	3.8	72.0	24.2	186
	3.1 - 4.6	9.3	33.1	57.6	774	13.1	55.5	31.3	632
	4.7 - 6.0	39.7	18.0	42.3	983	37.2	36.1	26.8	452
	6.1 - 7.6	83.3	6.3	10.3	126	96.6	1.4	2.0	148
	7.7 - 9.1	84.5	11.1	4.4	297	50.5	48.4	1.1	93
	9.2 - 10.7	81.8	6.1	12.1	33	90.5	0.0	9.5	21
	Subtotal	36.4	24.7	38.9	2552	30.4	45.4	24.2	1594
Hill	3.1 - 4.6	50.0	13.7	36.3	256	56.0	28.3	15.7	382
(n = 14)	4.7 - 6.0	20.8	27.6	51.5	293	45.2	23.3	31.5	73
	6.1 - 7.6	98.5	0.0	1.5	67	100.0	0.0	0.0	34
	Subtotal	41.4	18.8	39.8	616	57.5	25.5	17.0	489
Ridge	1.6 - 3.0	96.8	0.0	3.2	63	75.0	25.0	0.0	4
(n = 13)	3.1 - 4.6	36.8	0.0	63.2	87	13.8	0.0	86.2	29
	4.7 - 6.0	66.6	0.0	33.4	293	82.4	4.0	13.6	427
	6.1 - 7.6	95.9	2.0	2.0	244	91.9	2.7	5.4	74
	Subtotal	76.0	0.7	23.3	687	80.0	3.7	16.3	534
Total		33.6	30.7	35.7	7244	30.9	47.9	21.3	5345

[1]Grass-stage seedling: stems < 0.1 m tall, height growth not yet initiated.
[2]Advance regeneration: stems ≥ 0.1 m tall, height growth initiated.
[3]Top-killed individuals include those stems that were dead at the time of sampling and those that recovered vegetatively through living root systems.
[4]Resprout: new shoot initiated from a living root system (restricted to grass-stage seedlings).
[5]Reflush: new needles developed in the original crown (usually restricted to advance regeneration).
[6]Landform definitions are as follows: depressions (deep concave landforms, slopes > 5%); hollows (shallow concave landforms, slopes ≤ 5%); flats (no identifiable depression, slopes < 5%); slopes (linear features, slopes > 5%); hills (convex features, slopes < 5% on most sides); and ridges (linear convex features, slopes > 5% on two sides).

Like mortality, the best models for explaining reflushing of advance regeneration on depressions, flats, and slopes typically include plant height (and/or height^2), one or more elevation contours, soil texture parameters (except flats), and one or more two-way interaction terms between height (or height^2) and elevation contour (Tables IV and V). Two general trends for probability of reflushing are evident. First, the inverted bell-shaped curves for four of the elevation contours in depressions illustrate the disproportionately higher probability of resprouting in the smallest, but also the largest size classes (Figure 2d, Table V). Second, for most advance regeneration (Figures 2d-f) the probability of reflushing decreased with height. An exception is the 0.1-1.5 m contour in depressions and slopes, possible because of small sample sizes (n = 5 and 16, respectively). Relationships between soil texture and probability of reflushing were not consistent among landforms (Table V).

Discussion

A remarkable result of this study is that a large percentage of longleaf pine seedlings (70%) and advance regeneration (50%) survived, to the time of sampling, or recovered from the flood despite the catastrophic nature of the disturbance. Continued observations for several months after our initial sampling suggest that no additional flood mortality occurred in the study populations. Additional evidence suggests high survival of grass-stage seedlings with short periods of inundation. Submerged seedlings in another study all survived, although growth was less than in unflooded seedlings (Palik *et al.*, 1997). This is contrary to the belief that mortality of longleaf pine with submergence is generally high (Wahlenberg, 1946). However, repeated flooding, such as occurs on floodplains, may result in greater mortality over time than single floods. Indeed, the absence of longleaf pine

