Ice Damage in Loblolly Pine: Understanding the Factors That Influence Susceptibility

Doug P. Aubrey, Mark D. Coleman, and David R. Coyle

Abstract: Winter ice storms frequently occur in the southeastern United States and can severely damage softwood plantations. In January 2004, a severe storm deposited approximately 2 cm of ice on an intensively managed 4-year-old loblolly pine (Pinus taeda L.) plantation in South Carolina. Existing irrigation and fertilization treatments presented an opportunity to examine the effects of resource amendments on initial ice damage and subsequent recovery. Fertilized treatments showed more individual stem breakage, whereas nonfertilized treatments showed more stem bending; however, the proportion of undamaged trees did not differ between treatments. Irrigation did not influence the type of damage. Trees that experienced breakage during the storm were taller with larger diameter and taper and leaf, branch, and crown biomass compared with unbroken trees. One growing season after ice damage, relative height increases were significantly greater for trees experiencing stem breakage compared with unbroken trees; however, relative diameter increases were significantly lower for these trees. Relative diameter increases for broken trees were smaller for fertilized treatments compared with nonfertilized treatments. A reduction in wood strength was ruled out as the cause of greater breakage in fertilized trees; rather, fertilized trees had reached an intermediate diameter range known to be susceptible to breakage under ice loading. FOR. SCI. 53(5):580-589.

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CE ACCUMULATION during winter storm events can cause significant damage to trees in the southeastern United States. Permanent damage often occurs as excess weight from ice deposition causes stem bending and/or breakage, branch breakage, or uprooting (Cannell and Morgan 1989, Belanger et al. 1996, Smith 2000). The susceptibility of a tree to glaze damage depends on the amount of ice accumulation, residence time of ice, wind presence and speed, and tree size, as well as the tree's physical properties, such as wood strength, elasticity, growth form, and surface area (Croxton 1939, Carvell et al. 1957, Bruederle and Stearns 1985, Hauer et al. 1993, Warrillow and Mou 1999). For example, coniferous tree foliage is present during the winter months and catches and holds greater amounts of ice compared with leafless deciduous trees (Lemon 1961, Whitney and Johnson 1984, Boerner et al. 1988, Warrillow and Mou 1999).

Loblolly pine (Pinus taeda L.) is the most economically important tree species in the southeastern United States (Zeide and Sharer 2002), and an understanding of its sensitivity to ice damage is necessary to make sound timber management decisions (Amateis and Burkhart 1996, Zeide and Sharer 2002). Knowledge of initial damage and subsequent growth and recovery may allow for more productive utilization of these stands after severe ice storms. A better understanding of how common silvicultural treatments affect susceptibility to breakage will allow managers to minimize economic losses that result from ice storms. Loblolly pine is generally believed to be more tolerant of ice damage than some southern pines (i.e., longleaf pine [Pinus palustris Mill.], slash pine [Pinus elliottii Englem.], and sand pine [Pinus clausa (Chapm. ex Engelm.) Vasey ex Sarg.]) because of greater stem flexibility and shorter needles (McKellar 1942, Bennett 1959, Wahlenberg 1960, Brender and Romancier 1965, Hebb 1971, Williston 1974). This tolerance may also be due, in part, to the relatively sparse foliage of loblolly pine, resulting in less ice accumulation (Bennett 1959).

Despite its relative tolerance, loblolly pine remains susceptible to ice damage. Previous reports have documented the fact that loblolly pine is most susceptible to main stem breakage when the diameter range is 12-25 cm (Downs 1943, Wiley and Zeide 1991, Amateis and Burkhart 1996, Belanger et al. 1996, Bragg et al. 2002, 2003, 2004, Zeide and Sharer 2002). Trees with a diameter below this range generally experience stem bending, but most trees recover (Downs 1943, Shepard 1978, Bragg et al. 2002, 2004). Trees larger than this will primarily experience branch and terminal leader breakage, but main stem breakage and bending should be minimal (Downs 1943, Bragg et al. 2002, 2004).

The application of silvicultural techniques that increase growth rates (e.g., wide spacing, thinning, fertilization, and competition control) may reduce the threat of ice damage by

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allowing trees to grow through susceptible size ranges more quickly (Zeide and Sharer 2000, 2002, Bragg et al. 2004). These methods also result in increased stem taper, which may increase resistance of loblolly pine to damage (Zeide and Sharer 2000, 2002, Bragg et al. 2003). The literature has not, however, suggested fertilization as a method to alter tree susceptibility to ice damage. Loblolly pine responds positively to fertilization (Albaugh et al. 1998, Borders and Bailey 2001, Coleman et al. 2004, Jokela and Martin 2004). Therefore, fertilization should expedite tree growth and allow trees to grow out of susceptible size classes at a faster rate than would be achieved without nutrient amendments. Rapidly grown trees generally have greater stem taper than slowly grown trees (Larson et al. 2001), thus making them more resistant to damage. However, studies investigating the effect of fertilization on tree growth have shown that treatments may increase (Brockley and Simpson 2004) or decrease stem taper (Jokela et al. 1989, Zhang et al. 2002). In addition, fertilization may increase the susceptibility of trees to breakage during an ice storm by negatively affecting properties such as specific gravity that help determine wood strength.

