Uprooting and snapping of trees: structural determinants and ecological consequences

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The influence of mechanical and architectural properties of trees on growth rates, mortality rates, and relative probabilities of snapping and uprooting were examined on Barro Colorado Island, Republic of Panama. Of 310 fallen trees, 70% snapped, 25% uprooted, and 5% broke off at ground level. Stepwise discriminant analysis between snapped and uprooted trees indicated that of the variables measured, wood properties were the most important factors determining the type of death in trees. Uprooted trees tended to be larger, shorter for a given stem diameter, and to have denser, stiffer, and stronger wood than snapped trees. There were no significant differences between trees that snapped and trees that uprooted in the extent of buttress development or in the slope of the ground upon which they grew. Trees with low density wood grew faster in stem diameter than those with high density wood but also suffered higher mortality rates. After damage, many of the snapped trees sprouted; small trees sprouted more frequently than large trees. Sprouting is proposed as a means by which weak-wooded fast-growing trees partially compensate for being prone to snapping.

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L'étude traite de l'influence des propriétés mécaniques et structurales des arbres sur le taux de croissance, le taux de mortalité et la susceptibilité à la cassure et au renversement, sur l'Ile Barro Colorado, République de Panama. Des 310 arbres tombés, 70% étaient cassés, 25% déracinés et 5% brisés au niveau du sol. L'analyse discriminante progressive entre arbres cassés et arbres déracinés a fait ressortir l'importance des propriétés du bois comme facteurs déterminants du type de mortalité des arbres. Les arbres renversés avaient tendance à être plus larges et plus courts, pour un diamètre donné; leur bois était plus dense, plus rigide et plus robuste que celui des arbres cassés. L'étude ne révèle pas de différence significative entre arbres cassés et arbres renversés quant au développement de contreforts ou au degré de pente du terrain. Les arbres à bois de faible densité avaient une croissance en diamètre plus élevée que les arbres à bois dense, mais leur taux de mortalité était aussi plus élevé. Plusieurs des arbres cassés ont formé des rejets, surtout les arbres de faible taille. La formation de rejets est proposée comme moyen par lequel les arbres à croissance rapide et à bois fragile peuvent compenser leur prédisposition à se casser.

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Introduction

General introduction

Forests can be thought of as spatial-temporal mosaics of patches of land in different stages of recovery following disturbance (e.g., Jones 1945; Watt 1947; Whitmore 1978). Forest structure and species composition are influenced by both the rate (Whitmore 1974) and the size (Kramer 1926, 1933; Brokaw 1982) of disturbances. Large disturbed patches and chronically disturbed forests tend to be dominated by fast-growing light-demanding trees with good seed dispersal abilities, prolonged seed dormancy, or well-developed means for vegetative propagation (e.g., Marks 1974; Whitmore 1974; Brokaw 1982; Putz 1983). However, in addition to the frequency and size of disturbances, the particular type of disturbance is also important in determining the species composition in regenerating patches of forest. In many forest communities, the most common disturbance is the death of canopy trees. These deaths can occur in a variety of ways: trees can uproot, snap off, or die standing. Each of these types of disturbance has a different effect on the species composition in regenerating patches of forest.

A tree is uprooted when subjected to lateral forces on the crown and stem that exceed root–soil holding strength but which do not break the stem. When a tree is uprooted, the soil mass adhering to its roots is generally turned over resulting in characteristic pit-mound microtopography and inverted soil horizons (e.g., Brown 1976). In temperature forests, several plant species specialize on particular microsites within the pit-and-mound complex (Hutnik 1952; Falinski 1978; Beatty 1980). Tree uprooting also may expose buried dormant seeds to the environmental conditions required

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for germination (e.g., Guevera and Gomez-Pompa 1972; Putz 1983) and provide a suitable substrate for those species requiring mineral soil for establishment. On Barro Colorado Island, Panama, pioneer (early successional) trees are more concentrated on the soil disturbed by uprooted trees than elsewhere in tree-fall gaps (Putz 1983).

