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ABSTRACT

Some evidence suggests that longleaf pine might be more tolerant of high winds than either slash pine (Pinus elliottii Englem.) or loblolly pine (Pinus taeda L.). We studied wind damage to these three pine species in a common garden experiment in southeast Mississippi following Hurricane Katrina, a very large, Category 3 hurricane that directly affected the stand in August 2005. The experiment, a factorial arrangement of silvicultural treatments established in 1960, included 120 plots of 100 trees each, covering about 22 ha. Following the hurricane, dbh was measured on all trees, and each tree was rated with respect to mortality from wind damage. Longleaf pine suffered less mortality (7%) than the other two species (slash pine, 14%; loblolly pine, 26%), although the differences in mortality were statistically significant only between longleaf pine and loblolly pine. Longleaf pine lost significantly fewer stems per hectare and less basal area than the two other species. Differences in mortality among species were not a function of mean plot tree height or plot density. Our analyses indicate that longleaf pine is more resistant to wind damage than loblolly pine.

Keywords: wind damage, hurricane, loblolly pine, longleaf pine, slash pine

Longleaf (Pinus taeda L.) and slash (Pinus elliottii Englem.) pines have largely replaced longleaf pine (Pinus palustris Mill.) as the dominant conifer in the Gulf Coast region (Frost 2006), with longleaf pine now occupying just 3% of the area it did prior to European settlement. Among the factors contributing to this drastic shift in species composition are (1) large-scale logging in the early 1900s, (2) a large increase in fire suppression, (3) inadequate number of seed trees to provide adequate natural regeneration, (4) poor survival of planted longleaf partly because of its multiyear grass stage and competition with other species, and (5) a sharp increase in natural and artificial regeneration of loblolly and slash pines (Frost 2006).

Hurricanes (i.e., tropical cyclones with sustained winds ≥119 km hour⁻¹) can cause massive economic damage to forests. In 2005, winds from Hurricane Katrina damaged 22 million m³ of timber with an estimated value of 1.4–2.4 billion dollars. Effects are not limited to loss of wood volume and quality; ecosystem services provided by these forests can also be impaired. Damage from Katrina (which made landfall on the Louisiana and Mississippi Gulf Coast on Aug. 29, 2005) and subsequent decomposition of dead biomass is reducing carbon sequestration capacity of Gulf Coast forests equal to the total U.S. net annual forest carbon sink (Chambers et al. 2007). Hurricane activity has increased since the mid-1990s, and this higher activity has been projected to last for the next 10–40 years (Goldenberg et al. 2001).

Four main factors are related to the extent and intensity of wind damage on forests: climate, soils, topography, and stand conditions (Wilson 2004). Hurricanes obviously represent an extreme climatic event. Trees growing under soil conditions that restrict root growth and depth are more prone to uprooting. Variation in windthrow along topographical gradients is more complicated and is often confused with species and soil variation. There are many stand attributes that help determine the susceptibility of stands to windthrow. These include height-to-diameter ratios, height, spacing, recent thinning and impacts of previous disturbance on creating exposed edges that contain trees more vulnerable to windthrow. Species composition may also affect the degree of damage from hurricanes and represents a stand attribute that can be manipulated by forest managers.

Longleaf pine has evolved morphological attributes to coexist with fire (Boyer 1990), but it is not clear whether frequent hurricanes and tropical storms have resulted in any selection for wind resistance. Here we examine whether longleaf, loblolly, and slash pines were differentially damaged by Hurricane Katrina, a very large, Category 3 hurricane (Saffir Simpson scale; see Moran and Morgan 1996). Our study used a common garden experiment located in southeast Mississippi that was within the highest wind-field zone on the northeast quadrant of the land falling storm. The common garden experiment minimizes the effects of differential effects of climate, soils, and topography, while allowing identification of variation due to stand attributes.