On January 26-27, 2004, an ice storm deposited over 2 cm of ice across 15 South Carolina counties, affecting over 250,000 ha of forestland and causing over \$67 million in damage to pine timber (A.J. Boone, pers. comm., South Carolina Forestry Commission, Dec. 8, 2005). This event also provided an opportunity to investigate the damage incurred on a 4-year-old intensively managed loblolly pine plantation within the storm-affected area. Our objective was to measure initial damage and monitor the recovery of loblolly pine receiving irrigation and fertilization after the ice storm. We predicted that fertilized trees would be more susceptible to damage due to larger crown surface area available for ice deposition and lower wood quality. However, based on loblolly pine's positive response to nutrient additions, we also expected that trees receiving fertilization would recover more quickly than nonfertilized trees experiencing similar types of damage (i.e., stem breakage or bending).

Materials and Methods

The original fertilization experiment was established in 2000. A detailed account of the study site and experimental design is available (Coleman et al. 2004, Coyle and Coleman 2005); a brief description follows.

Study Site

The study was located on the US Department of Energy Savannah River Site, a National Environmental Research Park, near Aiken, SC, in the Carolina Sand Hill physiographic region (33°23'N, 81°40'E). The soil is predominately Blanton sand with loamy subsoil 120-200 cm deep across the site (Rogers 1990). We chose a site with deep sandy soil because it favored wet season access and drip irrigation methods. Also, low endemic soil moisture and nutrient levels provided low inherent soil resources with which to compare the effects of fertilization and irrigation amendments.

Plant Material

Four tree species were hand-planted in February of 2000. The hardwoods (Liquidambar styraciflua L., Platanus occidentalis L., and Populus deltoides Bartr.) suffered no apparent or lasting ice damage, whereas loblolly pine (Pinus taeda L.) did. Therefore, this report focuses only on loblolly pine. The pine genetic material used for planting was International Paper family 7-56.

Experimental Design

The experiment was a completely randomized block design consisting of four treatments: control (C), irrigation (I), fertilization (F), and irrigation plus fertilization (IF). Each treatment was replicated in three blocks. We planted seedlings at 2.5 × 3-m spacing in 0.22-ha treatment plots. Each treatment plot contained a central 0.04-ha measurement plot with 54 trees. Using drip irrigation, we applied up to 5 mm of water daily to irrigated treatment plots (I and IF) depending on evaporative demand. In 2003, the year before the ice storm, we applied 347 mm of additional water to irrigation plots. In 2004, we applied 346 mm of additional water. We applied liquid fertilizer (delivered in 5 mm of water via drip irrigation) to F and IF treatments at the rate of 120 kg N ha-1 year-1 split into 26 weekly applications from April to October. Control plots received 5 mm of water weekly to maintain experimental consistency. Thus, nonirrigated plots (i.e., C and F) received 130 mm of additional water annually.

Damage

Damage assessments were based on stem breakage and bending. As part of our original experiment, annual height and dbh (diameter outside bark at 1.37 m above ground, hereafter referred to as diameter) were recorded during the dormant season and had been measured before the storm. Stem taper was estimated from height and diameter (diameter/height). We used these measurements as a baseline for damage comparisons and also to investigate the relationship between tree size and damage. Note that early in our study, fertilization resulted in significantly taller trees with significantly larger diameters and overall biomass; however, irrigation did not always affect growth characteristics (Coleman et al. 2004).

Another part of our original experiment, annual destructive harvests, allowed us to examine the differences in crown surface area available for ice deposition. In December 2003, we harvested loblolly pine and collected branches and fascicles from five trees per treatment. Individual trees were selected to represent the size ranges found in each treatment. All branches were removed from each tree, and fascicles were removed from representative branches of the different crown sections (i.e., top, middle, and bottom). Branch fresh weights were measured in the field, representative subsections of branches were removed, and fresh weight and dry weight measurements were obtained to determine the water content of the branches. Similarly, fascicle fresh and dry weights were measured from each sample branch and scaled up in relation to branch biomass of each crown section. Nonlinear regression (PROC NLIN, version 8.1; SAS, Inc., Cary, NC) was performed to estimate leaf biomass and branch biomass as a function of diameter for each tree. The sum of leaf and branch biomass was used as a surrogate measure of available surface area for ice deposition, hereafter referred to as crown biomass. We also calculated the ratio of crown biomass to diameter (CB:D).

