

COMPARISON OF HURRICANE DAMAGE TO SEVERAL SPECIES OF URBAN TREES IN SAN JUAN, PUERTO RICO

by John K. Francis

Abstract. Percent defoliation and percent crown loss were estimated, and a count of stem failure was taken for 24 species of urban trees in San Juan following Hurricane Georges. Differences among species were significant, and detailed comparisons are presented. Wood-specific gravity, branch resistance to flexing, and leaf retention strength were measured for the study species. Many significant correlations were noted between pre-storm height, diameter, wood-specific gravity, branch resistance to flexing, leaf retention strength, defoliation, percent crown loss, and stem failure. A regression equation predicting defoliation is presented. Tree height was the most influential variable followed by branch resistance to flexing, leaf retention strength, and wood-specific gravity. If tree height was eliminated from the model, specific gravity then entered the stepwise regression first.

Key Words. Defoliation; crown loss; hurricanes; Puerto Rico.

For the second time in a decade, most of the trees in metropolitan San Juan, Puerto Rico, USA, were damaged by a major hurricane. On September 19, 1989, Hurricane Hugo passed northeast of San Juan with maximum gusts of 148 kph (92 mph) (Francis and Gillespie 1993). After 9 years, the trees surviving Hurricane Hugo had recovered so completely that the damage was not noticeable. On September 21, 1998, Hurricane Georges traversed the full length of Puerto Rico. The northern eye wall reached approximately 15 km (9 mi) south of the southern edge of San Juan (U.S. Geological Survey 1999) with sustained winds of 177 kph (110 mph) and maximum gusts to 208 kph (129 mph) (Bennett and Mojica 1999). Maximum gust speeds at the Muñoz Marín International Airport (at the north edge of the metropolitan area) reached 148 kph (92 mph) (Bennett and Mojica 1999), exactly the same as with the previous hurricane. The southern edge of San Juan probably experienced maximum gusts of around 160 kph (99 mph). Once again, the damage (defoliation, twig and limb breakage, trunk snap, and tipping) to trees was very great.

It is obvious to even the casual observer that some tree species suffer less in hurricanes than others. There have been published comparisons of damage (Wadsworth and Englerth 1959; Lugo et al. 1983; Walker 1991; Zimmerman et al. 1994; Duryea et al. 1996; Asner and Goldstein 1997; Weaver 1999) and much informal observation of various species' susceptibility to storm damage. Sometimes the perception and folk wisdom about susceptibility of tree species is inconsistent. Moreover, the quantitative data on wind damage to trees in Puerto Rico have been collected in the form of percentages of populations suffering broad classes of damage. If quantification of damage to individual trees is possible, more precise data can be collected, which would enable additional statistical tests and construction of better models.

Hurricanes are exceedingly complicated processes. Equally complex are the trees they affect. The mean damage to certain tree species may differ from the damage to others by an order of magnitude or more in a given storm. These variations in resistance may arise from differences in 1) height relative to surrounding trees, hills, and structures; 2) crown form and structure; 3) root morphology; 4) soil characteristics; 5) wood strength; 6) flexibility of stem and branches; and 7) strength of leaf retention (including resistance to shredding) (Putz et al. 1983; Francis and Gillespie 1993; Hedden et al. 1995; Asner and Goldstein 1997).

It is recognized that the aforementioned characteristics are not all independent of each other, are not equally important, and have been studied to different degrees. Measurements of tree size (height, dbh, and crown class) have been repeatedly shown to correlate with degree of damage to trees (Putz et al. 1983; Gresham et al. 1991; Reilly 1991; Walker 1991; Francis and Gillespie 1993; Duryea et al. 1996; Parresol and Alemañy 1998). Asner and Goldstein (1997), however, could not show a significant correlation between stem diameter and stem

failure (snapped plus tipped) of Hawaiian trees. King (1986) concludes that the greater vulnerability of larger trees to damage is due to loss of flexibility caused by increased girth and to increased wind speeds at greater heights. Quantifying the forces causing damage is complicated and has not been attempted in Puerto Rico. Studying damage or potential damage as a function of root morphology has been conducted in temperate and tropical trees (Putz et al. 1983, Schaetzl et al. 1989). The influence of soil characteristics is related to and influences root morphology. The influence of the wind forces and the sources of wind resistance in trees, however, are only conceptually understood. In this study, the relative importance of 4 structural factors affecting wind resistance, tree height, wood strength, flexibility of branches, and leaf retention strength, is addressed.