Trees snap when subjected to forces that exceed stem strength but that are not strong enough to dislodge and break the roots and roll the root ball. Less soil is disturbed by snapped than by uprooted trees and, on Barro Colorado Island, pioneer trees are consequently less common in tree-fall gaps caused by snapped than by uprooted trees (Putz 1983). Furthermore snapped trees that are capable of resprouting have larger root systems and a positional advantage over smaller trees and may often succeed in reoccupying vacated canopy positions (Smith 1972).

Trees die standing due to fire, lightning, or the attack of pathogenic organisms. Generally, dead-standing trees gradually disintegrate, falling over when the trunk is sufficiently rotten. Canopy gaps opened by dead-standing trees are small and narrow because, by the time the trees fall over, many of their branches have already fallen off. The small size and slow opening rate of gaps created by dead-standing trees favors the growth of seedlings and saplings present at the time of canopy tree death relative to plants that germinate after gap formation.

On Barro Colorado Island, approximately 1% of the trees more than 20 cm diameter at breast height (dbh) (diameter at 1.3 m or above the buttresses) die each year. In 5 ha of mature forest monitored for 5 years, the mode of death is known for 78 trees more than 20 cm dbh; 51 (66%) snapped, 15 (19%) uprooted, and 12 (15%) died standing (Putz and Milton 1982). In this paper we discuss factors influencing the way trees die. We concentrate on snapped and uprooted trees because these are the most common types of tree falls and because of the difficulties of identifying trees that died standing.

Factors potentially influencing whether trees snap or uproot

The overall root system strength of large trees is notoriously difficult to measure (but see Fraser 1962; Fraser and Gardiner 1967), and varies with soil type and moisture status (Day 1950; Sutton 1969). Stem strength is easier to measure, or at least estimate, using the engineering properties of the wood. Trees with weak wood would be expected to snap rather than uproot. However, in predicting whether a particular tree will snap or uproot, factors other than wood strength also may be important.

Soil depth decreases with increasing slope of the terrain on Barro Colorado Island (Dietrich *et al.* 1982), and Fraser (1962) demonstrated with tree-pulling experiments that small increases in rooting depth result in considerable increases in resistance to uprooting. Therefore, an increase in the proportion of uprooted trees is expected on steeper terrain. Field data on the relationship between slope and the incidence of uprooting are contradictory; Neustein (1971) found uprooting to be common on slopes in Scotland, but Kennedy (1974) observed a decrease in the incidence of uprooted trees with increasing slope in Northern Ireland. We will examine the importance of slope as an indirect indication of soil depth in determining the occurrence of uprooted and snapped trees in a natural, mixed-species tropical forest.

Empirical and theoretical evidence indicate that buttresses increase trees' resistance to mechanical stress (for reviews see Richards 1952; Smith 1972; Henwood 1973). Whether or not buttresses reduce the likelihood of damage, Henwood (1973) suggested that by lengthening the lever arm of a tree's base, buttresses serve to reduce the tensile forces acting on the roots. If roots are less stressed, proportionately more stress will be manifest in the trunk and the probability of snapping will increase. Smith (1972) pointed out that in the buttressed region wood is peripherally displaced to where most of the tensile force is acting, thus reducing the probability of snapping near the ground. In a temperate forest in the United States, Mergen (1954) observed that structural failure of unbuttressed tree trunks almost invariably occurred within a few feet of the ground. These findings suggest that stem sections near the ground but above the buttresses are subjected to the most stress. One might expect that the proportion of snapped trees relative to uprooted trees would increase with the amount of buttressing and that snapping would occur above rather than within the buttressed portion of the trunk.

Increases in height of solidly anchored vertical beams lead to increases in the probability of snapping (local buckling; Wainwright *et al.* 1976). Beam theory has been applied to trees (e.g., Greenhill 1881; McMahon 1973; King and Loucks 1978) even though trees are clearly not solidly anchored and fail to satisfy several of the other simplifying assumptions. However, in spite of problems with the model, the relative probabilities of snapping and uprooting may change as trees approach their calculated critical heights.