Methods

The experiment was established in 1960 (Schmidtling 1973) on a cut-over second-growth longleaf pine stand 32 km north of Gulfport, Mississippi (30.65N, 89.04W, elevation 50 m). The soils are well-drained upland, fine sandy loams in the Poarch series and the
Saucier-Susquehanna complex. Slope in this complex varies from 0 to 8%, but it was closer to 1–4% on the study site.

Five treatments were established: (1) no cultivation or fertilization; (2) cultivated with no fertilization; (3) cultivated with a single application of 112 kg ha$^{-1}$ of NPK fertilizer (type unknown); (4) cultivated with a single application of 224 kg ha$^{-1}$ of NPK fertilizer; and (5) cultivated with a single application of 448 kg ha$^{-1}$ of NPK fertilizer. Cultivated plots were cleared of all stumps and slash, plowed, and then disked prior to planting. They were then disked three times each season for 3 years to reduce woody competition and then mowed in years 4 and 5. Fertilizer was applied with an agriculture spreader and disked into the soil in May, 1 year after planting. In addition to the cultural treatments, the loblolly, longleaf, and slash pine seedlings for the experiment were grown in a nursery using seed from local source parents that were classified by their measured wood specific gravity. Two groups were used in study, those with high specific gravity (HSG) and low specific gravity (LSG) (Clark and Schmidtling 1988).

The experimental design was a randomized complete block with split plots, replicated four times, creating 120 subplots (three species × two specific gravity treatments × five silvicultural treatments × four blocks). Whole plots within replications represent the species treatment and they consisted of 10 (two specific gravity treatments × five silvicultural treatments) 100-tree plots. Subplots consisted of 100 1-year-old bare root seedlings that were bar-planted in 3.05 × 3.05 m spacing in February and March of 1961. No operational thinning has been carried out. Fire records are incomplete prior to 1994, but since January 1994 (age 33 years), the study site has been burned in the dormant season five times: 1994, 1998, 2001, 2002, and 2003. Growth through 25 years (fall 1984) has been reported by Smith and Schmidtling (1970), Schmidtling (1973), and Clark and Schmidtling (1988).

Height and dbh (DBH) were measured on all trees in the winter of 1999–2000 (40 years in the field). Mean stocking (stems per hectare), height (m), dbh (cm) and basal area (BA, in m$^2$ ha$^{-1}$), for loblolly, longleaf and slash pine respectively were: stocking (449, 552, 579); height (19.8, 21.0, 22.1); dbh (23.2, 24.6, 25.8); and BA (21.1, 26.7, 28.7).

Hurricane Katrina struck the experiment in Aug. 29, 2005 with sustained winds greater than 145 km hr$^{-1}$ (US Geologic Survey 2008) with peak gusts up to 225 km hr$^{-1}$ (Kupfer et al. 2007). In Dec. 2006, all trees in the experiment were measured for dbh and rated with respect to damage from the storm. Trees were rated in three categories: undamaged, downed, or boles snapped. Killed trees include those that were downed or with boles snapped. The dbh just prior to the storm for killed trees was estimated by adjusting individual tree dbh growth by the average annual growth between the 1999 and 2006 measurements.

Earlier research demonstrated that the initial phenotypic selections for wood specific gravity resulted in no difference between selection types in specific gravity or tree growth across species and treatments (Schmidtling 1973, Clark and Schmidtling 1988). Because there was no specific gravity treatment effect, the HSG and LSG treatments represent noncontiguous plots. For our experimental design, we combined the two noncontiguous 100-tree specific gravity treatment plots into single 200-tree plots resulting in one-half the original number of subplots (three species × five treatments × four blocks = 60 plots). In addition, initial analyses of pre-Katrina basal area provided a rationale to create three treatments from the five installed in the field. The fertilization treatments (treatments 3, 4, and 5) were not significantly different from each other and so were combined and named cultivated fertilizer applied (C-F), whereas the remaining treatments were left as they were and named no cultivation (NC, treatment 1) and cultivated no fertilizer applied (C-NF, treatment 2). This resulted in a further reduction in the number of subplots to 36 (three species × three treatments × four blocks).