We surveyed trees 2 weeks after the ice storm (Feb. 5, 2004) to assess the type and magnitude of damage resulting from the disturbance. Each living tree in the measurement plot was examined to determine either the height of main stem breakage or the degree of stem bending. The height at which the stem broke was measured. We determined the degree of stem bending by aligning a pole between the base of the tree and the terminal leader. A protractor with a weighted pointer was used to measure the pole's angle from vertical. The margin of error for measuring stem bending was found to be 3°. Therefore, any stem with a measured angle <3° was considered undamaged. We did not quantify branch loss, but observations indicated that bent trees lost little crown area. Broken trees obviously lost substantial crown area above the breaking point.

Bending Moment Model

To investigate the susceptibility of stem breakage as a function of fertilization, we adapted a bending moment model (Peltola et al. 1999). The modulus of rupture (MOR), or the maximum bending load to failure, is a wood property that is strongly related to breakage resistance. In turn, MOR is highly dependent on wood specific gravity (Panshin and de Zeeuw 1970, Bragg et al. 2003). Studies show that fertilization results in slight to moderate (4-9%) reductions in wood specific gravity (Posey 1964, Megraw 1986, Blanche et al. 1992, Jokela and Stearns-Smith 1993, Clark and Edwards 1999, Albaugh et al. 2004, Borders et al. 2004). Specific gravity also varies considerably among sites, possibly due to differences in site quality, genotype, or tree ontogeny (Jokela et al. 2004), and differs with respect to the sampling location on the tree. For example, the specific gravity of wood within the crown of loblolly pine was found to be 25% less than that measured at the base of the tree (Lenhart et al. 1977).

MOR can be estimated as

$$MOR = aG^{1.25}$$
, (1)

where the coefficient a equals 121 when the wood is green and G is the wood specific gravity, and the exponent remains constant (Panshin and de Zeeuw 1970). We used previously reported wood specific gravity values for 4-yearold loblolly pine (G = 0.40; Bentdsen and Senft 1986) to calculate MOR for nonfertilized trees. For fertilized trees, we used the maximum reported reduction of 9% (i.e., G =0.36) and an exaggerated reduction of 25% for wood specific gravity (i.e., G = 0.30), which exceeded the previously reported 0-9% decrease in wood specific gravity due to fertilization (Clark and Edwards 1999, Albaugh et al. 2004, Borders et al. 2004).

After solving the equation for MOR, we estimated the maximum bending moment (R_C) as

$$R_{\rm C} = \frac{\pi \times \text{MOR} \times D^3}{32},\tag{2}$$

where D is the diameter (m) of the stem, and the divisor remains constant (Petty and Worrell 1981, Cannell and Morgan 1989, Peltola et al. 1999). This equation illustrates that R_C is proportionally related to MOR and exponentially related to stem diameter (Peltola et al. 1999). R_C is a measure of tree resistance to force. When a force on the tree exceeds its R_C, breakage occurs (Petty and Worrell 1981, Peltola et al. 1999). Using these equations, we were able to further evaluate differences in MOR and determine how these differences affect R_C and, thus, resistance to breakage.

Recovery

Tree recovery was monitored by measuring stem straightening and the characteristics of poststorm crown structure. The angle of stem bending was re-measured 11 (Apr. 8, 2004) and 28 weeks (Sept. 8, 2004) after the storm to track bent stem recovery. We measured the degree of lower stem deviation, hereafter referred to as the angle of inflection, 28 weeks after the storm. To measure the angle of inflection, a pole was aligned tangent to the curve formed by the terminal righting toward vertical. To quantify stem form 28 weeks after the storm, we recorded stem straightness and the number of leaders present on each tree. We used three discrete levels of form: a value of 1 was used to represent good form (straight tree and single terminal); a value of 2 was used to represent intermediate form (obvious horizontal to vertical bend and/or one or two branches assuming leader); and a value of 3 was used to indicate poor form (stem not straight, often times sigmoidal in shape and/or multiple leaders in a cyme or umbel form). A broken tree could still be assigned a form of 1 if it appeared that a single lateral branch had assumed the terminal position without noticeable affect on stem straightness.

Poststorm Growth

Poststorm tree growth was evaluated through changes in diameter and height. Height and diameter were recorded 1 year after the ice storm. We used these measurements, in conjunction with prestorm height and diameter, to determine the absolute change of these characteristics (i.e., poststorm variable minus prestorm variable) and the relative change of these characteristics (i.e., log of poststorm variable minus log of prestorm variable).