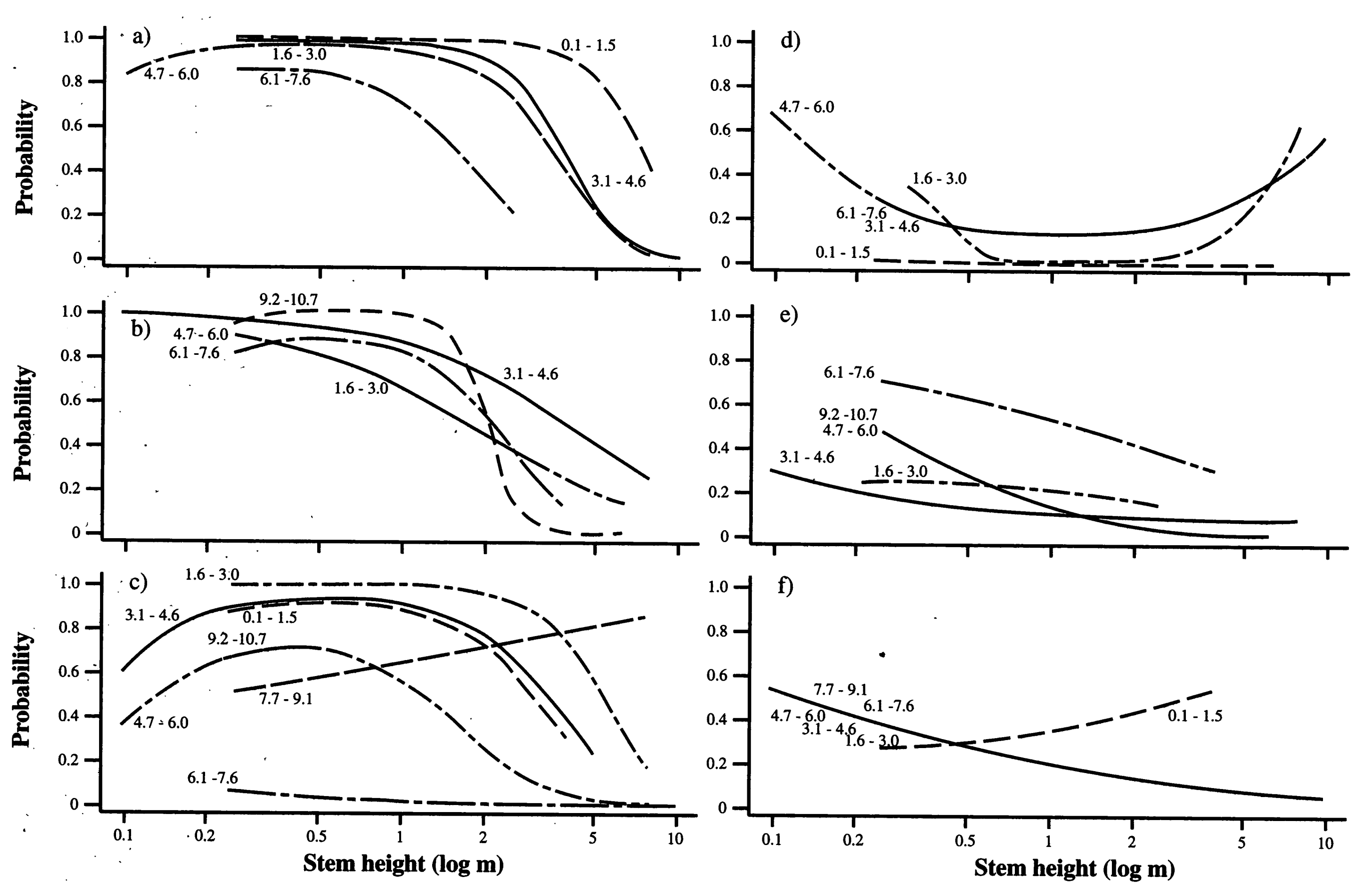

FIGURE 2. Estimated probability of longleaf pine advance regeneration mortality in (a) depressions, (b) flats, and (c) slopes, and crown reflushing ability in the same landforms (d - depressions, e - flats, f - slopes), for each elevation zone (1.5 m contours) based on logistic multiple regression. Mortality values are based on initial mortality, *i.e.*, the combination of stems that were dead at the time of sampling plus those that were top-killed but had reflushed by the time of sampling. Individual models are based on average soil texture characteristics for specific landforms. Note: in some instances, several elevation contours shared identical response curves on the graphs (*e.g.*, 9.2-10.7 and 4.7-6.0 m in graph e); only one curve is visible in these instances.

TABLE II. Summaries of logistic multiple regression models by landform for probability of longleaf pine grass-stage seedling mortality and resprouting

Landform[1]	Model fit -2 Log likelihood Statistic	Indices of model predictive ability Concord. (%)	Discord. (%)	Somer's D
a) GRASS-STAGE SEEDLING[2] MORTALITY				
Depression	219.78*** (5 df)	80.4	16.1	0.643
Hollow	48.55*** (4 df)	79.3	10.5	0.688
Flat	456.06*** (7 df)	80.7	17.2	0.635
Slope	1050.63*** (9 df)	84.7	13.8	0.709
Hill	255.15*** (4 df)	79.1	18.5	0.606
Ridge	246.00*** (6 df)	80.9	14.3	0.66
b) GRASS-STAGE SEEDLING RESPROUTING[3]				
Depression	219.12*** (5 df)	72.5	23.9	0.486
Hollow	112.15*** (3 df)	70.8	16.7	0.541
Flat	216.86*** (3 df)	72.8	24.7	0.480
Slope	151.88*** (6 df)	62.8	33.6	0.292
Hill	75.64*** (2 df)	65.6	27.5	0.381
Ridge	ns			

[1]Landform definitions are as follows: depressions (deep concave landforms, slopes > 5%); hollows (shallow concave landforms, slopes ≤ 5%); flats (no identifiable depression, slopes < 5%); slopes (linear features, slopes > 5%); hills (convex features, slopes < 5% on most sides); ridges (linear convex features, slopes > 5% on two sides).