The strength of wood in roots, stems, and branches directly determines how much drag force a tree can withstand before the trunk or limbs snap or the tree tips. Modulus of rupture (the stress needed to rupture standard wood samples) is a logical predictor of a tree bole's ability to withstand lateral stress. However, because wood-specific gravity is easily measured and is highly correlated with breaking strength of wood as well as its ability to withstand torsion forces (USDA 1974), it was used in this experiment. Putz et al. (1983) found wood-specific gravity to be the most efficient indicator of resistance to snapping and uprooting. Asner and Goldstein (1997), however, failed to obtain significant correlations between wood-specific gravity and stem failure in Hawaiian trees. Drag force is shed when trunks and branches of trees bend in the direction of the airflow and present smaller profiles to the wind (Hedden et al. 1995). In Hawaii, more flexible species (with low elastic modulus) suffered less snapping than other species (Asner and Goldstein 1997). Likewise, profiles are reduced and lower drag forces are experienced when leaves are shed under the prolonged battering of gusts. Although the ability to predict damage to individual trees may not yet be possible, an understanding of the relative importance of the factors contributing resistance or susceptibility to storm damage in a number of important urban forest species will contribute to our confidence in recommending and managing these species in Puerto Rico.

METHODS

A single study area was used in order to keep the wind speeds affecting study trees as nearly equal as possible. The area selected was the University of Puerto Rico Botanic Garden and surrounding neighborhoods extending out for a few species about 5 km (3 mi). Twenty-four species of ornamental, shade, and greenbelt trees were chosen (Table 1). All suitable trees of each species were evaluated until a sample of 30 to 50 individuals per species had been obtained. Trees were rejected only if they were growing in a sheltered position under the forest canopy, were very young (sapling size), were growing in the lee of a tall building, or had gross defects (such as hollow or decayed trunks, large cracks, and previous major crown damage) that obviously affected their ability to withstand wind stress. The diameters at breast height (dbh) were measured with a diameter tape, and the pre-hurricane total heights were estimated from the current height and thickness and form of trunk and branches. It was noted whether the sample trees had snapped (between the ground level and base of the crown) or had been thrown (tipped). Thrown trees were trees leaning 45 degrees or more as a result of the storm. This often involved breaking or pulling of part of the roots. Because snap and throw rates were relatively small figures and similarly reduce trees' survival, they were combined in the analysis and called stem failure. The percent defoliation was obtained by comparing the current leaf complement with a visualization of the fully leafed former crown and estimating the percentage of leaves that had been lost. Percent crown volume loss was similarly estimated by comparing the volume (envelope) of the current crown structure (defined by limbs and twigs) with a visualization of the pre-hurricane crown structure. The latter 2 estimates, being subjective, were both determined by a single person (the author). The evaluations were conducted between 2 and 14 days after the storm.

Because trunk and branch breaking strength (the ability of branches and trunks to flex under stress) and the ease with which leaves are shed in wind could not be directly and holistically measured, three index measurements were used: bole wood-specific gravity (density), resistance of small branches to flexing, and leaf retention strength. Wood-specific gravity was determined by the auger method, in which a sample of

known volume is extracted with a carpenter's auger or brace and bit (Stanley) from a living tree at breast height (from just inside the current growth ring for 10 cm [4 in.] inward), dried at 105°C (220°F), and weighed (Francis 1994). Samples were collected from 5 of the previously evaluated trees per species. Resistance of small branches to flexing was determined by collecting 5 branches per species. These branches were 5 to 10 mm (0.3 to 0.4 in.) in diameter at the butt end, except for 2 species, trumpet tree (*Cecropia schreberiana*) and matchwood (*Schefflera morototoni*), in which only somewhat thicker branches are produced. The leaves on each branch were removed and passed through a leaf area meter (Licor LI-3100) to determine total leaf area per branch. The branches were clamped in a horizontal position and the inside bark diameter measured at the axis point. Weight was slowly added at a point 30 cm (12 in.) from the axis until the branch flexed to an angle of 45 degrees or broke (method adapted from Hedden et al. 1995). Three indexes were calculated: Newtons/cm² of leaf

area, Newtons/cm² of branch cross-sectional area, and Newtons/(branch cross-sectional area)(leaf area). Leaf retention strength was determined for leaves on branches in 2 orientations. In the "up" position, branches were clamped vertically with the acute angle of the leaf petioles upward. The "down" position was opposite. Orientation is important because retention strength may differ as much as an order of magnitude between these 2 directions. A clamp was attached to the leaf and weight was added slowly until the petiole failed. Then the leaf area was determined. Five leaves per orientation for each species were evaluated in this way.