Statistical Analyses

The proportion of bent, broken, and undamaged stems per plot, degree of stem bending, angle of inflection, and relative breaking point were each analyzed using plot means in a univariate 2 × 2 factorial analysis of variance for a randomized complete block design with fertilization and irrigation treated as fixed effects and block (n = 3) treated as a random effect. We performed a repeated measures analysis on the degree of stem bending as it was measured at three different time intervals after the storm. We analyzed the data set using four common covariance structures (unstructured, first-order autoregressive, toeplitz, and ante-dependence) and used Akaike's Information Criterion (Burnham and Anderson 1998) to determine which structure best fit the model. The Akaike's Information Criterion suggested that the ante-dependence structure be used.

Pre- and poststorm height and diameter, prestorm taper, leaf biomass, branch biomass, crown biomass, CB:D, R_C , relative and absolute growth rates, and poststorm number of leaders and growth form were each analyzed using a splitplot design for a randomized complete block. Fertilization and irrigation were treated as fixed whole-plot effects and breakage (broken versus intact) was treated as the subplot effect. We performed these analyses using individual tree measurements rather than plot means. All analyses were performed using the mixed model procedure of SAS (PROC MIXED) with an α level of 0.05. Proportional data were arcsine transformed to achieve normality (Zar 1996). When interactions occurred, we performed tests of simple main effects using the SLICE option in the LSMEANS statement of PROC MIXED (Littell et al. 2006, Schabenberger et al. 2000). Treatment means were compared using Fisher's least significance difference test (LSD) with an α level of 0.05.

Results

Prestorm Tree Size

Before the storm, fertilization had significantly influenced tree size and crown structure, but irrigation had no effect. One month before the storm, fertilized trees were 17% taller with 22% larger diameter and 7% larger taper than nonfertilized trees (Table 1). Fertilized trees had 32% larger branch biomass than nonfertilized trees (Table 2). Although fertilized trees had 11% larger leaf mass, 22% larger crown biomass (Table 2), and 5% larger CB:D than nonfertilized trees, there was no detectable statistical effect of fertilization on these variables. Irrigation did not affect any of these variables (P > 0.05), and there were no fertilization-by-irrigation interactions.

Initial Damage

At the first measurement (2 weeks poststorm), ice had melted from trees, and some bent stems had partially or fully recovered. Averaged over all treatments, 15% of all trees experienced stem breakage, 71% experienced stem

Table 2. Prestorm leaf, branch, and crown biomass (mean ± SE) for nonfertilized (n = 306) and fertilized trees (n = 318) and for intact (n = 527) and broken trees (n = 97)

	Biomass (Mg ha ⁻¹)		
	Leaf	Branch	Crown
Nonfertilized	5.92 ± 0.16	4.87 ± 0.20	10.79 ± 0.35
Fertilized	6.68 ± 0.12	6.68 ± 0.12	13.85 ± 0.32
P	0.4593	0.0470	0.1288
Intact	6.06 ± 0.11	5.64 ± 0.15	11.70 ± 0.26
Broken	7.65 ± 0.22	8.22 ± 0.38	15.86 ± 0.58
P	< 0.0001	< 0.0001	< 0.0001

bending, and 14% had no measurable damage. Prestorm size influenced the type of damage inflicted by the ice storm. Trees that experienced breakages during the storm were 12% taller with 17% larger diameter, 7% larger stem taper, 21% larger leaf biomass, 31% larger branch biomass, and 26% larger crown biomass than those that did not break (Tables 1 and 2). Within I and F treatments, CB:D was higher for broken trees than for intact trees, but there was no difference between broken and intact trees within the C or IF treatments (i.e., fertilization-by-irrigation-by-breakage interaction, P = 0.0272, Fig. 1).

The proportion of damaged relative to undamaged trees was not affected by fertilization or irrigation (P > 0.10), but there was a fertilization effect on the proportion of broken trees relative to bent trees. The proportion of trees experiencing stem breakage was higher among fertilized (23.2 ± 4.3%) than among nonfertilized trees (7.6 \pm 3.0%, P = 0.0045), but the proportion of trees experiencing stem bending was higher among nonfertilized (78.7 ± 5.2%) than among fertilized trees (62.1 \pm 3.5%, P = 0.0132). Irrigation did not affect the type of damage (P > 0.05). The relative height of breakage was similar between fertilized and nonfertilized trees, with mean breakage occurring at the very center of tree height (P = 0.6322). One broken tree died because breakage occurred beneath the crown, and there were no shoot meristems to resume growth. All other trees lived through the 2004 growing season. The degree of initial stem bending (21° averaged over all treatments) was not affected by fertilization or irrigation (P > 0.05).