Analysis of variance was used to test for statistical differences among treatments, species, and their interactions. Comparisons between means were made using Tukey’s multiple range test. Analysis of covariance was used to examine the impact of tree height, plot density, and the diameter/height ratio on species variation in tree mortality. Because tree heights were not measured prior to or following the hurricane, we used tree heights measured in 1999 (6 years before the storm). For these regression analyses, all 120 plots (100 trees each) were used with $\alpha = 0.05$.

**Results**

Treatment and treatment × species interaction effects in hurricane damage were rarely significant and, when so, were minor and/or difficult to interpret. In contrast, the amount of damage caused by the hurricane consistently differed significantly across species; thus, this article reports only species effects. Longleaf pine generally suffered less damage than the other two species, although it was only significantly different from loblolly pine (and not slash pine) in percentage of mortality (Figure 1). However, longleaf pine lost fewer stems in absolute numbers (data not shown) and BA (Figure 2) during Hurricane Katrina than the two other species. With longleaf pine, mortality was evenly distributed between downed trees and snapped boles. In both loblolly and slash pines mortality resulted predominantly (75% for both species) from snapped boles.

We also examined species variation in mortality using analyses of covariance, using mean plot tree height, plot density, and the height-to-diameter ratio as continuous variables in the model. When using tree height as a covariate, species and mean plot height were statistically significant sources of variation, whereas the species × height interaction term were not. Mortality generally increased with mean plot height, but at any given height, mortality...
was greatest in loblolly pine, followed by slash pine and lowest in longleaf pine (Figure 3).

In contrast, when using plot density as a covariate, species, plot density, and the species \times height interaction terms were statistically significant sources of variation. The variation in both the slopes and intercepts resulted in a set of curves that were difficult to interpret biologically. However, visual inspection of Figure 4, showing the relationship between plot density and mortality, clearly indicates differential damage among the species, particularly between longleaf and loblolly pine. Figure 4 displays the mean relationship and 95% confidence interval for longleaf pine indicating damage occurred across a wide range of plot density; 85% of the loblolly plots and 63% of the slash pine plots lie above the longleaf pine confidence interval. No relationship was observed between height-to-diameter ratio and mortality.

Discussion

Wind damage due to a catastrophic storm event such as a hurricane is primarily a function of its strength and proximity of a forest to the eye of the storm. In this case, Hurricane Katrina hit our study site directly with sustained winds of at least 145 km hour \(^{-1}\). Katrina caused massive damage to forests along the Louisiana and Mississippi gulf coasts (Chambers et al. 2007, Kupfer et al. 2007, Stanturf et al. 2007). McNulty (2002) estimated that a single hurricane can obviate the equivalent gain of 10% of the annual carbon sequestered in the United States. Owing to its size, intensity, and trajectory, Hurricane Katrina may have had 6–14 times that impact (Chambers et al. 2007). Using nearly 450 plots in southern Mississippi, Kupfer et al. (2007) developed predictive damage models to examine the importance of storm meteorology, stand conditions, and site characteristics to predict forest damage. Although their analyses provided insights into broad-scale patterns, our study provides a rare opportunity to examine the effects of wind damage on three important pine timber species in a large replicated study populated with mature trees.

Damage to longleaf pine from Hurricane Katrina was clearly the least severe, followed by slash and loblolly pines. As this study is replicated on one site, variation among neither soil conditions nor topography was responsible for differential species mortality. Other stand attributes do not appear to be responsible for the species differences. As per Foster and Boose (1992) and Stanturf et al. (2007), more damage occurred with taller trees; however, the species differences were apparent across all tree heights. The experiment area had not been recently thinned, but it did vary in stocking among plots. Unlike a recently thinned study, variation in stocking in this study had agraged over time; thus, even trees in sparsely stocked plots appeared windfirm. Again, species differences in mortality were clear even when taking stocking into account.