Crown size and shape determine the amount of stress wind, rain, and other loads exert on a tree's stem and roots. Shedding of lateral branches, either by abscission (Millington and Chaney 1973) or because of mechanical damage, results in a reduction in wind resistance (bluffness). This should lessen the probability of stem breakage and uprooting. Pruning spruce trees resulted in smaller wind induced root movements (Hutte 1968) and presumably lowered the probability of uprooting. Do certain species characteristically lose large branches during storms and do these species share wood or architectural properties?

In this paper we document the relative frequencies of different types of damage to trees on Barro Colorado Island (BCI) and show that the relative likelihoods of uprooting and snapping are size related and very much dependent upon wood properties. The relationships among mortality rates, growth rates, and wood density are explored along with the probability and importance of sprouting after damage.

Study site

Barro Colorado Island (BCI, 9°09′ N, 79°51′ W) was created when the Chagres River was dammed to form Gatun Lake, part of the Panama Canal. The climate, soils, and vegetation of BCI have recently been described by Knight (1975), Croat (1978), and Foster and Brokaw (1982); we provide only a brief summary. The vegetation of BCI is semideciduous and classified as tropical moist forest in the Holdridge Life – Zone System (Holdridge *et al.* 1971). Approximately one-half of the 15.6 km^2 island was intermittently used for agriculture before establishment as a biological preserve in 1923. The terrain is hilly and dissected by stream-cut ravines except for the relatively flat central plateau. Elevations range from 25 to 165 m above sea level. Most of the island has well-drained clay–loam soil, but there are also small areas of poorly drained gley soil (Bennett 1929; Knight 1975).

Annual rainfall on BCI between 1929 and 1975 averaged 265 cm (s = 40, Rand and Rand 1979). Rainfall is markedly seasonal; the dry season usually commences in mid-December and ends in mid-April.

Methods

Field methods

We censused freshly fallen trees in a nonsystematic but intensive fashion from July 1979 through February 1980. N. Brokaw (personal communication) generously supplied data on trees which fell between 1976 and 1978. We also included fallen trees blown down during an intense local storm in 1979. We obtained the remainder of our sample by searching the island for recent tree falls.

We classified fallen trees >10 cm dbh as snapped near ground level, snapped above the ground, or uprooted. Trees that snapped near ground level were considered in a separate category because, generally, they were partially uprooted and thus difficult to classify. Uprooted trees were those which overturned taking at least some soil along with their roots. Trees that snapped above the first live major branch (i.e., in the crown) and those that lost large branches were recorded as having dropped branches. Only trees that were alive when they fell were included. The following measurements were made on each tree: dbh, height of snap (where applicable), total height, estimated terrain slope, and basal diameter (average distance between buttress edges measured along and perpendicular to the widest basal diameter). Snapped trees were inspected for signs of previous damage (e.g., heartrot, termites, or woodpecker holes). We checked fallen trees for new sprouts at least 6 months after they fell.

Species-specific mortality rates and growth rates were estimated by following 782 trees of 68 species (>20 cm dbh) in five 1-ha study plots over a 5-year period. Plot descriptions can be found in Putz and Milton (1982) and Thorington *et al.* (1982). Growth rate estimates were supplemented by data provided by D. H. Knight and G. E. Lang for trees in a 1.5-ha plot on BCI they monitored for 10 years.

Measurement of wood properties

In addition to measurements made in the field, values for specific gravity, modulus of elasticity, and modulus of rupture were taken from the literature, primarily from a survey of Panamanian woods (Anonymous 1971). Supplementary wood-property data came from Dickinson *et al.* (1949), Wangaard *et al.* (1955), Longwood (1962), and Echenique-Manrique *et al.* (1976). All tests were conducted on straight-grained wood free of defects according to procedures set by the American Society for Testing Materials (Anonymous 1952).

Of the strength measures available, the modulus of rupture (in kilograms per square centimetre) i.e., the stress needed to rupture a material, seems the most logical indicator of a material's ability to withstand lateral stress. However, it should be pointed out that trees sometimes break under torsional stress.