Bending Moment Model

Based on our assumptions of how fertilizer affects wood specific gravity, we found that prestorm R_C was larger among fertilized trees than among nonfertilized trees and larger among broken trees than among intact trees. Fertilized trees with a 9% reduction in G had 40% larger Rc than

Table 1. Prestorm height, diameter, and taper (mean ± SE) for nonfertilized (n = 306) and fertilized trees (n = 318) and for intact (n = 527) and broken trees (n = 97)

	Height (m)	Diameter (cm)	Taper (cm m ⁻¹) ⁸
Nonfertilized	5.28 ± 0.06	7.61 ± 0.13	1.42 ± 0.01
Fertilized	6.33 ± 0.05	9.76 ± 0.11	1.53 ± 0.01
P	0.0085	0.0029	0.0009
Intact	5.70 ± 0.05	8.44 ± 0.10	1.46 ± 0.01
Broken	6.45 ± 0.08	10.19 ± 0.18	1.57 ± 0.02
P	0.0008	< 0.0001	0.0002

^{*} Taper was estimated from height and diameter measurements (diameter/height).

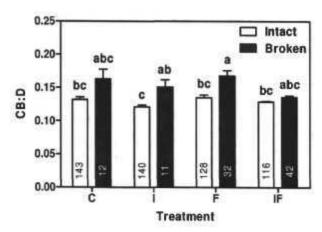


Figure 1. Relationship between treatments and breakage for prestorm ratio (mean \pm SE) of crown biomass to diameter (CB:D). Sample sizes are embedded in columns. Means sharing a letter are not significantly different (Fisher's LSD, $\alpha=0.05$).

nonfertilized trees (P < 0.0001). Broken trees had 35% larger $R_{\rm C}$ than intact trees (P = 0.0062). At a 25% reduction in G, there was no detectable statistical difference between $R_{\rm C}$ of fertilized trees and nonfertilized trees even though $R_{\rm C}$ of fertilized trees was 24% larger (P = 0.1784). However, broken trees had 31% larger $R_{\rm C}$ than intact trees (P < 0.0001).

Recovery of Broken Stems

Recovery from stem breakage involved lateral branches assuming the terminal leader position. After 28 weeks, broken trees had more leaders than intact trees, but the numbers of leaders were always larger in broken trees than in intact trees except in I treatments (i.e., fertilization-by-irrigation-by-breakage interaction, P=0.0352) (Fig. 2). Fertilization and irrigation effects on the number of leaders were evident among broken trees but not among intact trees. There were fewer leaders in irrigated trees except when fertilizer was applied, in which case there were more.

Within all treatments, broken trees had poorer form than

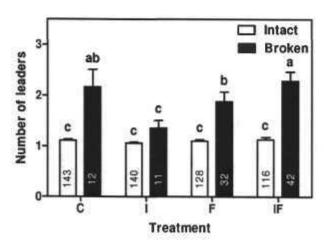


Figure 2. Relationship between treatments and breakage for poststorm number of leaders (mean \pm SE). Sample sizes are imbedded in columns. Means sharing a letter are not significantly different (Fisher's LSD, $\alpha = 0.05$).

intact trees after 28 weeks (Fig. 3). Fertilization and irrigation effects on form were evident among broken trees but not among intact trees (i.e., fertilization-by-irrigation-by-breakage interaction, P < 0.0001) (Fig. 3). Irrigation alone resulted in better form than any other treatment; however, irrigation combined with fertilization resulted in poor form.

Recovery of Bent Stems

Assessment of the recovery from stem bending was measured by the degree of straightening (return of bent terminal to vertical), including the departure of the lower stem. Bent stems straightened significantly throughout the growing season (P < 0.0001). Within 11 weeks, 15.3 \pm 3.7% of previously bent trees had returned to vertical, and within 28 weeks, 83.3 \pm 6.3% had returned to vertical. Neither fertilization nor irrigation affected bent stem recovery rates (P > 0.05) after the ice storm.

Poststorm Growth

Poststorm growth was influenced mainly by the type of damage incurred. Broken trees experienced significantly smaller relative diameter increases (0.16 ± 0.07 cm cm⁻¹) than intact trees (0.29 \pm 0.02 cm cm⁻¹, P < 0.0001), but these differences did not translate into differences in absolute diameter increases (P = 0.43). Trees responded to breakage with relative height increases (0.64 ± 0.07 m m⁻¹) more than three times that of intact trees (0.19 ± 0.03 m m^{-1} , P < 0.0001) and absolute height increases $(2.45 \pm 0.13 \text{ m})$ more than twice that of intact trees $(1.17 \pm$ 0.09 m). The effects of fertilization and irrigation on relative height growth were minimal and evident among broken trees but not among intact trees (i.e., fertilization-by-irrigation-by breakage interaction, P < 0.024) (Fig. 4). Although the same interaction was detected in absolute height growth, it was subtle and had little biological meaning. Tests of simple main effects could not identify relevant differences

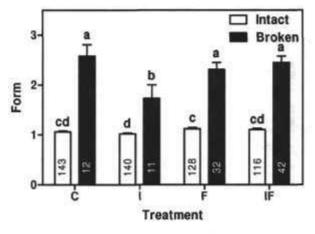


Figure 3. Relationship between treatments and breakage for poststorm growth form (mean \pm SE). A value of 1 indicates the best form whereas a value of 3 indicates poor form. Sample sizes are embedded in columns. Means sharing a letter are not significantly different (Fisher's LSD, $\alpha = 0.05$).

