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Tree Damage and Annual Mortality in a Montane Forest in Monteverde, Costa Rica¹

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ABSTRACT

In four hectares of primary montane wet forest in Monteverde, Costa Rica, 1403 live trees (>10 cm diameter at breast height) were censused for major damage and mortality during a four-year period. Overall tree damage and mortality after four years was 15.9 trees ha⁻¹ yr⁻¹, with over 80 percent due to snapping of trunks and uprooting of whole trees. Of the 73 stems that snapped during the study interval, 20 regenerated live foliage from their broken stems. This resulted in an actual mortality rate of 12.7 trees ha⁻¹ yr⁻¹, or 2.2 percent, which is in the mid-range of annual tree mortality reported for other forests. Tree death occurred during all seasons of the year, but rates were highest during the wet season. Individuals of gap-colonizing species died at a higher rate than expected from their representation in the population. This study suggests that although montane sites are subject to high winds and unstable soils, overall rates and types of mortality are similar to lowland forest sites.

Key words: tree mortality; tree crown damage; vegetative regeneration; forest dynamics; montane forest; snags; Monteverde; Costa Rica.

THE LOSS OF TREE CROWNS and the death of whole trees affects forest nutrient cycling, regeneration, and species richness. The frequency and types of small-scale forest disturbances such as loss of crowns and treefalls (hereafter “tree damage”) are determined by local climatic forces, physical characteristics of the substrate, and biological attributes of the trees (Brokaw 1982, Putz & Milton 1982, Putz *et al.* 1983, Denslow 1987, Putz & Brokaw 1989). When whole trees, tree parts, and their associated epiphytes fall to the forest floor, they: cause pulses of organic material and nutrients that can subsequently become available to terrestrially rooted plants (Denslow 1987); increase the biomass of the forest floor, thus creating additional habitats for terrestrial organisms; reduce resources used by arboreal animals and epiphytes, but at the same time creating snags for nesting by key avian seed dispersers (*e.g.*, Wheelwright *et al.* 1984); crush seedlings, saplings, and understory plants (Aide 1987, Gartner 1989, Kinsman 1990); and affect the microclimate of the en-

suing gap that may subsequently deter or facilitate seed germination of some species (Putz & Milton 1982, Brandani *et al.* 1988, Swaine *et al.* 1990).

Although many damaged trees die, some continue to live by producing new shoots from above- or below-ground parts. Regeneration from broken plant segments (hereafter “resprouting”) has been documented in a number of cloud forest trees (Lawton & Putz 1988) and shrubs (Kinsman 1990). Documentation of resprouting in tropical forests is scarce, since most research has centered on regeneration from seeds, seedlings, or clonal regrowth (Clark & Clark 1989, Eriksson & Ehrlén 1992). The species composition of regeneration of gaps depends on the type of disturbance that created the gap (*e.g.*, Connell 1989, Whigham 1991). Resprouting from standing broken stems might replace the lost canopy and affect the form and duration of gap regeneration faster than regeneration from seedlings. The ability to resprout might allow a species to maintain its frequency in the population (Knight 1975, Putz & Brokaw 1989, Whigham *et al.* 1991).

Most studies of tree damage and mortality have been carried out in lowland tropical forests, with relatively few studies in tropical montane forests. The rates and frequency of tree damage might be

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TABLE 1. *Date of initiation and number of months in which tree damage and mortality were measured in the study area. The dates given are when trees were tagged and monitoring began. The final census for all areas was in September 1992. The total number of months of monitoring is in brackets. (N.M. indicates not measured.)*

Location	Stem diameter	
	> 30 cm DBH	10–30 cm DBH
Hectare 1	12–87 [45]	6–89 [39]
Hectare 2	2–87 [45]	N.M.
Hectare 3	5–89 [40]	5–89 [40]
Hectare 4	4–90 [29]	N.M.

expected to be greater in higher elevation forests because of steeper slopes, less stable soil, and exposure to more wind. Plant adaptations to these environmental characteristics might also be expected in montane forests. In this paper, we describe the types, rates, and seasonality of tree damage and mortality, and report the frequency of resprouting of snapped trees in a lower montane forest in Monteverde, Costa Rica.