Density (dry weight/green volume) can also be used as an indicator of strength and is correlated with more direct measures of strength, e.g., modulus of rupture (Anonymous 1974). Deviations from predictions of wood strength based on density are due to histological and chemical features of the wood, such as fiber length and overlap, cell wall pitting, and silica inclusions (Forsaith 1926; Esau 1958). Since density is related to the ability of wood to resist torsional as well as lateral stress (Anonymous 1974), it may be better than the modulus of rupture as a measure of a tree's breaking strength.

Flexibility, expressed as Young's modulus (10^3 kg/cm^2), may influence the fates of trees in several ways. By shedding wind, flexible trees can withstand more wind-induced stress than rigid trees of similar strength. However, when a tree's crown is displaced from its balance point, although wind-induced stress on the tree is reduced, stress on the roots owing to gravity may increase. This should lead to an increased incidence of uprooting among flexible trees that do fall.

Allometrical and architectural measures

We express the degree of buttressing as the ratio of the dbh (or the diameter above the buttresses) to the average basal (ground level) diameter. Buttress height is not included in this index owing to the ambiguity involved in its measurement and because the major theoretical analysis of buttress strength is based solely on buttress width (Henwood 1973).

To calculate each tree's theoretical critical (buckling) height, i.e., the height at which the slightest lateral displacement will cause a vertical beam to buckle under its own weight, we used McMahon's (1973) formulation of Greenhill's (1881) equation. Assuming that a tree trunk approximates a cubical paraboloid in which mechanical stresses are evenly distributed over the entire tapering column, critical

TABLE 1. Comparisons of uprooted and snapped trees. Different sample sizes (N) reflect availability of data

Variable	Uprooted		Snapped
dbh (cm)	$N = 78$		$N = 217$
	$x = 44.6$	$P < 0.05$	$x = 33.6$
	$s = 28.9$		$s = 23.9$
Height (m)	$N = 78$		$N = 217$
	$x = 21.6$	$P < 0.01$	$x = 19.0$
	$s = 6.9$		$s = 7.4$
Modulus of rupture (kg/cm^2)	$N = 63$		$N = 145$
	$x = 881.2$	$P < 0.01$	$x = 641.9$
	$s = 346.6$		$s = 245.1$
Modulus of elasticity (10^3 kg/cm^2)	$N = 63$		$N = 145$
	$x = 148.8$	$P < 0.01$	$x = 111.4$
	$s = 114.9$		$s = 84.0$
Density (dry weight/green volume)	$N = 74$		$N = 210$
	$x = 0.53$	$P < 0.0001$	$x = 0.41$
	$s = 0.13$		$s = 0.12$
Slope (degrees)	$N = 78$		$N = 217$
	$x = 11.0$	$P = 0.16$	$x = 12.6$
	$s = 11.8$		$s = 13.7$
Buttressing	$N = 64$		$N = 178$
	$x = 2.5$	$P = 0.78$	$x = 2.2$
	$s = 1.1$		$s = 1.2$
Height/critical height	$N = 63$		$N = 145$
	$x = 0.38$	$P = 0.27$	$x = 0.40$
	$s = 0.11$		$s = 0.11$
Height/dbh	$N = 78$		$N = 217$
	$x = 58.2$	$P < 0.001$	$x = 68.1$
	$s = 22.0$		$s = 24.3$

NOTE: Probabilities calculated using Student's t-test. For the two heteroscedastic variables (dbh and slope) we used the separate variance estimate (Nie *et al.* 1975) to calculate the t-statistics.

height would be

$$[1] \quad H_{cr} = 0.792\sqrt[3]{\frac{E}{\text{density}}}\ \sqrt[3]{\text{dbh}^2}$$

where E is equal to Young's modulus (10^3 kg/cm^2).

Multivariate statistical analysis

In addition to comparing trees which suffered different types of damage using each of the 9 variables separately (Table 1), we analyzed the data with discriminant-function analysis (Klecka 1975). This technique selects the set of variables which best separates the means of the groups, in our case the damage classes, in multivariate space. To reduce the problems of assigning weights to correlated discriminating variables (e.g., density with modulus of rupture), we also present the correlation of each variable with the discriminant function as an estimate of its contribution to group separation.

