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PRODUCTION AND DECOMPOSITION RATES OF A COASTAL PLAIN FOREST FOLLOWING THE IMPACT OF HURRICANE HUGO

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Abstract: Recovery of a coastal plain mixed hardwood-pine forest following the impact of Hurricane Hugo in 1989 was monitored for four years, 1991–1995. Eight 400 m^2 plots were set in each of two treatment areas-an Unsalvaged and a Salvaged site. Wind-downed trees were kept on the site in the Unsalvaged Site and removed in the Salvaged Site. It was hypothesized that leaving hurricane generated debris in place would lead to higher production and decomposition rates, and therefore greater nutrient retention, over decade-long terms.

No significant differences in production or decomposition rates were found as a result of treatments; and so production and decomposition data from the two treatments were subsequently combined into a single data set to provide baseline estimations of these parameters for possible future permanently plotted studies. Net primary production of herbs was 94.5 g m^{-2} yr^{-1}. Litter mass production was *664.3* g m^{-2} yr^{-1}.

Several parameters, other than production and decomposition, were measured and were also not 'significantly different between Salvaged and Unsalvaged treatments. The relatively short duration of the study may have influenced the results, but the data are suggestive of possible contrasting ***long-term*** trends with respect to the treatments. This additional data indicated that: 1) the mean root : shoot ratio of volunteer pine seedlings in the Salvaged site was three times that of the Unsalvaged Site; 2) estimated soil organic matter was 1½ times greater in the Unsalvaged Site compared to the Salvaged Site; 3) the mean percentage of wood ash of newly germinated pine seedlings was 1% times greater in the Unsalvaged Site compared to 'the Salvaged Site; and 4) mean post-Hugo radial increase of surviving loblolly pine trees on both plots was 0.21 cm yr^{-1} compared to 0.18 cm yr^{-1} pre-Hugo growth.

These short-term data sets, although not statistically different between treatments, at least suggest that long-term rates of recovery of forests following hurricane impacts might be greater if the forests are left undisturbed. Long term studies are needed to increase data, and discover if, over successional--decades long-time frames, coastal plain forests respond differently with hurricane detrital material removed compared to being left in place. Such data have implications with respect to management of coastal forests following hurricane and even human-generated impacts.

Key Words: Coastal forests, forest production and decomposition, forest hurricane recovery.

INTRODUCTION

Hurricane Hugo struck the South Carolina coast on 22 September 1989 with sustained winds of >200 km hr^{-1} 33 km southwest of Santee Experimental Forest, a part of Francis Marion National Forest (Purvis et al., 1990).

The storm heavily impacted coastal forests, uprooting or severely damaging a high proportion of trees in these forests. This study was based on the expectation that the uprooted and broken trees and branches, as well as understory debris, would create a high organic matter and tissue nutrient load on the forest floor which would soon begin decomposing and releasing nutrients to the forest soil. Plants growing in the nutrient rich soil following the hurricane could be expected to use released nutrients from decomposing vegetation to potentially generate high production rates. The hurricane-generated nutrients and the now higher light levels reaching the forest floor would result in new vigorous plant growth replacing hurricane-killed vegetation.

The United States Forest Service (USFS) began salvaging fallen trees from some areas of the national forest during the months following the storm (Marsinko et al., 1993), and a research project was proposed to monitor post-Hugo recovery of a forest where hurricane-generated debris was removed (Salvaged) compared to a forest where debris was left in place (Unsalvaged). The basic premise of such a study was that southern U.S. coastal plain forests are evolutionarily adapted to hurricane impacts and that removal of hurricane-generated debris would be detrimental to recovery of these forests during the years following hurricane impact. This would be a result of depletion of nutrients and organic matter that would accompany any debris removal, which in turn would lead to a less than robust recovery of the forest community from the devastation caused by the storm.

The hypothesis for this study was that the Unsalvaged Site would recover more robustly than the Salvaged Site, as measured by herbaceous and tree production rates.