[2]Grass-stage seedling: stems < 0.1 m tall, height growth not yet initiated.
[3]Resprout: new shoot initiated from a living root systems.
*** $p < 0.001$; ns = not significant.

on floodplains (Goebel *et al.*, 1996) suggests that the species is intolerant of frequent flooding.

The second important result of our study is that high survival and vegetative recovery are not population- or landscape-wide phenomena; both vary with plant size and flood-zone geomorphology. Probability of mortality generally increased with decreasing stem height of advance regeneration. This occurred because complete crown submergence was more likely for smaller stems, particularly at lower elevations in the landscape. However, as a group, grass-stage seedlings had lower mortality rates than advance regeneration, perhaps because faster height growth rates in the latter reduce carbohydrate reserves available for recovery (Brown, 1964). The 10-m height threshold for mortality that we observed reflects the position of live crowns above maximum water depth in the flood zone. Stems taller than 10 m had some live crown above the water, even in the lowest landscape positions.

The mechanism causing increased mortality with crown submergence may have been oxygen deficiency of submerged tissue. Lack of oxygen may be the primary cause of mortality in inundated trees, although toxic metabolites (*e.g.*, iron, fatty acids, ethylene) also inhibit root growth of submerged conifers (Sanderson & Armstrong, 1980). Complete or nearly complete inundation could have

TABLE III. Logistic regression parameter estimates for percent mortality and resprouting ability of longleaf pine grass-stage seedlings (Note: intercept represents parameter estimates for the 4.7-6.0 m elevation class)