Results

Field observations

Of 310 fallen trees (>10 cm dbh) censused on BCI, 25% uprooted, 70% snapped between their lowest branch and the ground, and 5% snapped off at ground level. Although most trees died by falling, in 5 ha of permanent study plots monitored over a 5-year period, 14% of the dead trees died standing (Putz and Milton 1982). Heartrot was observed in 13% of the snapped trees. No attempt was made to determine the proportion of hollow trees in the other damage classes. Trees snapped at various points along their boles with no tendency for damage to be concentrated near the ground (Fig. 1).

There was little difference in the proportions of snapped and uprooted trees between the blowdown of July 1979 and more or less isolated tree falls. During the storm 117 trees fell, 23% uprooted, 74% snapped, and 3% snapped at ground level. It appeared that trees with propensities towards either snapping or uprooting did so regardless of the nature of the tree-fall event in which they were involved.

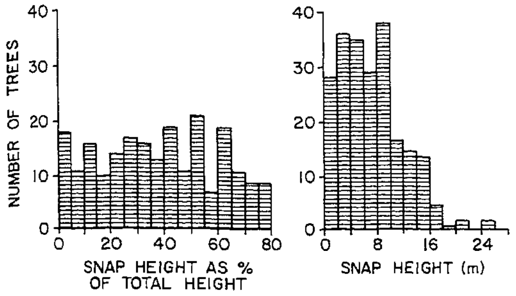

FIG. 1. Height at which trees on Barro Colorado Island snapped. Those which snapped above the first large live branch are not included.

New leafy branches (sprouts) developed on 111 (51%) of the 217 snapped trees and 5 (6%) of the 77 uprooted trees. Of the snapped trees, a significantly greater fraction of the trees smaller than the median size (dbh = 22 cm) sprouted compared with large trees ($\chi^2 = 17.48$, $P < 0.005$). We could not ascertain how long these sprouted trees will survive but observed that many lived long enough to reproduce. Furthermore, casual observation of canopy tree form suggests high incidence of breakage and crown regrowth.

Thirty-one trees were observed to have lost large branches during wind storms. Owing to a likely big-tree bias in our field methods, (i.e., we were more likely to observe branches lost from large trees) we are confident only in suggesting the following list of species which seemed characteristically to drop branches: *Anacardium excelsum* (Bertero and Balb.) Skeels (Anacardiaceae), *Cavanillesia platanifolia* (H. and B.) H.B.K. and *Ceiba pentandra* (L.) Gaertn. (Bombacaceae), *Enterolobium cyclocarpum* (Jacq.) Griseb. (Leguminosae), *Poulsenia armata* (Miq.) Standl. (Moraceae), *Virola sebifera* Aubl. and *V. surinamensis* (Rol.) Warb. (Myristicaceae), *Pouteria stipitata* Cronq. (Sapotaceae), *Terminalia amazonica* (J. F. Gmel.) Exell in Pulle (Combretaceae), and *Jacaranda copaia* (Aubl.) D. Don (Bignoniaceae). The trees recorded as having lost large branches on the average had lower modulus of rupture, less dense, and more elastic wood than both the snapped and the uprooted trees, but *P. stipitata* and *T. amazonica* were exceptions to this trend.

For the 46 species for which we have both diameter growth rate and wood property data, growth rates are negatively correlated with specific gravity of the wood ($r = 0.44$, $P < 0.01$).

To test the hypothesis that certain wood properties confer overall resistance to damage, we examined the correlation between wood-density and tree-mortality rates. We chose density because it is correlated with other wood properties, it was the best discriminator between uprooted and snapped trees in the multivariate model (see below), and it was the variable for which we had the most complete data. There is a significant negative correlation ($r = 0.72$, $P < 0.05$) between mortality rate and wood density for 782 trees (68 species; 78 died during the 5-year observation period) in permanent study plots on BCI.