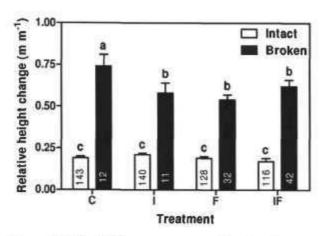


Figure 4. Relationship between treatments and breakage for poststorm relative growth rate (mean ± SE). Sample sizes are embedded in columns. Means sharing a letter are not significantly different (Fisher's LSD, $\alpha = 0.05$).

and thus support the main effect of breakage (P < 0.0001) (Fig. 5).

Discussion

Damage

Fertilized and nonfertilized trees experienced similar proportions of overall damage, but the type of damage was different. Fertilized trees experienced more main stem breakage, whereas nonfertilized trees experienced more stem bending. Irrigation did not affect the type of damage because it did not affect prestorm growth, with a few exceptions. The most severe type of damage witnessed in our study was main stem breakage. Trees broken in our study had a mean diameter (9.8 ± 0.3 cm) below the previously reported range of susceptibility to breakage. This observation may be due to the fact that other researchers looked at a wider range of size classes in their studies, rather than confining their observations to stands of similar age. Trees that experienced breakage in our study would most likely have been classified as bent had they not broken.

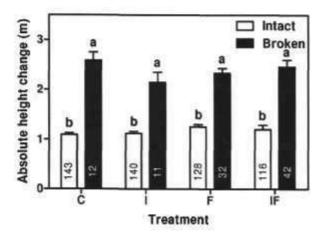


Figure 5. Relationship between treatments and breakage for poststorm absolute growth rate (mean ± SE). Sample sizes are embedded in columns. Means sharing a letter are not significantly different (Fisher's LSD, $\alpha = 0.05$).

The results of our modeling exercise suggest that R_C is 24% higher in fertilized trees than in nonfertilized trees even under an exaggerated reduction of wood specific gravity. Furthermore, broken trees had 31% higher Rc than intact trees, suggesting that factors other than wood strength have greater influence on susceptibility to breakage. Ice accumulation represents the major component of the bending force acting on the tree and is a function of available surface area (primarily branch and foliar); therefore, trees with greater amounts of crown surface area will experience greater ice loading (Lemon 1961, Warrillow and Mou 1999). Ice accumulation on needles and branches may cause up to a 30-fold increase in crown weight (Baxter 1952). Therefore, the force imposed through the accumulation of ice must be at least 24% greater to cause breakage in a mean diameter fertilized tree than a mean diameter nonfertilized tree simply because of the resistance gained by increased

The fact that trees receiving fertilization had larger diameters and branch biomass before the storm than nonfertilized trees helps explain the difference in the frequency of stem breakage between treatments. Specifically, a greater proportion of fertilized trees experienced breakage because the proportion of larger, less pliable trees with greater crown surface area was higher in these treatments (i.e., more trees were in the susceptible size range). Although we were not able to detect a fertilization effect on leaf biomass, crown biomass, or CB:D ratio, our data suggest that the pattern exists. The lack of effect is most likely attributed to the power of the experimental design required to test the effect of breakage (i.e., split-plot designs test the subplot effects with higher power than the whole-plot effects). Other analyses of these data (i.e., a 2 × 2 factorial with fertilization and irrigation) indicate significant divergence of biomass components as a function of fertilization (M.D. Coleman, US Forest Service unpublished data, 2007). Furthermore, numerous studies involving weed control, fertilization, and a combination of the two also suggest larger aboveground allocation toward leaf and branch biomass relative to stem biomass at this stage of loblolly pine development (Albaugh et al. 2004, Borders et al. 2004, Martin and Jokela 2004, Samuelson et al. 2004, Sayer et al. 2004). A similar study investigating ice storm damage in a sweetgum (Liquidambar styraciflua L.) plantation showed that fertilization did not directly influence breakage, but bole thickness and crown diameter were positively correlated to the likelihood of breakage (Guo 1999). Irrespective of fertilization, broken trees were clearly taller, with larger diameters and larger leaf, branch, and crown biomass than nonbroken trees. Consequently, this observation supports our prediction that larger crown surface area increases susceptibility to breakage. Furthermore, stem taper was larger for broken trees than for intact trees, suggesting that this characteristic alone does not infer increased resistance to breakage. Susceptibility to breakage is related to developmentally specific relationships between crown surface area and stem diameter.