STUDY AREA

Santee Forest study sites before Hurricane Hugo consisted of natural well-stocked mature stands, 90-150 yr old, of loblolly (*Pinus taeda* L.) and longleaf pine (*P. palustris* Miller) mixed with overstory hardwoods of sweetgum (*Liquidambar styraciflua* L.), tulip poplar (*Liriodendron tulipifera* L.), maples (*Acer* spp.), oaks (*Quercus* spp.), hickories (*Carya* spp.), elms (*Ulmus* spp.) and other hardwoods of lesser importance (USFS, 1995). Braun (1950) classified the forest region as a mixed loblolly pine-southern hardwood forest. An estimated 90% of all trees were broken or uprooted at these sites by the storm (pers. obs.), an impact noted also at other nearby sites (Hook et al., 1991) and within ranges found by a study on Hugo storm-related tree damage within a forest in Puerto Rico (Walker, 1991). Eighty percent of these damaged or killed trees were salvaged from the Salvaged (S) Site of this study (pers. obs.), while no storm debris was removed from the Unsalvaged (U) Site.

Mean diameter at breast height (DBH) of surviving trees, following the storm, was 17 cm, leaving a tree basal area of about 35 m^2 ha^{-1}. Mean DBH of destroyed trees, whose average age was 63 yr was 28 cm (pers. obs.), a finding in accordance with Reilly (1991) and others (Gresham et al., 1991; Pittman et al., 1996) who found that the storm lolled or damaged a higher proportion of larger trees than smaller ones. The sites are probably N-limited. Blood et al. (1989) reported that coastal loblolly pine forests receive only 0.24 g m^{-2} of N through precipitation, and with generally sandy or clayey soils (Hook et al., 1991) nutrient holding capacity is probably very low.

METHODS

Salvaged and Unsalvaged study sites were established in the fall of 1990 within the Santee Experimental Forest, South Carolina. Four 20 X 20 m plots were set in place at each site and permanently marked with 3 m aluminum poles. Plots were separated by 10 m medians. Within each of two of these permanent plots at each site, 50 one-year old loblolly pine seedlings, obtained from the nearby state nursery, were planted and marked in the spring of 1991.

Thirty-seven surviving trees (nearly all of the survivors >10 cm DBH) of the major species (sweetgum, loblolly pine, tulip poplar, red maple, oaks) throughout all the plots were banded with aluminum dendrometers on 1 July 1991 to track annual circumference growth rates.

Three randomly selected 0.5 X 0.5 m subplots were established within each 20 X 20 m plot (12 each per Salvaged and Unsalvaged Sites) and were used to estimate herbaceous productivity, and litter production and decomposition rates. Ten 2 X 2 m plots were also established within alternate 20 X 20 m plots at each site (20 plots total) to estimate natural pine seedling recruitment.

Over the next four years, biology students from JCSU collected semiannual late fall and early spring samples (n = 8 sampling events X -20 samples/event = -160 samples) of herbaceous cover and litter from the small subplots for estimation of herbaceous net primary productivity and litter production, and three 10 cm-deep soil samples from Salvaged and Unsalvaged areas. They also measured diameter growth of banded trees and the height and base diameter changes of planted pine seedlings. A mesh (2 mm) bag of 10.0 g of dried (60°C) litter, and one or two dried and weighed sticks from the sites (<3 cm diameter) were set out in each of the subplots at each visit and collected on subsequent visits. Collected samples were brought ‘back to the laboratory at JCSU and dried and weighed. Soil samples were heated to 60°C for two days to determine soil moisture and 400°C for five hours in a muffle oven to estimate organic matter and ash content..

Herbaceous net primary productivity was estimated by harvest of live herbaceous growth occurring within the 0.25 m^2 subplots since the previous sample date. This method was used because it was the most practical way to estimate this parameter given the logistical situation of twice yearly measurements with student labor. These- plots were also used to estimate litter production rates by collection of dead plant material in each plot during semi-annual sampling periods.

Two additional studies were initiated during the course of the study. A root-shoot dry weight ratio of 25 Unsalvaged and 25 Salvaged (total of 50) three-year-old volunteer loblolly pine seedlings was determined. Samples were dug up, the shoot separated from the root, and both washed and dried at 60°C, and weighed. The root-shoot mass ratio was calculated for each seedling. A second study compared mean annual ring widths of three years of pre-storm and five years of post-

Table 1. Summary means (± standard deviations) of Santee Forest Hurricane Hugo recovery parameters, July 1991–October 1995. Data are combined means of both Salvaged and Unsalvaged Sites except where noted.