		Grass-stage seedling[1] mortality			Grass-stage seedling resprouting[2]		
Landform[3]	Variable	ϑ	SE	χ^2_i	ϑ	SE	χ^2_i
Depression	Intercept	-0.1652	0.4295	0.15 ns	0.00619	0.3405	0.0003 ns
	6.1-7.6 m	2.3577	0.3996	34.81**	ns		
	3.1-4.6 m	0.5243	0.1945	7.26**	0.6933	0.1526	20.65**
	1.6-3.0 m	4.5740	1.0209	20.07**	-1.2792	0.2311	30.63**
	Med. sand	0.0782	0.0102	58.70**	-0.0169	0.00714	5.57*
	Coarse sand	ns			-0.0394	0.00757	27.10**
	Silt/clay	-0.0166	0.0081	4.19*	0.0222	0.00704	9.92**
Hollow	Intercept	10.3284	2.4872	17.24**	3.7783	0.6244	36.61**
	3.1-4.6 m	-3.6147	1.2601	8.23**	-3.8270	0.6377	36.01**
	Med. sand	-0.1717	0.0389	19.51**	ns		
	Coarse sand	-0.0880	0.0360	5.99*	-0.1133	0.0159	50.79**
	Silt/clay	0.0870	0.0260	11.22**	0.0532	0.0122	18.91**
Flat	Intercept	1.4076	0.2490	31.95**	1.2295	0.1480	68.98**
	7.7-9.1 m	4.9252	0.6048	66.32**	2.9282	0.5231	31.34**
	6.1-7.6 m	0.3360	0.1692	3.94*	ns		
	3.1-4.6 m	2.0653	0.1794	132.50**	-1.5274	0.1413	116.85**
	1.6-3.0 m	1.8629	0.2030	84.25**	ns		
	Med. sand	-0.0597	0.0077	60.13**	ns		
	Coarse sand	0.0917	0.0121	57.51**	ns		
	Silt/clay	-0.0415	0.0053	62.09**	-0.0298	0.00548	29.60**
Slope	Intercept	-1.5697	0.2291	46.95**	-0.6926	0.2549	7.38**
	9.2-10.7 m	-2.1664	0.4655	21.66**	ns		
	7.7-9.1 m	-1.5499	0.1999	60.11**	-1.5899	0.3663	18.84**
	6.1-7.6 m	-0.9991	0.2659	14.12**	ns		
	3.1-4.6 m	2.1120	0.1504	197.28**	ns		
	1.6-3.0 m	3.1616	0.3559	78.91**	-1.5170	0.1851	67.16**
	0.1-1.5 m	-0.4052	0.1771	5.23*	-0.8822	0.2300	14.71**
	Med. sand	0.0385	0.0072	28.49**	0.0563	0.0079	51.49**
	Coarse sand	0.0745	0.0079	88.88**	-0.0139	0.0034	16.51**
	Silt/clay	0.0129	0.0049	6.91**	0.0173	0.0059	8.52**
Hill	Intercept	-1.4899	0.3654	16.63**	3.7490	0.5192	52.14**
	6.1-7.6 m	-4.9861	1.0207	23.86**	ns		
	3.1-4.6 m	-2.1758	0.2943	54.66**	ns		
	Med. sand	0.1221	0.0167	53.42**	-0.0932	0.0126	54.94**
	Silt/clay	0.0671	0.0117	32.85**	-0.0451	0.0124	13.32**
Ridge	Intercept	-5.4987	1.1121	24.45**	ns		
	6.1-7.6 m	-2.3010	0.4194	30.10**	ns		
	3.1-4.6 m	-4.0915	0.7567	29.23**	ns		
	1.6-3.0 m	-4.5575	0.8469	28.96**	ns		
	Med. sand	0.2806	0.0496	32.05**	ns		
	Coarse sand	-0.3820	0.0614	38.68**	ns		
	Silt/clay	0.1192	0.0278	18.44**	ns		