Damage estimates (percent defoliation, percent crown loss, and stem failure) for the 24 tree species were analyzed assuming a one-way classification with a linear model including fixed effects of tree species and random effects of tree nested in species and sample nested in tree and species. Contrasts among least squares means for species were done using t-statistics; a difference was deemed significant if the observed significance level was less than 0.01. Product-moment

Table 1. Comparison of storm damage by Hurricane Georges to 24 species of trees growing in and near the University of Puerto Rico Botanic Garden.

Species	Dbh (cm)	Height (m)	Mean				No.
			Def.	CL	S+T		
<i>Swietenia mahagoni</i>	28.5	10.7	70.7	22.7	0	50	
<i>Hymenaea courbaril</i>	38.0	17.3	89.6	40.6	2	50	
<i>Calophyllum calaba</i>	34.8	15.2	77.3	41.0	6	50	
<i>Pinus caribaea</i>	37.2	17.7	51.8	41.8	6	50	
<i>Melaleuca quinquinervia</i>	26.6	8.8	52.4	43.2	10	39	
<i>Delonix regia</i>	36.3	10.9	70.2	43.8	2	49	
<i>Lagerstromia speciosa</i>	48.5	11.5	77.0	44.0	2	50	
<i>Terminalia catappa</i>	46.6	14.6	86.6	46.5	2	41	
<i>Tabebuia heterophylla</i>	23.7	10.3	73.2	47.4	4	50	
<i>Cassia javanica</i>	43.9	10.5	87.7	47.4	10	31	
<i>Casuarina equisetifolia</i>	54.0	20.6	62.0	49.8	4	50	
<i>Pterocarpus macrocarpus</i>	76.4	20.7	94.5	50.7	6	50	
<i>Bucida buceras</i>	33.6	13.4	80.7	50.7	2	50	
<i>Enterolobium cyclocarpum</i>	113.6	17.5	87.6	50.8	9	33	
<i>Mangifera indica</i>	64.5	12.6	66.8	51.7	2	50	
<i>Clitoria fairchildiana</i>	26.0	4.7	62.0	51.9	38	32	
<i>Ficus benjamina</i>	68.6	9.1	56.5	52.5	30	50	
<i>Schefflera morototoni</i>	16.4	10.1	91.3	56.4	30	50	
<i>Albizia procera</i>	34.2	18.8	97.3	59.7	22	50	
<i>Cecropia schreberiana</i>	24.5	12.7	94.5	60.6	24	34	
<i>Sterculia apetala</i>	33.1	12.9	94.9	63.7	21	34	
<i>Peltophorum pterocarpum</i>	38.6	15.4	89.5	65.6	12	33	
<i>Senna siamea</i>	30.3	16.2	94.9	66.5	10	50	
<i>Spathodea campanulata</i>	41.6	16.9	98.1	81.1	34	50	

Dbh = diameter at breast height; Height = estimated pre-storm tree height; Def. = estimated percent defoliation; CL = percent of crown volume (space occupied by the envelope of limbs and twigs) lost, based on a visualization of former crown volume; S+T = sum of snapped and thrown (tipped) trees; No. = number of trees sampled.

correlations (Pearson correlation coefficients) with significance level set at $P = 0.01$ were calculated between tree diameters and heights and damage estimates, percent crown loss, percent defoliation, and stem failure for all 1,076 trees evaluated. Also, the mean (per species) index values, leaf retention strength, and wood-specific gravity were correlated ($P = 0.05$) with mean percent defoliation, crown loss, and stem failure. More complete estimates of association of damage with predictor variables were obtained using multiple stepwise regression of damage on the index values and tree diameter and height. Observed significance levels of 0.05 were required to retain a variable in the regression model.

RESULTS AND DISCUSSION

The means for dbh, estimated pre-storm height, estimated percent defoliation, estimated crown loss, and stem failure of the 1,076 trees from 24 species are listed in Table 1. The species are ranked according to ascending percent crown loss. Small-leaf mahogany (*Swietenia mahagoni*) suffered the least crown loss (22.7%), and African tuliptree (*Spathodea campanulata*) lost the most crown (81.1%). The differences in crown loss among species are significant (Figure 1). While these results may not be representative of the effects of all possible storms on these species, their relative resistance to defoliation, breakage, and tipping should be taken into consideration when selecting trees for planting in urban settings.

Although less important physiologically than crown loss, defoliation was extreme, ranging from 48.5% for queen-of-flowers (*Lagerstromia speciosa*) to 98.1% for African tuliptree (*Spathodea campanulata*). The differences among species were significant, but the distribution of differences was complicated (Figure 2). Refoliation was rapid, visibly commencing in some of the species within 1 week of the storm.