STUDY SITE

Field work was conducted from April 1987 to September 1992 in a lower montane wet forest (Holdridge 1967) in the Monteverde Cloud Forest Reserve in Costa Rica (10°18'N, 84°48'W) (1480 m in elevation). The study area was in leeward cloud forest (Lawton & Dryer 1980), the floristic composition and structural characteristics of which are described in Nadkarni *et al.* (in press). The forest floor soils are wet throughout the year (Bohlman *et al.* 1995), are derived from volcanic rhyolites, and are classified as Typic Dystrandept (Vance & Nadkarni 1990). The study site encompassed slopes of 5 percent to 20 percent.

This forest is noted for its windiness throughout the year due to its location on the continental divide, with air funnelled through the adjacent Penas Blancas Valley. Wind gusts in the area have been estimated as high as 100 km hr⁻¹ (Lawton & Putz 1988). Although variable from year to year, the climate of Monteverde can be divided into three seasons. The misty-windy season (November–February) is characterized by substantial mist carried by strong northeast trade winds. The dry season (March–April) has strong winds and some cloud water and mist deposition, but low measurable rainfall. The wet season (May–October) is characterized

by low windspeeds and convective storms originating in the Pacific lowlands. Measured annual rainfall is 2000–2500 mm yr⁻¹, but total wet deposition is higher due to substantial wind-driven mist (Hartshorn 1983, Clark & Nadkarni 1990).

METHODS

A four-hectare study area was established and divided into 100 20 × 20 m subplots. Trees were measured and classified by size (diameter at breast height, DBH) and tagged. In two of the hectares, all trees > 10 cm DBH were measured; in two other hectares, all trees > 30 cm DBH were measured (Table 1). Tree locations were ascribed to 20 × 20 m subplots. In April 1990, half of all trees in the study site were identified to species by W. A. Haber and E. Bello (Nadkarni *et al.*, in press). Tagged trees that died before being identified (*i.e.*, prior to April 1990) were designated as unknown. All extant standing broken stems > 10 cm DBH were tagged and numbered.

In our frequent visits to the study area (*ca.* two times per week), we made note of the trees that sustained major crown damage, snapped, or fell. We censused the entire site for damaged, snapped, or fallen trees annually (September 1990, 1991, and 1992). Tree damage and mortality were divided into five categories: standing broken stems—classified by the height of the break relative to the total tree height (high, middle, low); uproot—fallen trees with exposed root-balls; knockdown—a broken or uprooted tree falling as a result of a neighboring tree hitting it; standing dead—tree dead, but stem not broken or uprooted; or missing—tree that was not found again. During the final census, all standing broken stems were checked for evidence of sprouting of foliage anywhere on the stem. Stems with foliage were recorded alive, and those with no evidence of sprouting of foliage were recorded as dead.

We recorded the standing broken stems that fell to the ground during the study period. Longevity of standing broken stems was calculated by counting the number of months between the time of damage and when we noted the stem fallen to the ground. We could not be certain of the actual time of falling for 8 of the 16 standing broken stems that fell.

RESULTS

TREE DAMAGE AND MORTALITY.—Of the 1403 live trees (742 10–30 cm DBH, 661 > 30 cm DBH)

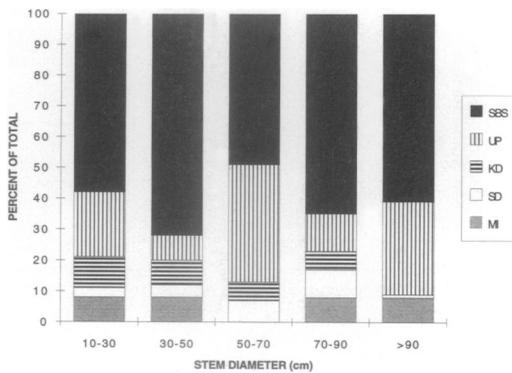


FIGURE 1. Size class distribution (percent of total stems) of the 147 trees that were damaged or died during the study divided into five categories (MI, missing; SD, standing dead; KD, knockdown; UP, uproot; SBS, standing broken stem).