[1]Grass-stage seedling: stems < 0.1 m tall, height growth not yet initiated.
[2]Resprout: new shoot initiated from a living root system.
[3]Landform definitions are as follows: depressions (deep concave landforms, slopes > 5%); hollows (shallow concave landforms, slopes ≤ 5%); flats (no identifiable depression, slopes < 5%); slopes (linear features, slopes > 5%); hills (convex features, slopes < 5% on most sides); and ridges (linear convex features, slopes > 5% on two sides).
* $P < 0.05$; ** $P < 0.01$; ns = not significant.

deprived leaves and bark of oxygen. Diffusion of oxygen from leaves and lenticels on bark occurs in a number of pines (Hahn, Hartley & Rhoads, 1920). We do not know the extent to which longleaf pine is able to transport oxygen from exposed portions of the stem to submerged tissue. The ability to do this may help explain why mortality is lower when crown submergence is low.

Our results also show that mortality of longleaf pine from the flooding varies with landform shape and elevation above the stream channel. Mortality was highest on landforms that retained water even after the flood receded (depressions, hollows), whereas it was lowest on water-shedding landforms (ridges, hills). Landform elevation above the stream channel added an additional geomorphic control to flood response. In particular, longleaf pine on slopes located low in the flood zone had higher mortality rates than those growing on slopes higher in the flood zone. The mechanism behind these patterns could be the relationship between plant size and probability of submergence. In addition, the duration of inundation and exposure to reduced oxygen concentrations was probably high on concave and low elevation landforms.

TABLE IV. Summary of logistic multiple regression models for probability of longleaf pine advance regeneration mortality and reflushing among landforms

Landform[1]	Model Fit -2 Log likelihood Statistic	Indices of model predictive ability Concord. (%)	Discord. (%)	Somer's D
a) ADVANCE REGENERATION[2] MORTALITY				
Depression	283.10*** (9 df)	86.2	12.9	0.733
Flat	297.29*** (11 df)	79.7	19.9	0.598
Slope	629.82*** (12 df)	84.5	15.1	0.695
b) ADVANCE REGENERATION REFLUSHING[3]				
Depression	228.94*** (10 df)	77.9	21.4	0.565
Flat	177.54*** (6 df)	74.8	21.8	0.530
Slope	126.07*** (5 df)	69.4	29.9	0.395

[1]Landform characteristics are as follows: depressions (deep concave landforms, slopes > 5%); flats (no identifiable depression, slopes < 5%); slopes (linear features, slopes > 5.

[2]Advance regeneration: stems ≥ 0.1 m tall, height growth initiated.

[3]Reflush: new needles developed in the original crown.

*** $p < 0.001$.

Our results illustrate clearly how geomorphology can control ecological pattern across a landscape through mediation of an ecosystem process (Swanson *et al.*; 1988); in our case, the effects of flooding on longleaf pine populations. Interactions between landforms and flooding are unquestionably important for controlling the distribution and demography of plants in bottomland ecosystems (DéCamps, 1996; Hodges, 1998). Our study illustrates how floods interact with geomorphology to affect even upland landscapes and tree populations in dramatic ways. These results serve to extend the concept of land-water interactions (Gregory *et al.*, 1991) spatially, into upland landscapes, and temporally, to return intervals of centuries. In upland settings, infrequent floods may interact with other (better-studied) natural disturbances (*e.g.*, fire, wind, and lightning in longleaf pine ecosystems [Platt & Rathbun, 1995; Palik & Pederson, 1996]) to control population structure and dynamics of long-lived species.