Parameter	Summary Mean	
Planted loblolly pine, final diameter, cm	3.2 (1.1)	
Planted loblolly pine, final height, cm	372.0 (150.5)	
Circumference increase, surviving trees, cm	6.6 (4.6)	
Net herbaceous production, g m^{-2} yr^{-1}	94.5 (80.4)	
Litter accumulation, g m^{-2} yr^{-1}	664.3 (562.1)	
Decomposition rate-leaves, % loss yr^{-1}	45.6 (20.0)	
Decomposition rate-wood, % loss yr^{-1}	25.6 (16.4)	
Stem radial increase of storm-surviving loblolly pine trees, cm yr^{-1}:		
pre-Hugo	0.18 (0.02)	
post-Hugo	0.21 (0.06)	
	Treatment Means	
Parameters by site treatment:	Salvaged	Unsalvaged
Soil organic matter, %	9.6 (5.9)	14.2 (2.7)
Soil moisture, %	18.7 (8.6)	21.9 (8.7)
Wood ash, %	0.86 (0.3 1)	1.07 (0.79)
Root to shoot ratio, pine seedlings	1.08 (0.52)	0.63 (0.43)

storm tree growth, by study of 25 tree cores taken from undamaged storm-surviving loblolly pine trees (-10-30 cm DBH).

Student's *t* tests were calculated for all sets of data. No significant differences were found between treatments / sites; thus production and decomposition data for Salvaged and Unsalvaged plots were combined (averaged) into a single data set.

RESULTS AND DISCUSSION

Estimated aboveground herbaceous net primary production (NPP) was 94.5 (±80.4) g m^{-2} yr^{-1} (Table 1). Monk et al. (1970) reported 12.4 g m^{-2} yr^{-1} for an eastern U.S. piedmont oak-hickory forest, while Ralston (1973) and Nemeth (1973) reported 120-200 g m^{-2} yr^{-1} in a southeastern U.S. pine forest. Whittaker et al., (1974) reported 280 g m^{-2} yr^{-1} NPP for the Hubbard Brook Forest in New 'Hampshire.

Newly planted one year old loblolly pine trees had a nearly six fold increase in both diameter (3.2 cm) and height (372.0 cm) over four years (Table 1). It is not known if these growth rates differed substantially from growth rates of loblolly seedlings in similar areas not impacted by hurricanes; however, Sluder (1996) reported a three year average height growth of newly germinated longleaf pine seedlings of 24.5 cm in Francis Marion National Forest. Tree growth rates estimated by dendrometers showed a mean circumference increase after four years of 6.6 (±4.6) cm (Table 1).

Analysis of tree cores from loblolly pine trees that survived the hurricane revealed an average radial increase of 0.211 cm yr^{-1} in post-Hugo growth rings compared to an average 0.178 cm yr^{-1} pre-Hugo (3-year) annual increase (Galloway 1996). The rates are somewhat less than increases (-0.350 cm yr^{-1}) found by Johnson and Young (1992) in loblolly pines along the Virginia coast following a hurricane impact there. The findings are correspondent with those of Whigham et al. (1991) who found that diameter growth of nearly all species of trees in a Yucatan, Mexico, forest was greater in the first year after Hurricane Gilbert than the average of the five years before the storm.

Litter production following the storm was 664.3 (±562.1) g m^{-2} yr^{-1} (Table 1). a figure similar to data from Gresham (1982) who reported 400 gm m-2 yr^{-1} of leaf litter production within South Carolina pine stands Whigham et al. (1991) have suggested that forest recovery following hurricanes is assisted by the large amounts of nutrients transferred to the soil in new litter. This leads to high post-storm biomass production rates followed by high post-storm litter production rates. They found a leaf litter mass of 836 g m^{-2} yr^{-1} following Hurricane Gilbert in Yucatan which was twice the pre-storm rate of litter production. Whigham et al. (1991) in Mexico and Gardner et al. (1992) in South Carolina found that soil water nutrient levels were higher for at least a year following hurricanes than before them. The latter study also reported that projected forest soil N inputs from hurricane generated litter decomposition would be 10.9 gm m^{-2} during the year following the hurricane. This would be four times "normal" annual inputs.

Annual mass loss rate of post-storm leaf litter was 45.6% (±20.0) of original mass. Wood loss rates were 25.6% (± 16.4) of original mass (Table 1). This translated into an overall average mass loss rate of 0.47 g m^{-2} yr^{-1}, comparable to the stem mass loss rate 0.44 g m^{-2} yr^{-1} for a forest in Puerto Rico (Odum, 1970). Decomposition rates have implications for the long-term production rate of forests because the gradual release of nutrients through this process sets the limits of forest NPP.