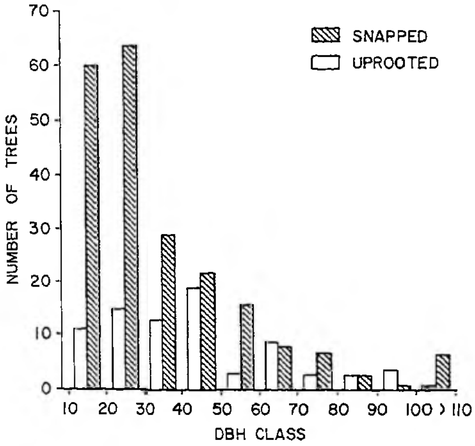

FIG. 2. Number of trees that snapped and uprooted as a function of dbh (diameter at 1.3 m or above buttresses).

Comparison of snapped and uprooted trees

Snapping and uprooting were the most common forms of tree damage. Trees obviously knocked down by other trees and those with signs of prior damage (e.g., hollow or rotten; $N = 30$ trees) were excluded from the analysis. Although for each of the nine variables there was considerable overlap between the two damage classes, six showed significant differences (Table 1). Trees that uprooted were significantly larger in dbh than trees that snapped though there was substantial overlap of ranges (Fig. 2). Uprooted trees were also taller than snapped trees, although for a given diameter, uprooted trees were shorter. However, when wood properties and trunk taper were considered, snapped trees were no closer to their calculated buckling height (h/h_{cr}) than uprooted trees. Wood of uprooted trees had higher moduli of rupture and elasticity and was denser than wood of snapped trees. There was no relationship between slope of the ground and type of damage.

There was no difference in the extent of buttress development on snapped and uprooted trees (Table 1). The low correlation of buttressing with the discriminant function (see below) suggests that if buttresses conferred some resistance to snapping, it was slight for the trees in our study (Table 2). Furthermore, in 5 ha of permanent study plots, there was no difference between the mortality rates of prominently buttressed and unbuttressed trees ($\chi^2 = 2.06$, $P = 0.17$). It should be pointed out that buttressed trees had less dense wood than unbuttressed trees (buttressed trees: mean = 47.9, $N = 25$; unbuttressed trees: mean = 58.1, $N = 31$; $t = 2.12$, $P < 0.05$).

TABLE 2. Discriminant-function analysis results and the number and percent of trees correctly classified by the model

Variables	Standardized discriminant-function coefficients	Correlation with discriminant functions
Density	−1.02	−0.88
Modulus of rupture	0.22	−0.75
Height/dbh	0.30	0.37
Modulus of elasticity	−0.21	−0.35
Buttressing	−0.31	−0.28
Slope	−0.09	0.11

	Number of trees	Number correctly classified
Uprooted	52	31 (60%)
Snapped	124	90 (73%)
Overall	176	121 (69%)

Multivariate statistical comparison of snapped and uprooted trees

We used stepwise discriminant analysis to assess the relative importance of each of the variables in determining whether a tree snapped or uprooted. The discriminant function is most closely correlated with wood density, wood strength (modulus of rupture), and the height−diameter ratio (Table 2). The modulus of elasticity also contributes discriminatory power although much less; slope and buttressing contribute little. The function describes a dimension from trees with rupture resistant and dense wood that have a low height-to-diameter ratio, that tend to uproot, to relatively slender trees with low density low modulus of rupture wood that tend to snap. There is a significant difference between the centroids (multivariate means) of the two damage categories (function eigenvalue = 0.258; canonical correlation = 0.453; Wilk's lambda = 0.794; χ^2 of Wilk's lambda = 39.34, $P < 0.001$). However, the distributions of the discriminant scores overlap considerably when projected onto a two-dimensional graph (Fig. 3).