TABLE V. Logistic regression parameter estimates for percent mortality and reflushing of longleaf pine advance regeneration[1] (Note: intercept represents parameter estimates for the 4.7-6.0 m elevation class)

Land form[3]	Variable	Crown mortality ϑ	SE	χ^2_i	Reflushing ability[2] ϑ	SE	χ^2_i
Depression	Intercept	-6.728	2.504	7.22**	7.302	2.422	9.09**
	Height	13.302	2.758	23.27**	-10.122	2.898	12.20**
	Height^2	-4.049	0.755	28.76**	2.481	0.849	8.54**
	1.6-3.0 m	ns			-60.818	29.414	4.28*
	0.1-1.5 m	2.744	0.875	9.84**	ns		
	Medium sand	-0.056	0.018	9.41**	0.069	0.011	42.80**
	Coarse sand	0.125	0.021	35.41**	-0.082	0.010	64.48**
	Silt/clay	-0.052	0.012	18.15**	0.025	0.007	12.85**
	Height*(6.1-7.6 m)	-0.956	0.241	15.76**	ns		
	Height*(3.1-4.6 m)	1.886	0.655	8.28**	ns		
	Height*(1.6-3.0 m)	ns			81.69	39.520	4.27*
	Height*(0.1-1.5 m)	ns			-5.245	1.287	16.61**
	Height^2*(3.1-4.6 m)	-0.689	0.329	4.40*	ns		
	Height^2*(1.6-3.0 m)	ns			-27.200	13.142	4.26*
	Height^2*(0.1-1.5 m)	ns			1.882	0.661	8.10**
Flat	Intercept	4.057	0.376	116.70**	1.514	0.361	17.61**
	Height^2	-0.656	0.074	79.69**	-0.852	0.151	31.70**
	9.2-10.7 m	-46.211	21.407	4.66*	ns		
	6.1-7.6 m	-16.047	4.285	14.03**	ns		
	3.1-4.6 m	1.128	0.199	32.15**	ns		
	1.6-3.0 m	ns			-4.623	1.618	8.16**
	Medium sand	-0.040	0.008	25.76**	ns		
	Coarse sand	0.070	0.013	28.14**	ns		
	Silt/clay	-0.034	0.005	42.64**	ns		
	Height*(9.2-10.7 m)	54.323	25.066	4.70*	ns		
	Height*(6.1-7.6 m)	17.169	4.955	12.01**	ns		
	Height*(3.1-4.6 m)	ns			-2.937	0.636	21.32**
	Height*(1.6-3.0 m)	ns			2.584	1.056	5.99*
	Height^2*(9.2-10.7 m)	-14.809	6.855	4.67*	ns		
	Height^2*(6.1-7.6 m)	-4.366	1.389	9.89**	0.501	0.084	35.68**
	Height^2*(3.1-4.6 m)	ns			1.384	0.376	13.54**
Slope	Intercept	-8.540	1.650	26.78**	1.668	0.510	10.68**
	Height	12.818	1.905	45.29**	-1.480	0.266	30.94**
	Height^2	-3.983	0.543	53.79**	ns		
	7.7-9.1 m	9.041	4.293	4.43*	ns		
	1.6-3.0 m	4.164	0.528	62.15**	ns		
	0.1-1.5 m	ns			-1.703	0.825	4.26*
	Medium sand	-0.035	0.009	16.20**	0.025	0.007	12.85**
	Coarse sand	0.026	0.010	7.22**	ns		
	Silt/clay	-0.023	0.007	10.51**	-0.028	0.007	16.75**
	Height*(7.7-9.1 m)	-12.935	4.755	7.40**	ns		
	Height*(6.1-7.6 m)	-2.447	0.317	59.65**	ns		
	Height*(3.1-4.6 m)	0.980	0.102	92.89**	ns		
	Height*(0.1-1.5 m)	0.865	0.196	19.54**	ns		
	Height^2*(7.7-9.1 m)	4.281	1.251	11.71**	ns		
	Height^2*(0.1-1.5 m)	ns			0.602	0.233	6.67**

[1]Advance regeneration: stems ≥ 0.1 m tall, height growth initiated.

[2]Reflush: new needles developed in the original crown.

[3]Landform characteristics are as follows: depressions (deep concave landforms, slopes > 5%); flats (no identifiable depression, slopes < 5%); and slopes (linear features, slopes > 5%).

* $p < 0.05$; ** $p < 0.01$; ns = not significant.

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