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SHORT COMMUNICATIONS

Defoliation of an island (Guam, Mariana Archipelago, Western Pacific Ocean) following a saltspray-laden 'dry' typhoon

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Tropical cyclonic storms with sustained winds above 120 km h^{-1} are called hurricanes, typhoons or cyclones depending on their geographic location. They can cause considerable damage to forests. This damage may be in the form of pruned and fallen trees from intense winds (Boucher *et al*. 1990, Walker *et al*. 1992), defoliation from a combination of winds and torrential rains (Vandermeer *et al*. 1997), or mortality from marine inundation of low-lying land (Gardner *et al*. 1991). Occasionally, extensive defoliation of forests can also occur from wind-driven saltwater when winds are onshore and precipitation is insufficient to dilute the seaspray (Chen & Horng 1993). Below I report the dramatic consequences of an unusual seaspray-laden typhoon on the vegetation of the western Micronesian island of Guam.

Guam (14°N, 145°E) is the southernmost island in the Mariana Archipelago and lies approximately 1800 km east of the Philippines (Figure 1). Comprehensive treatments of Guam's vegetation are found in Fosberg (1960), Stone (1970), Raulerson & Rinehart (1991, 1992), and Mueller-Dombois & Fosberg (1998). The island lies near the centre of the cyclonic-storm basin in the western North Pacific Ocean and has experienced gale-force winds (>60 km h^{-1}), nearly always from cyclonic storms, on average once per year since 1945

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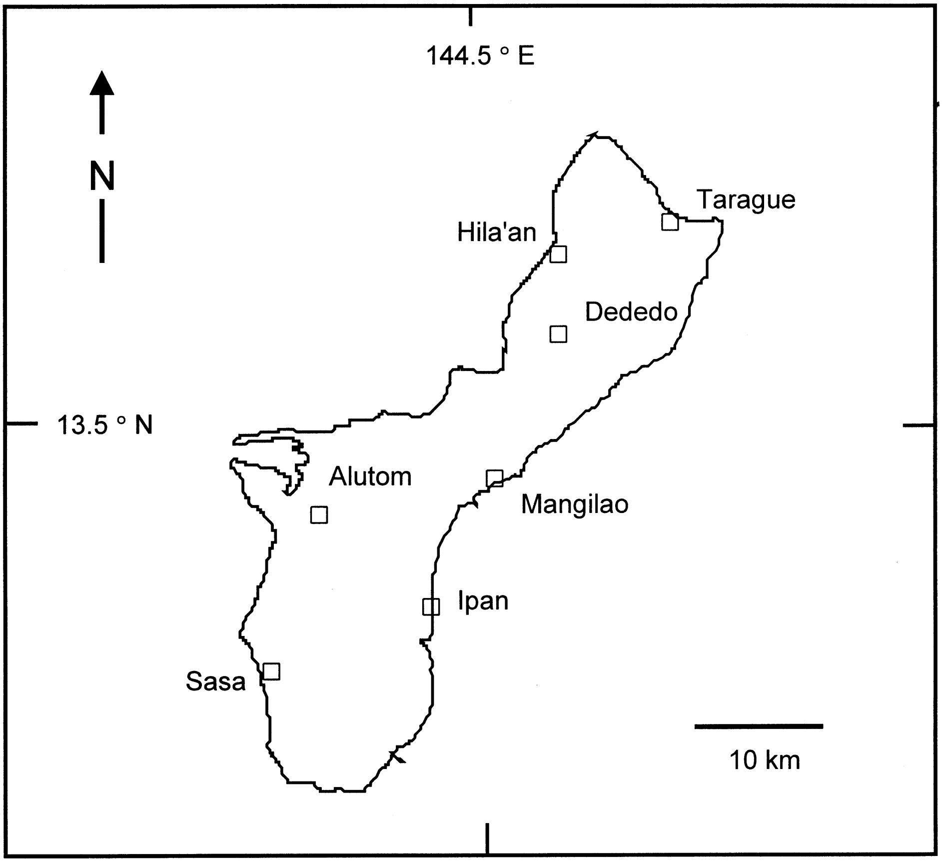

Figure 1. Map of Guam, Mariana Islands, showing general location of plots used in qualitative assessments.