Although many individual trees sprout and re-grow following loss of canopy, snap and throw (or stem failure) are the most extreme forms of storm damage. They are especially important in an urban setting because trees damaged in these ways are usually removed for aesthetic or safety reasons. Percentages of stem failure ranged from 0.0 for small-leaf

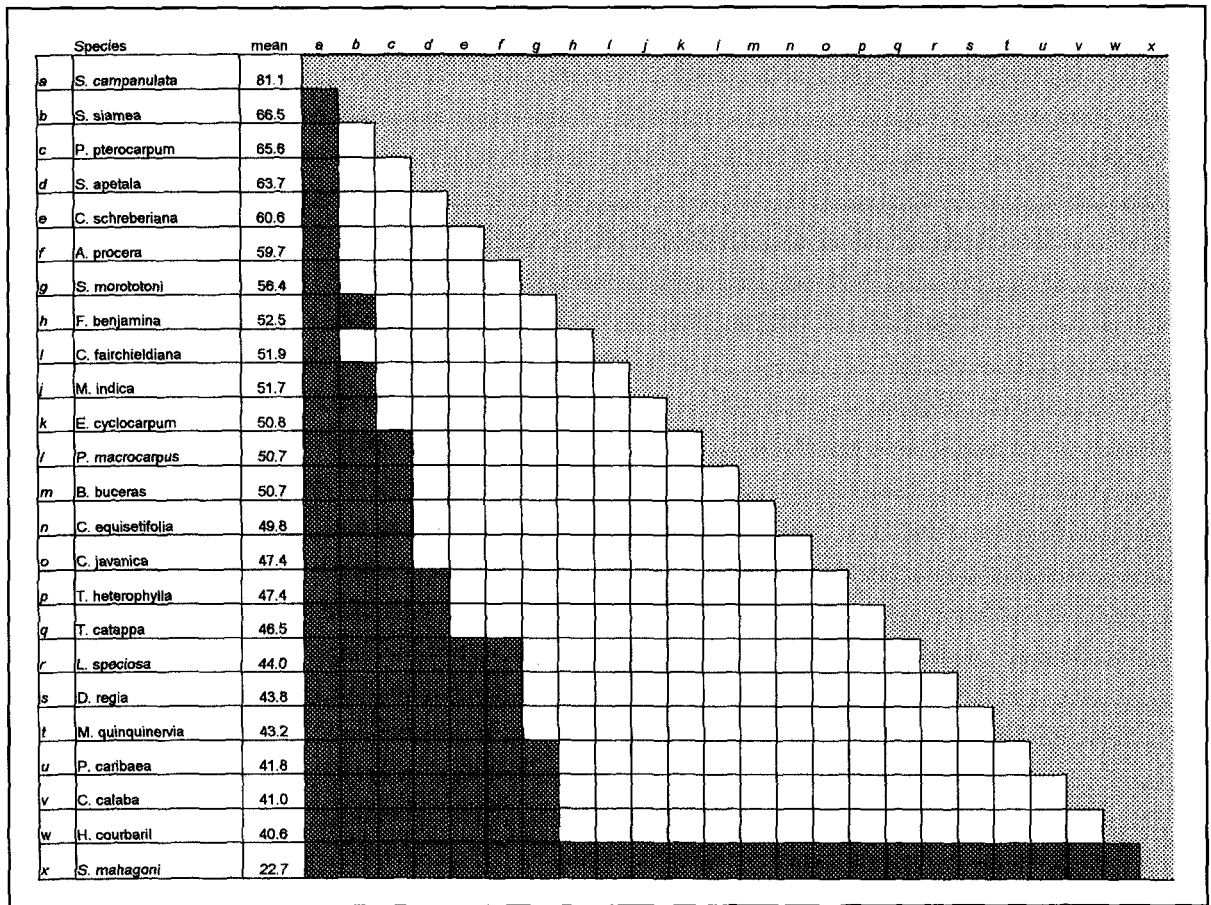


Figure 1. Comparison of means of percent loss of crown volume of various species affected by Hurricane Georges by the least significant difference (t) method. Squares in black represent individual comparisons between species' means that are significantly different at $P = 0.01$.