In contrast to other reports (Wilson 2004), height-to-diameter ratio was not related to mortality, although loblolly pine had a 5% lower ratio, owing to its shorter height, than the two other species. Thus, the major stand attribute that appeared related to variation in damage was species itself, with longleaf suffering significantly less than loblolly pine, consistent with Stanturf et al. (2007). Although
not statistically different from longleaf pine, slash pine had intermediate damage compared with the other two species. The physical mechanism(s) causing species differences in damage are unknown but may be related to stem strength and or canopy characteristics such as the display of foliage along branches. The latter may cause differences among the species in capturing wind energy.

In a study of the Hobcaw Forest in coastal South Carolina, after Hurricane Hugo, Gresham et al. (1991) reported that longleaf pine suffered less damage than loblolly pine. It was noted that species native to the coastal plain are possibly better adapted to the disturbance regimes found there; for example, longleaf pine, baldcypress (Taxodium distichum), and live oak (Quercus virginiana) suffered less damage than forest species with broad distribution ranges. Unlike Gresham et al. (1991), who sampled across a diverse forest landscape covering over 3,000 ha, our study took place in a replicated, common garden study covering 22 ha, where variation in topography and soils are minor and the trees are all the same age. Thus, this increases the confidence with respect to our conclusions on the relative wind resistance of longleaf pine compared with loblolly pine.

Analysis of ice storm damage on loblolly pine in North Carolina indicated that besides the immediate loss of biomass due to the storm, decreases in leaf area resulted in decreased productivity for years following the storm (McCarthy et al. 2006). Such effects also likely occurred because of the hurricane. Besides Katrina, the experiment reported here has been affected by five other major hurricanes since its establishment. Therefore, reductions in productivity due to major wind events likely contributed to the fact that although loblolly pine initially grew faster than longleaf pine in the early years (Schmidtling 1986), longleaf pine has outperformed loblolly pine over the long run.

One definition of resilience is “an ability to recover from or adjust easily to misfortune or change” (Merriam-Webster 2009). Stanturf et al. (2007) promote the conversion of loblolly pine plantations to longleaf pine stands to increase the resiliency of pine forests to hurricane damage. Our study supports this recommendation. Such restoration to longleaf pine via artificial regeneration may increase the timber value, carbon storage, and carbon sequestration relative to the other major pine species (loblolly and slash pines) along the Gulf Coast via decreasing direct impacts of hurricanes, as well as subsequent damage due to increased fire and insect infestations. Also, longleaf pine is less susceptible to major insect damage and diseases than the other two species, furthering their resilience (Boyer 1990). Thiscobenefit of greater resiliency provides further rationale to restore these ecosystems on sites currently occupied by loblolly and perhaps even slash pine, augmenting the role of restoration in improving other desirable characteristics of longleaf pine forests, such as increased productivity, timber value, and increased native biodiversity relative to slash and loblolly pine plantations (Frost 2006).

It is not possible to unequivocally state that longleaf pine has adapted to be more tolerant of wind damage than loblolly or slash pines. Wind damage increases with tree size, but the frequency and severity varies with species, site, wind parameters, and stand characteristics (i.e., canopy evenness and age distribution), perhaps making blanket statements regarding species fitness an oversimplification (Gresham et al. 1991, Peterson 2007). As per the risk map shown in Stanturf et al. (2007), the southern coastal plain of the United States (the center of the historical range of longleaf pine) is highly prone to hurricane events. Intense hurricanes occur in 2 out of every 3 years across the eastern United States (McNulty 2002). Similar to historical natural fire regimes, the selection pressure of frequent high velocity winds appears to have been high. We have shown that longleaf pine suffered less mortality due to damage from Hurricane Katrina than loblolly pine. This supports the supposition that longleaf pine has evolved to have higher resistance to wind damage than loblolly pine. Although trends also indicate the superiority of longleaf relative to slash pine, consistent statistical evidence was lacking.

**Literature Cited**