We propose that the relationship between diameter and crown surface area is the prevailing factor determining loblolly pine's susceptibility to breakage (Fig. 6). Although

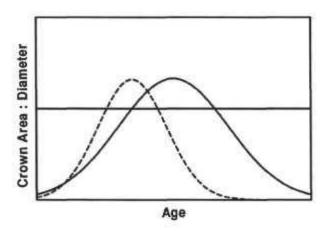


Figure 6. Conceptual model illustrating how the relationship between crown area and diameter influences susceptibility to breakage. Trends through time have been plotted for nonfertilized (——) and fertilized trees (——). The solid horizontal line indicates the threshold, above which breakage occurs, for the crown area to diameter ratio.

the main effect of breakage was confounded by the interaction with fertilization and irrigation, there was an apparent trend of higher CB:D among broken trees than among intact trees. Some have suggested that larger trees experience more stem breakage than do smaller trees (e.g., Hebb 1973), but it has also been argued and our modeling results support the fact that larger stem size offers greater resistance to breakage (Amateis and Burkhart 1996). However, as diameter increases through the early stages of development, so does the crown surface area available for ice deposition and, thus, increased force acting against a stem. Our results agree with previous studies that have suggested a modal response, with loblolly pine being most susceptible to main stem breakage at intermediate diameters (Downs 1943, Wiley and Zeide 1991, Amateis and Burkhart 1996, Belanger et al. 1996, Bragg et al. 2002, 2004, Zeide and Sharer 2002).

This pattern follows a continuum where at a smaller diameter trees relieve the stress of ice loads by bending rather than breaking (Downs 1943, Shepard 1978, Bragg et al. 2002). In the center of the continuum is the vulnerable stage where more ice accumulates than the stem can support and failure occurs (Downs 1943, Wiley and Zeide 1991, Amateis and Burkhart 1996, Belanger et al. 1996, Bragg et al. 2002, 2004, Zeide and Sharer 2002). At the other end of the continuum, large, structurally sound trees are capable of supporting the excess weight, and although some branches may be shed, little stem breakage occurs (Downs 1943, Bragg et al. 2002). Physiologically and developmentally (and assuming the tree is not weakened by insect damage, decay, or wet soils or further stressed by wind), this pattern occurs because branch and leaf biomass increases with diameter until canopy closure occurs. After canopy closure, allocation toward branch and leaf biomass declines as allocation toward stem biomass and diameter continues to increase (Dougherty et al. 1995, Jokela and Martin 2000, Albaugh et al. 2004, Borders et al. 2004, Martin and Jokela 2004, Samuelson et al. 2004, Sayer et al. 2004) (Fig. 6). Once the tree is past the susceptible diameter range, the crown surface area available for ice accumulation decreases as the capacity of the bole to resist breakage increases.

Changes in wood specific gravity due to treatments that accelerate growth, such as fertilization, need to be quite large to affect the relationship between diameter, crown surface area, and susceptibility to breakage. To illustrate this point, we calculated that a 0.4 cm increase in diameter is necessary to overcome a 9% decrease in wood specific gravity. The mean absolute diameter increase for fertilized trees in this plantation between 2002 and 2003 (prestorm) was 3.5 ± 0.4 cm. Thus, any resistance to breakage that may be lost due to lower wood specific gravity is outweighed in annual diameter growth. Consequently, we reject our prediction that a reduction in wood strength resulting from fertilization leads to a higher probability of breakage. We suggest that the relationship between diameter and crown surface area is the major factor determining loblolly pine's ability to withstand the accumulation of ice, but major decreases in wood properties would increase the susceptibility to breakage. Reported reductions in wood specific gravity due to fertilization (Clark and Edwards 1999, Albaugh et al. 2004, Borders et al. 2004) do not appear sufficient enough to drastically reduce wood strength with regard to ice susceptibility. Also, fertilization expedites tree growth and stand development so that fertilized trees will reach the susceptible size range earlier and progress through the range at a faster rate than nonfertilized cohorts (Miller 1981) (Fig. 6).

Recovery of Broken Stems

Recovery 1 year after the ice storm was more closely related to damage type than to resource amendments. Compared with intact trees, diameter growth was suppressed for broken trees. This might be expected as broken trees had lost some of their crown and, thus, their photosynthetic capacity. Although we did not measure branch loss after the storm, broken trees lost all branches above their breaking point. Major losses in leaf surface area result in reduced diameter growth until the leaf surface is replaced (Kuprionis 1970, Smith and Shortle 2003). For example, Wiley and Zeide (1991) reported a reduction in loblolly pine diameter growth for 8 years after ice storm damage; the following 6 years showed similar or increased diameter growth of broken trees relative to unbroken trees. Other studies have shown the same pattern of suppressed diameter growth for broken loblolly pine (Belanger et al. 1996) and sweetgum (Guo and VanderSchaaf 2002). This pattern may be further explained by the allocation of carbohydrates to dormant buds, branch formation, and stem elongation (Waring and Pitman 1985, Belanger et al. 1996, Smith 2000).