(USNOCC/JTWC 1990a). On 23 November 1992, the northern eye wall of Typhoon Gay with maximum sustained winds of 155 km h^{-1} passed over central Guam. As the wall approached the island, interaction with an adjacent, but distant typhoon disorganized Gay's thunderstorm structure, resulting in an unusual, nearly rainless 'dry' typhoon (USNOCC/JTWC 1993).

For seven sites around Guam (Figure 1), I qualitatively assessed the extent of defoliation of numerically dominant plant species (> 25 plants per site) three days following the passage of Typhoon Gay. I used 1-h meandering traverses through *c.* 1-ha plots in beach strand, residential/cultivated areas, native forest and savanna. Damage (browning and defoliation) to a species at a site was considered light if < 33% of the combined leaf area of all trees from a species was damage. Damage was considered moderate if plants lost from 33 to 67% green foliage, and categorized as severe if the combined leaf area was greater than 67% damaged. Most plants, though, were fully browned or without leaves, making scoring unambiguous and analyses of variance uninformative.

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The surveys, as well as an informal inspection of hillsides and plateaux islandwide, confirmed that the 540-km^2 island was almost completely defoliated by Typhoon Gay (Table 1). The light rain permitted salt spray driven by high winds to douse the narrow island, only 15 km at its widest, leaving exposed surfaces visibly coated with salt. Leaves on most dicot trees withered and fell within two days after the storm. In contrast, wind- and rain-defoliated trees often retain a few green leaves and begin greening shortly after a storm (Vandermeer *et al*. 1997). Other taxa on Guam such as palms, cycads and gymnosperms turned brown, but retained their foliage. Despite local winds gusting to 190 km h^{-1} (USNOCC/JTWC 1993), Typhoon Gay resulted in few windthrown trees or snapped branches. Most susceptible trees appeared to have been thrown or pruned by the six typhoons passing near or directly over Guam within the previous 2 y (A. Kerr, *pers. obs*.). Hence, damage to the vegetation appeared limited to defoliation from wind-driven seawater.

Despite Guam's location near the centre of the earth's most active cyclonic-storm basin (Frank 1988), island-wide defoliation from salt-laden typhoons appears to be a rare event. Only two other saltspray-laden typhoons have been recorded in the southern Mariana Islands since severe typhoons were first recorded there in 1671 (USNOCC/JTWC 1990a). In 1864 on Guam and in 1913 on the neighbouring island of Rota, typhoons accompanied by low precipitation left the islands 'coated with a salt rime' that devastated crops and trees (USNOCC/JTWC 1990a). In each of the three recorded instances, including that reported here, only one island, either Guam or Rota, was affected by salt spray. This occurred despite the islands' close proximity (35 km) and their small size relative to the diameter of a typical typhoon's inner wind field (>150 km). This suggests that salt-spray laden winds are usually quite localized within the wind field of a cyclonic storm.

Beach-strand vegetation withstands constant low-level exposure to salt spray and hence was initially expected to fare better than either native forest or introduced disturbed-ground and cultivated species. However, following the acute, typhoon-related dousing, the strand was completely defoliated (Table 1). Extensive shredding and subsequent browning of the fronds of a strand dominant *Cocos nucifera* L. by previous typhoons prevented a reliable tally of damage to this species by salt spray. The surveyed strand dominants, *Tournefortia argentea* and *Scaevola sericea*, have downy and lightly sclerotized leaves, respectively, yet neither form averted complete desiccation following the dry typhoon.

In contrast to beach strand, damage to native forest was less uniform. One possible reason for this difference is that coastal areas and the strand were more exposed to salt spray than were inland vegetation zones. This seems unlikely as defoliation to inland forest (Dededo) rivalled that of the most exposed coastal forest site (Mangilao). Several understorey forest species (*Cycas circinalis*, *Mammea odorata*, *Pandanus tectorius*, *Triphasia trifolia* and epiphytic

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Table 1. Severity of defoliation in hectare plots on Guam after Typhoon Gay. Lit: < 33% of the combined leaf area of species at a site experienced damage (browning or defoliation), Mod: 33 to 67% damaged, Sev: > 67% damaged, a dash indicates that the species was absent or too infrequent to be surveyed. ST: tree < 15 m height, TT: tree > 15 m, S: shrub < 5 m, H: herb or grass, V: vine.