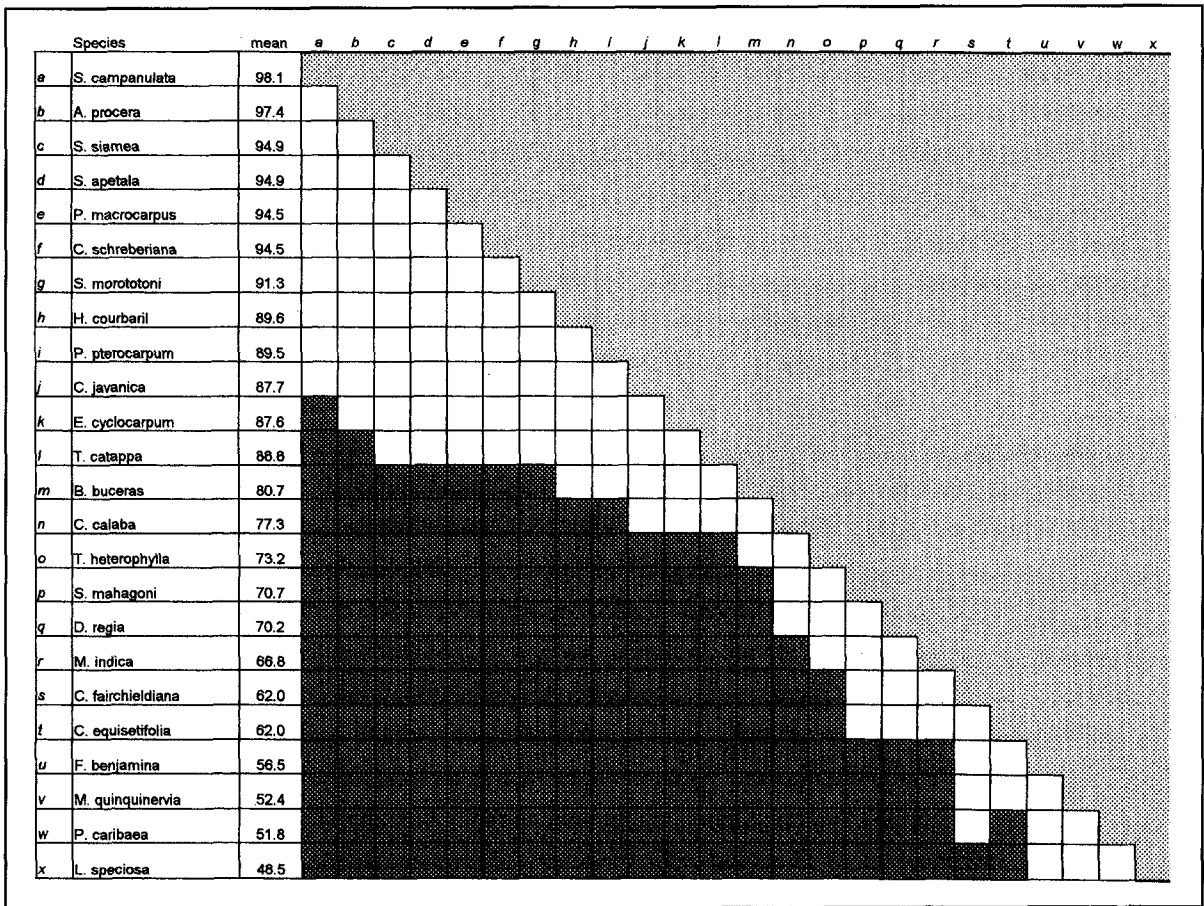


Figure 2. Comparison of means of defoliation of various species affected by Hurricane Georges by the least significant difference (t) method. Squares in black represent individual comparisons between species' means that are significantly different at $P = 0.01$.

mahogany (*Swietenia mahagoni*) to 37.5% for clitoria (*Clitoria fairchildiana*) (Figure 3). The species effect was significant and there were many differences among individual species (Figure 3). It is recognized that not all the differences in stem failure were species related. Soils, both natural and fills created during construction, may have imparted susceptibility, which was not evaluated.

It may legitimately be asked whether estimating percent defoliation and percent crown volume loss is possible, or rather, what degree of precision is possible when estimating such loss. Precision in estimating crown loss or defoliation depends on the practitioner's ability to visualize pre-storm crown dimensions and convert the present condition to a percent loss. Usually, researchers have classified defoliation and branch dam-

age of various grades into yes-or-no classes (Walker 1991; Basnet et al. 1992; Francis and Gillespie 1993; Zimmerman et al. 1994; Parresol and Alemany 1998). Even this classification requires visualizing the threshold condition, comparing it with the subject tree, and assigning the subject tree to one class or the other. One researcher felt confident enough to visually classify defoliation of individual trees and loss of canopy and cover into 25-percentile classes (Walker 1991). The consensus seems to be that estimates are possible (with limits to precision).