Broken trees experienced greater height growth during the season following the storm compared with intact trees. Other studies have also demonstrated significantly higher annual height growth for loblolly pine and sweetgum immediately after stem breakage (Wiley and Zeide 1991, Belanger et al. 1996, Guo and VanderSchaaf 2002). The measured growth may be somewhat exaggerated and does not represent true height growth because much of this increase can be attributed to lateral branches stretching vertically. After stem breakage, one or more of the uppermost lateral branches assumed the role of terminal leader and moved

from horizontal to vertical. Loblolly pine vigorously exploits newly available space (Burton 1981, Belanger et al. 1996). If there was only one lateral branch competing for the terminal position, the overall growth form was restored.

In many cases, we witnessed multiple lateral branches competing for the terminal position, which generally resulted in poor growth form. Ultimately, we expect one of these laterals to replace the broken terminal or two of these laterals will remain dominant and the tree will be forked. Managers wishing to improve overall stand form after ice damage could prune multileader trees to a single leader. We assumed that stem form would be more likely to recover if breakage is higher on the stem where branch plasticity is greatest. Our observations indicate that the potential for form recovery is best when breakage occurs in the upper one-third of tree height; however, breakage in this region does not necessarily infer that the best form will be recovered.

Intact trees responded similarly after the storm regardless of irrigation or fertilization, whereas both fertilization and irrigation affected recovery, to some extent, in broken trees. Although resource amendments affected some components of recovery, our data suggest that damage type is much more important in the process of recovery immediately following ice damage. Fertilization did not increase the rate of recovery as we predicted. However, as recovery continues and photosynthetic tissue is replaced in the crown, we expect that resource amendments will continue to expedite growth as observed in prestorm responses.

Recovery of Bent Stems

Numerous studies have documented the ability of loblolly pine to straighten bent stems after ice damage (Downs 1943, Muntz 1947, Brender and Romancier 1960, Cayford and Haig 1961, Kuprionis 1970), and our data concur with these studies. Neither fertilization nor irrigation appeared to influence stem straightening in any way. Stems began to straighten to prestorm levels immediately after the ice melted. Straightening gradually continued over the course of the growing season, and the majority of bent stems had straightened within 28 weeks after the ice storm. Although the majority of stems straightened, they were still somewhat offset. As the terminal leader straightened and the upper stem bent upward, the lower stem shifted underneath the bend. Thus, many recovered bent stems were not completely straight and often times were sigmoidal in shape.

Synthesis

Intensively managed loblolly pine plantations are becoming increasingly common in the southeastern United States (Borders et al. 2004). Because these plantations require considerable resource investments, minimizing losses to ice storms should be a key objective. It has been suggested that one way to reduce losses in pine stands is to help trees grow through the vulnerable stage as fast as possible using silvicultural techniques such as wide spacing, thinning, and competition control, which increase stem taper (Zeide and Sharer 2000, 2002, Bragg et al. 2003). Fertilization has been shown to increase stem taper (Larson et al. 2001) but has not been recommended as a tool for expediting loblolly pine growth, presumably because fertilization has been linked to a reduction in wood strength (Posey 1964, Albaugh et al. 2004).

Our results show that fertilized trees experienced more serious damage than nonfertilized trees because the storm event occurred while fertilized trees were within a susceptible diameter range. However, the results of our modeling exercise suggest that the increased diameter resulting from fertilization infers greater resistance than would be expected for a nonfertilized cohort; even if specific gravity is reduced substantially through fertilization. However, with greater stem resistance comes greater crown surface area on which ice can accumulate, hence causing a greater force acting on the stem. Therefore, the relationship between diameter and crown surface area appears more intrinsically related to loblolly pine's susceptibility to ice damage than does wood strength. The extent to which fertilization may increase the risk of loblolly pine to ice damage depends on when the storm event occurs in relation to the developmental stage of the stand. If trees are being grown on short rotations for pulp or fiber, fertilization may not pose a great risk as trees appear to have recovered rapidly with little mortality attributed to the disturbance. However, if trees are being grown for wood products, deformation from breakage and bending may considerably reduce quality harvest yield. Fertilization can expedite tree growth and stand development so that fertilized trees enter the susceptible size range earlier than nonfertilized cohorts; however, fertilized trees will spend less time in the susceptible range relative to nonfertilized cohorts.

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