tagged in the four-ha research area, 147 were severely damaged during the four-yr study period. The mean number of damaged and dead trees was 15.9 trees ha⁻¹ (std = 6.2) (9.9 10–30 cm DBH, 6.0 > 30 cm DBH) or 2.8 percent of the tagged trees. Of these, 61 percent suffered broken stems, 22 percent were uprooted, 7 percent were knocked down, 4 percent were standing dead, and 10 percent were missing (Fig. 1). The 91 standing broken stems that were created during the study period were divided into three height categories: high-break (35%), mid-break (32%), and low-break (33%). The proportions of standing broken stems by DBH relative to the total tagged population was significantly different from random ($X^2 = 11.7$, $P < 0.01$), with more damaged and dead stems in the larger size classes than expected (Fig. 2). The total number of extant standing broken stems (stems already broken when tagged) was 77 (19.3 per ha) (std = 6.9), or 5 percent of the total number of tagged trees.

Seasonality of tree damage was determined by pooling the number of damaged stems by the season in which they were damaged, regardless of year. (The time of damage of 29 percent of the trees could not be determined and were not included in the calculations.) The largest proportion of damage occurred during the 6-month wet season (47%), intermediate amounts in the 2-month dry season (31%), and lowest in the 4-month windy-misty season (22%). This trend is consistent with the calculated monthly rates, which compensate for the unequal number of months in each season (Table 2).

Of the trees that were damaged or died during

TABLE 2. The number of trees sustaining damage by season expressed as an average per month to compensate for the unequal number of months in each season. The time of damage of 43 of the 147 trees could not be determined, and are not included in the calculations. The misty-windy season is November–February, wet season is May–October, and dry season is March–April. Damage types: standing broken stem (SBS), uproot (UP), knock-down (KD).

Season	SBS	UP	KD	Total
Wet	3.5	3.2	1.0	11.3
Dry	2.5	2.0	1.5	7.5
Misty-windy	3.0	1.8	0.3	5.3

the study, 73 (50%) were identified to species. They represented 19 plant families, 20 genera, and 21 species. Trees in most of the plant families were damaged at similar proportions to that expected from their distribution in the live population (Table 3). Trees in seven plant families, however, sustained damage at strikingly higher rates than expected (their proportion of individuals in the pool of damaged stems was more than twice their proportion in the total marked population). Nearly all of these were gap-colonizing, rapid-growing, short-lived trees (Table 4).

REGROWTH OF DAMAGED TREES AND “TRUE” TREE MORTALITY.—Of the 91 standing broken stems that were created during the study, 30 (34%) had live sprouts (resprouted) by the final census. Of these, most were high-breaks (43%) or mid-breaks (40%), whereas only 17 percent of the standing broken stems that were low-breaks had resprouted. One uprooted tree resprouted.

The identified damaged trees that resprouted were in 10 plant families; those that did not resprout were in 19 families (Table 3). Two of the most common genera (*Ocotea* and *Guarea*) accounted for 50 percent of the damaged trees that resprouted.

Of the 147 trees damaged, snapped, or fallen during the study, 116 appeared to be dead, as there was no evidence of resprouting. This “true mortality” was due to standing broken stems that did not resprout (53%), followed by uproots that did not resprout (28%), knock-downs (7%), extant standing dead (3%), and 9 percent due to missing trees that were presumed dead. The mean annual mortality was 12.7 trees ha⁻¹ (std = 5.9) (8.2 for 10–30 cm DBH, 4.6 for > 30 cm DBH). This is equivalent to an annual true mortality of 2.2 percent for all size classes (2.1% for 10–30 cm DBH, 2.8% for > 30 cm DBH). The expectation of further life

TABLE 3. *The composition of damaged trees by family. The percent of the total trees damaged, not resprouted, resprouted, and proportion of all tagged trees. The total number of individuals in each category is shown at the bottom. (Calculations do not include the 74 unidentified damaged trees in the study site.)*