Untrained volunteers were tested to get an approximation of the precision of estimates of defoliation that might be possible. A computer was used to create a diagram of the vertical view of a tree containing 1,000 leaves and then construct 14 diagrams

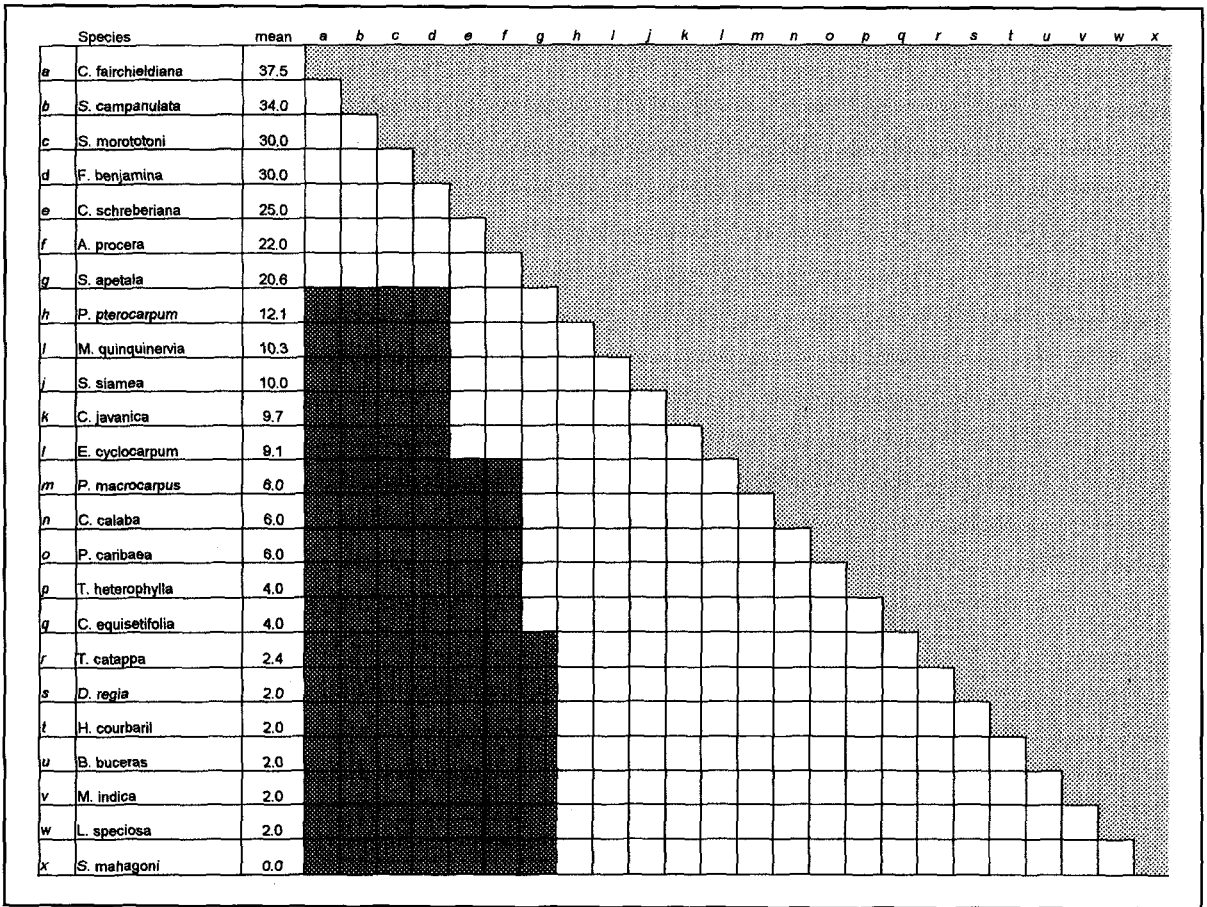


Figure 3. Comparison of means of percent failed stems (snapped plus tipped trees) of various species affected by Hurricane Georges by the least significant difference (t) method. Squares in black represent individual comparisons between species' means that are significantly different at P = 0.01.

of the same tree in various stages of defoliation. Thirty untrained participants from a variety of backgrounds were asked to view the diagram of the completely foliated tree and then without referring to it again, estimate the percentage of foliage remaining in the 14 cases that were shown to them in random order. Their estimates tended to exceed the actual percentage of foliage by a few percent (Figure 4). I believe precision of ± 10% is reasonable to expect from an experienced worker. Also, when comparisons are to be made, as long as bias is constant (as might be obtained with a single person estimating), mean differences are unbiased.