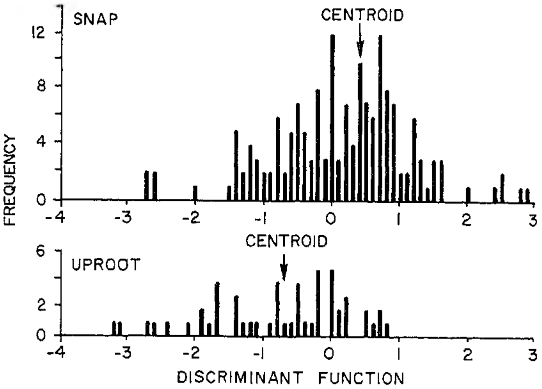

FIG. 3. Plot of tree frequencies on the discriminant function (see text and Table 2) which runs from uprooted trees (small values) to snapped trees (large values). Discriminant scores are standardized to an overall mean of 0 and a standard deviation of 1. Centroids are the actual group means.

Discussion

Factors influencing whether trees uproot or snap

Wood properties influence relative probabilities of uprooting versus snapping, as well as tree mortality rates. Wood density and strength (modulus of rupture) were higher for uprooted trees. That uprooted trees had less flexible wood (higher modulus of elasticity) than snapped trees is not surprising considering that the modulus of elasticity is highly correlated with both density and modulus of rupture (Anonymous 1974). However, in the discriminant analysis, the negative coefficient for modulus of elasticity suggests that even after the effects of this correlation are removed statistically, trees with less flexible wood tend to uproot.

There is a problem in assuming that the properties of materials (wood) can be used to predict the properties of structures (trees). Preliminary tree-pulling experiments designed to measure whole-tree flexibility found that, for the 16 species tested, the correlation between wood flexibility and tree flexibility was not statistically significant ($r = 0.078$, $P = 0.4$; Putz 1983).

Tree size, as measured by height and dbh, also influenced whether trees uprooted or snapped. Uprooted trees were generally larger, but we observed snapped trees up to 150 cm dbh with apparently defect-free wood. Larger trees may be prone to uprooting because, under stressed conditions, their mass increases both the strain on the root−soil interface and the likelihood of exceeding soil shear strength. Furthermore, trees asymptotically approach a maximum height while continuing to grow in diameter and resistance to snapping increases with decreasing height/diameter ratios.

Buttresses were no better developed on snapped than on uprooted trees and buttressed trees suffered both types of damage as often as unbuttressed trees. Buttressed trees, on the average, had less dense wood than unbuttressed trees and yet suffered approximately the same mortality rates. This suggests that buttressing confers at least a modicum of resistance to both snapping and uprooting. It was also noted that buttressed trees which snapped did so above the buttress zone and hence, when capable of sprouting, were in a good position for regaining a place in the canopy.

There was no relationship between slope and the relative frequencies of uprooting and snapping even on inclines greater than 35°. This may be because root systems on slopes differ from those on level ground (Fraser and Gardiner 1967). Although soil may be thinner on slopes, roots may still penetrate deep into the ground through cracks in the bedrock.

Using only mechanical and structural properties of trees it was possible to classify with 69% accuracy whether a tree snapped or uprooted (Table 2). Our predictive ability might increase with a greater knowledge of above- and below-ground tree architecture. Crown surface area, density, and location on the bole all affect wind drag and presumably susceptibility to different types of damage (Curtis 1943; Hutte 1968; Grace 1977). Trees with deep crowns and short stems are probably prone to uprooting, whereas long, clear-boled trees should more readily snap. Branch loss reduces crown wind resistance and may lower the likelihood of both snapping and uprooting (Hutte 1968). Stem taper may also affect the relative probabilities of snapping and uprooting, more conical trees being more resistant to snapping (Larson 1963). The omission of such architectural considerations from our analysis may explain why we found no difference in the critical height: observed height ratio for snapped and uprooted trees.

Heartrot may also be responsible for failure to predict a tree's fate. In some forests, many trees, especially the larger ones, are hollow (Hepting and Hedgecock 1937) but on BCI few trees are so affected. Although, on purely mechanical grounds, hollow trees are not necessarily weaker than solid trees, heartrot may increase the probability of snapping. After a windstorm in New York, "breakage was more common than uprooting in the case of the larger trees, probably because such a large percentage . . . were rotten, and uprooting was more common in the case of the smaller and hence younger trees which were still sound" (Behre 1921).