Two major factors related to decomposition rates and soil fertility, are soil moisture and soil organic matter. Both Salvaged and Unsalvaged Site soils held about 20% moisture. Soil organic matter measured by loss on ignition was 50% higher in the Unsalvaged Site (Table 1). Because soil organic matter is related to nutrient retention (Brady, 1974) and therefore long term sustainability of ecosystems (Nakane and Yamamoto, 1983), the effect of higher soil organic matter may be that. it leads to higher production rates within Unsalvaged Sites over long periods.

Ash is an indicator of nutrient contents of organic materials since it is the solid materials left after C, H, 0 have been removed by combustion. Wood ash of volunteer pine seedlings from Salvaged and Unsalvaged Sites were 0.86% (±0.31) and 1.07% (±0.79), respectively (Table 1). The difference may be attributable to differences in soil nutrient supplies, which in turn are related to soil organic content, which in turn is related to decomposition rates. The data are comparable to ranges reported by Gosz et al. (1972, 1973) and Whittaker et al. (1974) who found 1.7%–2.3% wood ash from dead branch bark and wood from trees in the Hubbard Brook Forest in New Hampshire.

While soil organic matter and tissue ash concentrations were not statistically different between the two treatments, the divergences that they do exhibit may become more pronounced over successional time frames as decomposition of resistant materials proceeds. This in turn may have effects on forest successional production and nutrient cycling trends by increasing soil nutrient retention capacities.

New naturally established post-Hugo pine seedlings harvested from Salvaged and Unsalvaged Sites had root : shoot ratios of 1.08 and 0.63, respectively (Table 1). Monk (1966a,b) reported that root : shoot ratios of pine seedlings are higher in drier, more nutrient poor habitats than in wetter or more nutrient rich sites. He found root : shoot ratios ranging from 0.130 to 4.04 in a study of 15 coastal plain herbaceous and woody species, and in a study of just loblolly pines (1966a) root: shoot ratios ranged from 0.20 to 0.83. The higher ranges were associated with smaller trees. Ericson (1995), Gleason and Tilman (1990), and Monk (1966b) noted that plants growing in disturbed sites alter energy devoted to their various parts depending on the available nutrient and energy (light) supplies. Such an effect may be operating at the sites of this study as well.

CONCLUSIONS

Hurricane generated debris is hypothesized to lead to higher forest production rates over the long term. While the short term production and litter data of this study do not statistically support this hypothesis, there are indications that over successional time frames, decomposing hurricane generated debris may hasten forest recovery and may increase net primary production. Higher (but not statistically significantly different) soil organic matter, wood ash, litter production, decomposition rates, and the lower root : shoot ratio in the Unsalvaged Site indicate that the site may ultimately have a higher production rate over the long term of forest recovery. Also, the growth rates of the surviving pine trees have so far been greater (but not statistically different) after the storm than before it. This (potential long-term) effect may be a result of increased nutrient supplies from decomposing hurricane generated litter (Lodge and McDowell, 1991; Gresham et al., 1991; Whigham et al., 1991), release from competition because of tree mortality, and higher-light levels following Canopy destruction.

Gresham et al. (1991), based on their observations and others' (Putz and Sharitz, 1991), have speculated that, ". . . it is possible that hurricanes have exerted selection pressure on traits of some tree species that are common in forests frequently damaged by hurricanes." Johnson and Young (1992) suggested, based on differential survival of individuals of loblolly pines, a genetic basis of variation to storm stresses. Speculation about the -existence of 'wind genes' may be extended to ecosystem process levels as well (Lodge and McDowell, 1991). Forest processes of production, decomposition, and nutrient cycling may be subject to selection pressures through the promotion of species adaptations that mold these interconnected processes about high impact events such as hurricanes.

The sites of this study could be used for long term tracking of forest recovery following a hurricane impact since the plots are permanently marked with aluminum poles. Coastal forest recovery following storms Should be monitored over long periods-successional time frames - to fully track forest recovery and further test the hypothesis that U.S. southeastern forests are adapted to hurricane impacts. Leaving these forests undisturbed following massive storms could be the best way to attain robust long term forest recovery.

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