To evaluate several factors potentially responsible for hurricane resistance in urban trees, height, dbh, wood density, branch flexibility, and leaf retention

strength were tested statistically (Pearson's correlation) for their influence on measures of storm damage. The correlations between dbh and height and percent defoliation and crown loss proved to be significant for nearly all species as expected. However, the correlations between dbh and defoliation, dbh and crown loss, height and defoliation, and height and crown loss were significant for only 1 to 3 of the species evaluated. Probably, the high variation in defoliation and crown loss and relatively narrow range of tree sizes within each species are responsible for lack of significance. Leaf retention strength in the "up" position and branch resistance to flexing divided by leaf area and resistance to flexing divided by leaf area times branch cross-sectional area had low correlation coefficients and were dropped from

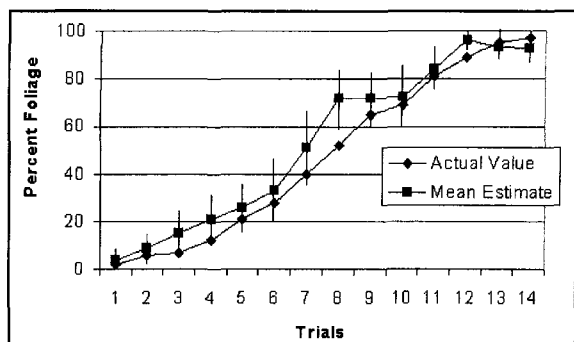


Figure 4. The results of estimation of computer graphic simulation of defoliation by 30 untrained participants. Whiskers on mean estimates represent 1 standard deviation.

further analysis. The Pearson's correlation matrix of leaf retention strength in the "down" position, branch resistance to flexing divided by cross-sectional area, and wood-specific gravity with percent defoliation, percent crown loss, and percent stem failure for means of the 24 species evaluated during this experiment is presented in Table 2.

Stem failure showed a negative correlation with wood-specific gravity, meaning that species with denser (stronger) wood are less likely to snap or throw. The fairly strong negative correlation between leaf retention strength and defoliation is logical: Defoliation decreases as leaf retention strength increases. Resistance to flexing increases as wood-specific gravity increases, as expected. There are significant auto-correlations between crown loss and defoliation and stem failure and crown loss. These correlations occur because total or partial crown loss automatically results in total or partial defoliation and so forth. Also, note significant relationships between wood density and defoliation and crown loss. Resistance to branch flexing, which is related to wood-specific gravity and leaf retention strength and between resistance to flexing and leaf retention strength. This may reflect the tendency for many species with low wood-specific gravity to hold their leaves weakly (per cm² of leaf area).

A least-squares linear multiple regression equation with height, leaf retention strength, resistance to branch flexing, and wood-specific gravity as independent variables and percent defoliation as dependent variable (adjusted R² = 0.712) is presented below:

$$\text{Percent DF} = 54.491 + 2.237\text{Ht} - 4.147\text{SG} - 0.275\text{LR} + 0.0017\text{RF}$$

where DF = defoliation, Ht = pre-storm tree height, SG = wood-specific gravity, LR = leaf retention strength with leaves in the "down" position, and RF = resistance to branch flexing per unit of branch cross-sectional area. The multiple regressions for percent crown loss and percent stem failure were not significant.

Stepwise multiple regression was used to judge the relative importance of the independent variables. For the dependent variable percent defoliation, height entered before branch resistance to flexing, followed by leaf retention in the "down" position, followed by wood-specific gravity.

While there are significant differences between tree species in resistance to storm damage, because of the complicated dynamics of storms, unevenness of the local environment, and the variable structure of trees, it is not yet possible to predict damage with much precision. Tree height, wood-specific gravity, branch flexibility, and leaf retention strength are all contributors, although all are intercorrelated. Reduced to the simplest terms, we could say that shorter trees are less frequently damaged directly by storms, trees with higher wood-specific gravity and

Table 2. Pearson's correlation coefficients and attendant P-values for averages of damage indices for 24 species affected by hurricane winds and mean values for indices of wind resistance.

Measured trait	DF	CL	S+T	SG	RF	LR
% defoliation (DF)	—					
P-value	—					
% crown loss (CL)	0.573	—				
P-value	0.003	—				
Stem failure (S+T)	0.168	0.546	—			
P-value	0.432	0.006	—			
Wood-specific gravity (SG)	-0.256	-0.294	-0.460	—		
P-value	0.227	0.164	0.024	—		
Resistance to flexing (RF)	-0.312	-0.134	-0.010	0.443	—	
P-value	0.138	0.534	0.961	0.030	—	
Leaf retention strength (LR)	-0.660	-0.232	-0.227	0.544	0.500	—
P-value	0.000	0.275	0.287	0.006	0.013	—

greater branch flexibility are less likely to suffer, and that it is to a tree's advantage to shed its leaves quickly. It may be possible to reduce the damage for at least some species of trees by pruning to reduce the crown profile exposed to winds (Duryea et al. 1996).

It should still be possible to dramatically improve the predictability of damage of trees in storms. Deficiencies in measurement technique and unmeasured effects certainly limit the power of these models. Static forces do not duplicate the whipping action of gusts on trees and limbs over many hours that ultimately results in breakage and throw. The stripping of twigs and small branches at their attachment frequently occurs and was not measured here and is probably not predicted by any of the measurements in this study. Much of the defoliation in hurricanes results from shredding of leaf blades rather than failure of petioles.