Trees uproot when roots or root–soil connections fail. Both are undoubtedly influenced by root size and distribution. Soil shear strength (i.e., the soil's ability to resist torsional forces) also plays a role in determining tree-fall rates on BCI perhaps because the shear strength of soils, particularly clay-rich soils, decreases with increasing soil-moisture content (Hough 1957). However, this is not the entire explanation for increased tree mortality rates during the rainy season since the proportion of trees that uprooted was the same as in the dry season.

Comparison of the ways trees die on BCI and in other parts of the world

The predominant modes of tree death varies from forest to forest. In mesic forests in eastern U.S.A., Runkle (1982) found that of the gap-making trees, 19% were uprooted, 67% snapped, and 10% died standing. Uprooting accounted for only 15% of damage to tropical hardwood plantations in Western Samoa (Wood 1970). In the forests of Sirena and Llorona on the Osa Peninsula in Costa Rica, 37 and 34%, respectively, of fallen trees were uprooted (P.D. Coley, personal observation). During a 5-year period in a *Fagus–Magnolia* forest in Texas, U.S.A., 77% of the trees that died did so before they fell over, 21% snapped, and not a single tree was uprooted (Harcombe and Marks 1983). Trees in the lowland dipterocarp forest in Malaysia mostly died standing; very few were either uprooted or snapped (F. E. Putz and S. Appanah, in preparation). Trees that die standing are also typical in longleaf pine (*Pinus palustris*) forests in Florida, U.S.A. (W. J. Platt, personal communication). In forests in Nigeria uprooting accounted for 30% of the tree falls (Jones 1956). In a fir (*Abies*) forest in California, Gordon (1973) observed that during a 2-year period 25% of the fallen trees uprooted but between-year variability in the proportion of trees uprooting was considerable (12% in 1 year, 72% in the other). In some forests, uprooting predominates over snapping as the major mode of tree fall. In *Tilia–Carpinus* and *Pinus–Quercus* forests in Poland, of the trees that died or fell, 48% uprooted, 7% snapped, and 45% died standing (Falinski 1978). Undoubtedly there are many factors determining whether trees uproot or snap. However, we suggest that wood properties are the most important. For instance, *Fagus*, *Quercus*, *Acer*, and *Carpinus* have sufficiently strong, dense wood that uprooting would be expected.

Not all reports of damage-class proportions fit our predictions. For example, in Warren Woods, Michigan, T. Poulson (personal communication) observed that only 31% of fallen *Acer* and *Fagus* trees uprooted during a tornado in 1979. Boe (1965) observed that more than 75% of fallen trees were uprooted in an old-growth redwood forest in California. Based on wood strength and density we would predict that conifers would be prone to snapping.

Although we found no difference in the proportions of uprooted and snapped trees in a large blowdown and in single tree falls on BCI, the nature and timing of disturbance may also influence whether a tree snaps or uproots.

Ecological significance of sprouting

The high percentage of trees that sprouted after they snapped indicates that snapping need not be fatal. The importance of sprouts in fields abandoned by slash-and-burn agriculturalists (Boaler and Schwale 1966; Kowal 1966; Blum 1968; Webb *et al.* 1972; Gentry 1978) and in forests after logging (Church 1961; Solomon and Blum 1967; Wilson 1968) is well-known, but their role in natural forest dynamics is seldom mentioned (but see Stearns 1949; Jones 1956; Spurr 1956).

Sprouts generally emerged from the tops of broken stems, the best possible location for avoiding aboveground vegetative competition and for regaining their canopy position. Uprooted trees which sprout do not have this positional advantage, but when some roots remain undamaged, the fallen trees are relatively better off below ground than are seedlings. Although sprouts from snapped trees grow faster than seedlings, they are prone to heartrot (Hepting and Hedgecock 1937). Growth rates and the probability of snapping are inversely correlated with wood strength. Sprouting is one means by which weak-wooded trees partially compensate for their propensity to snap.

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