Habitat		Site						
Species	Growth form	Alutom	Dededo	Hila'an	Ipan	Mangilao	Sasa	Tarague
Strand								
Cordia subcordata Lam.	TT	—	—	Sev	Sev	—	—	—
Guettarda speciosa L.	TT	—		—	—	—	Sev	—
Hernandia sonora L.	TT	—	—	Sev	Sev	—	Sev	Sev
Hibiscus tiliaceus L.	ST	—	Sev	—	Sev	Sev	Sev	Sev
Scaevola sericea Vahl	S	—	—	Sev	Sev	Sev	Sev	Sev
Tournefortia argentea L. f.	S	—	—	Sev	Sev	Sev	Sev	Sev
Savanna								
Casuarina equisetifolia L.	TT	Sev	—	—	Sev	—	Sev	Sev
Dimeria chloridiformis (Gaud.) K. Schum. & Lauterb.[1]	H	Sev	—	—	—	—	—	—
Miscanthus floridulus (Gaud.) Warburg	H	Sev	—	—	—	—	—	—
Stachytarpheta indica (L.) Vahl	H	Sev	—	—	—	—	—	—
Disturbed ground or cultivated								
Artocarpus altilis (Parkinson) Fosb.	TT	—	Sev	—	—	Sev	—	Sev
Bambusa vulgaris Schrad	TT	—	—	—	—	Sev	Sev	—
Carica papaya L.	ST	—	Sev	Sev	Sev	Sev	Sev	Sev
Chrysopogon aciculatus (Retz.) Trin.	H	Sev	—	—	—	Sev	—	—
Leucaena leucocephala (Lam.) De Wit	ST	Sev	Sev	—	Sev	Sev	—	Sev
Juniperus sp.	S	—	Sev	—	—	Sev	—	—
Mikania scandens (L.) Willd.	H	—	Sev	—	—	Sev	—	Sev
Musa spp.	ST	—	Sev	—	—	Sev	—	—
Native Forest								
Aglaia mariannensis Merr.	ST	—	Sev	Sev	—	Sev	—	Sev
Artocarpus mariannensis Trécul	TT	—	Sev	—	—	—	—	—
Chloris inflata Link	H	—	Sev	—	—	Sev	—	Sev
Cycas circinalis L.	ST	—	Lit	Lit	—	Lit	—	Lit
Cynometra ramifolia L.	ST	—	—	Sev	—	Sev	Sev	Sev
Epiphytic Pteridophyta[2]	H	—	Lit	Mod	Sev	Mod	Lit	Lit
Eugenia reinwardtiana DC.[1]	ST	—	Sev	Sev	—	Sev	—	Mod
Ficus spp.[3]	TT	—	Sev	Sev	Sev	Sev	—	Sev
Flagellaria indica L.	V	—	Sev	Mod	—	Mod	Sev	Mod
Guamia mariannae (Saff.) Merr.[1]	ST	—	Sev	Sev	—	Sev	—	Sev
Mammea odorata (Raf.) Kosterm.	ST	—	Lit	Lit	—	—	—	Lit
Maytenus thompsonii (Merr.) Fosb.[1]	ST	—	Sev	Sev	—	Sev	—	Sev
Merrilliodendron megacarpum (Hemsl.) Sleum.[a]	TT	—	—	Sev	—	—	—	—
Morinda citrifolia L.	ST	—	Mod	Sev	—	Sev	—	Sev
Nephrolepis hirsutula (G. Forst.) C. Presl	H	—	Sev	—	—	Sev	Mod	Sev
Pandanus tectorius Parkinson	TT	—	Lit	Lit	—	Lit	—	Lit
Piper guahamense DC.[1]	H	—	Lit	—	—	Mod	Lit	—
Pisonia grandis R. B.	TT	—	Sev	Sev	—	Sev	—	Sev
Thelypteris interrupta (Willd.) Iwatsuki	H	—	Mod	—	—	—	Sev	—
Triphasia trifolia (Burm. f.) P. Wils.	S	—	Lit	Mod	—	Lit	Lit	Lit