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Résumé. Les vents de l'ouragan Georges en 1998 avec des rafales excédant les 150 km/h ont endommagé sévèrement les arbres de la métropole San Juan à Porto Rico. Les études et les inventaires antérieurs de dommages calculaient un pourcentage d'arbres rencontrant certains critères subjectifs. Les comparaisons de résistance des espèces aux dommages par le vent s'étaient limitées à quelques espèces, principalement forestières, regroupées généralement dans de vastes catégories. Un pourcentage de défoliation et un pourcentage de cime perdue ont été estimés ainsi qu'un décompte des cassures à partir de 24 espèces d'arbres urbains de San Juan. Les différences entre les espèces étaient significatives et des comparaisons détaillées sont présentées. La densité du bois, la résistance des branches à la flexion et la force de résistance des feuilles ont été mesurées pour les espèces étudiées. Plusieurs corrélations significatives ont été notées entre la hauteur avant la tempête, le diamètre, la densité du bois, résistance des branches à la flexion, la force de résistance des feuilles, la défoliation, le pourcentage de cime perdu et le nombre de cassures. Les équations de régression pour prédire la quantité de dommages étaient significatives mais elles étaient des assez faibles quant à la prévision des dommages sur l'arbre. La hauteur de l'arbre était le facteur qui avait le plus d'influence suivi par la résistance des branches à la flexion, la force de résistance des feuilles et la densité du bois. Si la hauteur de l'arbre était éliminée du modèle, alors la densité du bois devenait la première variable prépondérante dans le calcul de régression.

Zusammenfassung. Die Sturmböen des Orkans Georges im Jahr 1998 erreichten eine Geschwindigkeit von 150 km/h und zerstörten und beschädigten Bäume in der Hauptstadt San Juan auf Puerto Rico. Die letzten Berichte über die Schäden und die Studien ermittelten einen Prozentsatz von Bäumen, die bestimmte subjektive Kriterien erfüllen. Die Vergleiche der Resistenzen der Baumarten wurden begrenzt auf wenige, meist forstlich genutzte Arten in großen Kategorien. Der Anteil der Entlaubung und des Kronenverlusts wurde geschätzt. Von 24 Baumarten in San Juan wurde der Stammbruch und -wurf ermittelt. Die Unterschiede

zwischen den Arten waren signifikant und es konnten detaillierte Vergleiche präsentiert werden. Die Holzdicke, Flexibilität der Äste und die Blattretentionskraft wurde bei diesen Bäumen gemessen. Viele signifikante Korrelationen konnten herausgefunden werden zwischen der Höhe vor dem Sturm, Durchmesser, Holzdicke, Biegelast der Äste, Blattretentionsstärke, Entlaubung, Anteil des Kronenverlustes und Bruch und Stammwurf. Die Möglichkeit der Einschätzung der Schadensmessungen über die Regressionsgleichungen war deutlich vorhanden, aber als Voraussage von Baumschäden taugten sie wenig. Die Baumhöhe war die größte Variable, gefolgt von der Biegelast der Äste, der Blattretention und der Holzdicke. Wenn die Baumhöhe aus dem Modell entfernt wurde, geriet die Holzdicke als erste in die schrittweise Regression.

Resumen. Los vientos del huracán Georges de 1998 con rachas arriba de 150 km/hr (93 mi/hr) dañaron severamente los árboles de la zona metropolitana de San Juan, Puerto Rico. La mayoría de los estudios e inspecciones previos han calculado el por ciento de daño con ciertos criterios subjetivos. Las comparaciones de la resistencia de las especies al daño por los vientos han estado limitadas a pocas especies, principalmente forestales, frecuentemente en categorías muy amplias. En este estudio fueron estimados el por ciento de defoliación y de pérdida de copa, y se hizo un conteo rápido para 24 especies de árboles urbanos en San Juan. Fue significativa la diferencia entre especies, aquí se presentan comparaciones detalladas. Se encontraron muchas correlaciones significativas entre la densidad de la madera, resistencia de las ramas a la flexión, intensidad de retención foliar, defoliación y por ciento de pérdida de copa. Las predicciones con las ecuaciones de regresión de las medidas de daño fueron significativas pero son predictores bastante débiles del daño a los árboles. La altura del árbol fue la variable más significativa seguida por la resistencia de las ramas a la flexión, retención foliar, y densidad de la madera. Si la altura del árbol fuera retirada del modelo, la densidad de la madera entraría primero en la regresión.