Family	Damaged trees			All trees
	Total	Not re-sprouted	Re-sprouted	
Annonaceae	2.7	3.8	—	1.4
Aquifoliaceae	1.4	1.9	—	0.7
Araliaceae	1.4	1.9	—	0.2
Asteraceae	4.1	5.7	—	2.7
Bombacaceae	2.7	3.8	—	2.7
Boraginaceae	2.7	3.8	—	1.9
Cecropiaceae	12.3	13.2	10.0	6.1
Flacourtiaceae	4.1	3.8	5.0	3.2
Lauraceae	17.8	13.2	30.0	14.5
Malvaceae	6.8	7.5	5.0	2.3
Melastomataceae	4.1	3.8	5.0	4.2
Meliaceae	5.5	—	20.0	6.6
Moraceae	4.1	3.8	5.0	2.0
Myrsinaceae	2.7	1.9	5.0	5.5
Myrtaceae	4.1	5.7	—	1.7
Rubiaceae	4.1	5.7	—	5.7
Tiliaceae	13.7	1.7	5.0	2.1
Urticaceae	4.1	1.9	10.0	1.6
Verbenaceae	1.4	1.9	—	0.6
Total number of trees	73	53	20	1403

TABLE 4. *The percent mortality and regeneration of the five most common tree species in the study site (and those with the highest rate of damage). Percent of stem density within the population; percent of stems damaged relative to the total population; number of stems damaged, percent of regeneration of damaged stems, number of stems that regenerated.*

Genus	Total live pop (%)	Dead		Regenerated		Temperament
		%	No.	%	No.	
All damaged trees	8.0	100	148	21	(31)	All
Ocotea	13.3	8	13	46	(6)	Climax
Guarea	7.6	9	8	50	(4)	Climax
Conostegia	4.4	4	2	50	(1)	Climax
Cecropia	7.1	12	10	39	(3)	Pioneer
Hampea	2.8	16	5	20	(1)	Pioneer
Heliocarpus	2.5	24	7	14	(1)	Pioneer

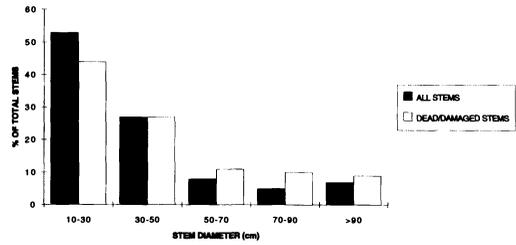


FIGURE 2. Proportional size class distributions of all trees (black bars) and of the 90 trees that died during the three-year study (white bars).

(calculated as the inverse of the average proportion of trees dying per year, Putz & Milton 1982) was 43.8 yr overall (48.3 yr for 10–30 cm DBH, 34.6 for > 30 cm DBH). Turnover time was calculated as the number of years necessary for all of the originally inventoried trees to die [number of originally tagged trees/(number of dead and snapped trees/time observed)] (Uhl 1982) and was 55.5 yr for 10–30 cm DBH, and 42.4 yr for trees >30 cm DBH.

We considered the population of standing broken trees in the original census separately from those that were created during the study period since the original standing broken stems were of undeterminable age. Of the 77 original standing broken stems, 69 percent remained standing, 18 percent fell, and 13 percent resprouted during the 4 yr of the study. The mean “longevity” (the amount of time dead standing stems remained standing) was 16.3 mo. This is an estimate because we were uncertain of the exact date of falling for half of the fallen broken stems.

DISCUSSION

The rate of true annual mortality in this study (2.2%) is in the mid-range of annual mortality rates of other tropical forests (1–3%) (Putz & Milton 1982, Uhl 1982, Brown *et al.* 1983, Lang & Knight 1983, Higuchi 1987, Manokaran & Kochummen 1987, Hartshorn 1990, Lieberman *et al.* 1990, Swaine *et al.* 1990), most of which are from lowland tropical regions. The length of expectation of further life, turnover rates, and seasonality of tree damage and death were also within the range of those documented for other forests.