[1]Endemic to the Mariana Archipelago.
[2] *Asplenium nidus* L., *Davallia solida* (G. Forst.) Sw. *Polypodium punctatum* L., *P. scolopendria* Burm. and *Pyrrosia lanceolata* (L.) Farwell.
[3]*F. prolixa* G. Forst. *F. tinctoria* G. Forst. and *F. microcarpa* L.f. var. *saffordii* (Merr.) Corner.

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pteridophytes) incurred variable damage (Table 1). It is unclear whether this is solely a result of greater resistance via their heavily sclerotized fronds and leaves or whether the understorey of the forest additionally offered refuge from the salty winds (Imbert *et al*. 1996). Nevertheless, many individuals of these species were severely affected and most other forest trees were completely defoliated. Note that the severity of defoliation made it difficult to identify some trees and probably explains the absence from the tally of otherwise prevalent forest species (e.g. *Cynometra ramiflora* L., *Macaranga thompsonii* Merr., *Neisosperma oppositifolia* (Lam.) Fosberg & Sachet, *Premna obtusifolia* R. Brown, *Psychotria mariannensis* Safford).

The island's vegetation appeared completely refoliated within one year. Within this time, I observed no stand-level mortality and death of isolated trees appeared limited to specimens in exposed locations such as residential areas, savannas and cliff-lines. However, extensive crown dieback was evident among the tallest individuals of the canopy-forming forest and backstrand (*Artocarpus mariannensis*, *Pisonia grandis*, *Ficus prolixa*, *Hernandia sonora*, *Cordia subcordata*). These trees generally lost the uppermost 2 to 3 m of crown foliage, as did monospecific stands of smaller trees such as *Leucaena leucocephala*. In all cases, the branches involved did not releaf and had clearly died.

The dry typhoon may have affected the forest in other ways, as well. For example, cyclonic storms can variably affect populations of forest invertebrates (Futura 1989, Willeg & Camillo 1991, McMahon & Blanton 1993, Secrest *et al*. 1996). On Guam, qualitatively noticeable increases in the abundance of litter-inhabiting fungus gnats (Sciaridae: cf. *Lobosciara* sp.) were apparent in the weeks following the defoliation by Typhoon Gay. In the weeks following the storm, windrows of the dead insects collected along shorelines and in wind eddies near buildings. According to long-time residents of the island, such an outbreak had not been observed within at least the last 50 y.

Isolating the effects of the salt spray on Guam's vegetation is confounded by the passage of several other storms. Within the 2 y prior to Typhoon Gay, six other typhoons, all with maximum sustained winds >120 km h^{-1}, passed over the island, three of them within 3 mo (USNOCC/JTWC 1990b–1993). Severe storms can alter below-ground nutrient pools through litter accumulation (Lodge *et al*. 1991), affect the outcome of competitive interactions (Vandermeer *et al*. 1996) and increase susceptibility to disease and herbivory (Everham & Brokaw 1996). It is possible that the vegetation of Guam was similarly affected by the numerous previous storms and that these factors indirectly contributed to the severity of the defoliation or the ability of the vegetation to recover. In addition, there may be less obvious future effects on growth, reproduction and species interactions.

Regardless, the observations reported here corroborate the empirical generalizations that the long-term consequences of severe storms can be more subtle than are suggested by the potentially catastrophic immediate effects (Basnet

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et al. 1992, Bellingham *et al*. 1995) and that a plant's ability to recover from damage can be more important than resisting such damage (Boucher *et al*. 1994). On Guam, defoliation was islandwide, severe, and appeared unrelated to a plant's ability to survive chronic, low-level exposure to saltspray. Strand species and forest endemics were about as likely to suffer damage as introduced taxa, though physical refuge and sclerophyllous leaves may have attenuated desiccation in some species. Yet, despite the vast defoliation, there was no stand-level mortality and most trees had regreened within one year.

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