The wet steep slopes of montane sites, coupled with strong seasonal winds and high epiphyte loads

might be expected to increase the incidence of tree damage. Mountain sites have higher epiphyte loads (Pócs 1980, Tanner 1980, Nadkarni 1984) and larger "rain loads" that add weight (Gloyne 1968) and possibly promote tree breakage. The rates of tree damage and mortality during the study period, however, were within the same range as lowland sites that experience less wind, have flatter topography, and support lower epiphyte loads (Putz & Milton 1982, Manokaran & Kochummen 1987, Lieberman *et al.* 1990).

The mode of damage and death in our site was also quite similar to some other tropical forests. In our study area, 65 percent of the seriously damaged trees snapped and 22 percent were uprooted. In the nearby elfin woodland on the windward side of the mountain, Lawton and Putz (1988) reported that 39 percent of treefall gaps resulted from snaps, and 41 percent from uproots. On Barro Colorado Island (BCI), Panama, a 1980 study reported 52 percent snapped and 17 percent uprooted (Putz & Milton 1982). In another study on BCI, 70 percent of mortality was attributed to snaps, and 25 percent to uproots (Putz *et al.* 1983). In Cocha Cashu, a Central Amazonian lowland forest, 46 percent of dead trees were snapped (Rankin-De-Merona *et al.* 1990). In La Selva, Costa Rica, in contrast, Lieberman and Lieberman (1987) reported that fallen dead trees (uproots and snaps combined) was 31 percent of total mortality.

The major difference between our montane site and the lowland sites described in the literature was that few trees died standing in the Monteverde forest (3% of total mortality), whereas this is far more common in some lowland tropical sites (Putz & Appanah 1987). For example, La Selva had 26 percent of mortality as standing dead (Lieberman & Lieberman 1987); Cocha Cashu, 25 percent (Rankin-De-Merona *et al.* 1990); Barro Colorado Island, Panama, 15 percent (Putz & Milton 1982); and tierra firme forest in Venezuela, 10 percent (Uhl 1982).

We documented that one-third of the standing broken stems formed during our study period resprouted (Table 3). Only a few studies have measured this phenomenon or incorporated it into their calculations of tree mortality so that the rates of annual "mortality" reported in some studies may overestimate actual tree mortality. Resprouting would be expected to be more common where wind and/or forceful storms are frequent agents of disturbance, such as in montane forests. In the forest

on BCI and on the Yucatan Peninsula, for example, frequent disturbance is thought to lead to local dominance by species that recover quickly from injury (Knight 1975, Putz & Brokaw 1989, Whigham *et al.* 1991). As predicted, the common main canopy species in Monteverde were those that sprout readily (Table 3).

Our data generally support the trend that in mature forests, gap-colonizing species suffer higher mortality rates than other taxa (Manokaran & Kochummen 1987) (Tables 3 and 4). The pioneer species *Cecropia polyplebia* (Cecropiaceae), *Hampea appendiculata* (Malvaceae) and *Heliocarpus appendiculatus* (Tiliaceae) had higher mortality rates and lower resprouting rates than the main canopy ("climax") species *Ocotea tonduzii* (Lauraceae) (Table 4).

Ocotea tonduzii, the most common species in our site (10% of basal area) had the highest incidence of damage of the climax species as well as the highest proportion of damaged trees that resprouted (46% of snapped trees). Gap regeneration could be affected by the incidence of trees that are capable of resprouting after snapping versus those that snap and die, thus needing to rely on regeneration from seeds and seedlings (Putz & Brokaw 1989). The ability to resprout could help maintain the dominance of common species, such as *O. tonduzii*, in the population. Live standing broken stems of *O. tonduzii* are important nesting sites for important local bird species such as the resplendent quetzal.

Long-term data are needed to record such phenomena as resprouting of broken stems and attrition of dead standing stems that appear to occur on a time scale of several years to several decades. More studies are also needed in other tropical montane forests for comparison with these results and to help determine the processes affecting the species richness and forest dynamics.

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