Wetlands (2010) 30:1077–1084
DOI 10.1007/s13157-010-0114-y

ARTICLE

Micronesian Mangrove Forest Structure and Tree Responses to a Severe Typhoon

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Received: 30 November 2009 / Accepted: 7 October 2010 / Published online: 12 November 2010

Abstract Tropical cyclones are common disturbances that have strong effects on mangrove composition and structure. Because there are numerous ecosystem services provided by mangroves, it is important to understand their adaptations and responses to these climatic events. In April 2004, Typhoon Sudal, a category 3–4 cyclone, passed over the state of Yap, Federated States of Micronesia. For four months following the typhoon we measured forest structure, above-ground biomass, tree mortality and response in six mangroves. The sites were dominated by species common in mangroves throughout the Indo-Pacific—*Sonneratia alba, Brugueira gymnorrhiza*, and *Rhizophora apiculata.* Total above-ground biomass (TAGB) of mangrove forests ranged from 211–573 Mg ha^{-1}. Tree mortality ranged from 6% to 32% among stands. Adaptations and responses to the typhoon varied by species, as well as by geographic location. *Sonneratia alba* had a higher frequency of mainstems broken (26%), but was the only species that vigorously sprouted from dormant basal or epicormic tissues. Standing live trees accounted for 80–95% of TAGB, suggesting that adaptations of mangrove trees can facilitate the persistence of an intact forest structure following typhoons of this intensity. Climatic changes such as sea level rise and increased severity of cyclonic events could alter this relationship.

Keywords Allometric equations · Disturbance ecology · Plant adaptations · Total above-ground biomass · Tropical wetlands · Typhoon impacts

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Introduction

Mangroves are important wetland ecosystems throughout the tropical and subtropical coastal areas of the world (Mitsch and Gosselink 2000), providing a variety of ecosystem services such as sources of food (fishes, crabs, etc.), wood, and protection from extreme events such as cyclones and tsunamis (Giesen et al. 2006). Tropical cyclones (typhoons) affect ecosystem structure in tropical coastal ecosystems in many islands of the western Pacific. In order to persist in an environment, the biota must possess adaptations that facilitate survival of such severe natural disturbances.

Most studies on the impacts of tropical cyclones on ecosystems have been conducted in the southern United States (Tilmant et al. 1994, Davis et al. 2004), the Caribbean (Sherman et al. 2001, Ostertag et al. 2003), and Central America (Fenner 1991, Cahoon et al. 2003). Despite the fact that typhoons are major, natural disturbances in the western Pacific (Schneider 1967), few studies have focused on the ecological and physical effects of typhoons on Pacific islands. Over the past 40 years, an average of ≈ 18 destructive typhoons have passed through the region annually (Furze and Preble 2003). Furthermore, based on a range of models, it is likely that future tropical cyclones will become more intense, with greater peak wind speeds and more heavy precipitation associated with ongoing increases of tropical sea surface temperatures (IPCC 2007).

Increased typhoon intensity associated with climate change could have severe negative consequences on Pacific islands because land areas are typically small and very isolated from continents and other islands which would affect recolonization rates and processes. Because of their importance as natural disturbances and potential interactions with anthropogenic perturbations of island ecosystems, it is important to better understand how Pacific Island ecosystems are affected by, and respond to typhoons. Our understanding of disturbance impacts and mangrove forest values is further limited by a lack of adequate allometric equations to predict aboveground biomass of trees which may have trunk diameters exceeding 1m (Saenger and Snedaker 1993, Komiyama et al. 2008).

The objectives of this study were to examine the effects of a severe typhoon on mangrove composition and structure in Micronesia, and to describe the short-term responses of the dominant mangrove tree species to the typhoon. In order to describe mangrove forest structure it was necessary to develop robust allometric equations to determine aboveground mangrove tree biomass for species of this region. We hypothesized that mangrove forest mortality and structural effects would vary among different stands due to differences in their location on the island, and their differences in species composition

Study Area

The study was conducted in Yap, the westernmost state of the Federated States of Micronesia (9°33′ N, 138°09′ E). Yap is composed of four islands separated only by mangrove-lined channels. The total land area is about 9700 ha. Mangrove forests comprise about 12% of the land area. The climate in Yap is humid, warm and tropical, with an average annual temperature of 27°C and an average rainfall of 3000 mm y^{-1}. The heaviest rains occur between June and October, while the months of November to May are drier with strong east to north-east tradewinds.

On 9 April 2004, Typhoon Sudal passed over the State of Yap, Federated States of Micronesia. The duration of the extreme weather event was approximately five hours. The storm over Yap had wind speeds ranging from 119 to 151 km h^{-1} along the north shore (leeward side), 155–161 km h^{-1} on the eastern shore, and 177–209 km h^{-1} on the southern shore (windward side) (Prior and Guard 2005). The typhoon hit Yap during a high, spring tide and as a result many of the lowland areas were submerged under 2–4 m of water or damaged by wave action (Mark Lander, University of Guam, pers. comm.).

In August 2004, we sampled six different mangrove forests dispersed throughout the perimeter of the islands that constitute Yap. Three of the sites were located on the windward (southern and eastern) coasts and three were located on the leeward (north-western) coasts. These sites were Qamun, Qaaf and Tabinifiy (windward), and Ruunuw, Qatliw and Maaq (leeward). Wind speeds during the typhoon were lower on leeward sites than the windward sites (Prior and Guard 2005).

Methods

In each of the six sites, we sampled forest structure and wood debris mass in five 6-m radius (0.0113 ha) circular plots established every 50 m along a 200-m transect. The initial starting point of each transect was ~10 m from the forest/seagrass ecotone. Transects were established perpendicular to the forest ecotone and at least 100 m away from the ecotones of other coastal communities (e.g., rock shoreline without mangrove). The start point and transect direction was selected prior to entering the mangrove stand minimizing any a priori knowledge of stand composition or condition.

The diameter at 1.3 m in height (dbh) and the species of all trees that were rooted in the plots were measured. If the trees were multi-stemmed, each individual stem was measured. From these data we calculated site characteristics of the stands (species composition, basal area, stand density, and tree biomass). Tree biomass was determined using species-specific allometric equations where diameter was the independent variable (Table 1). These equations were developed for this study from mangrove data collected from the Micronesian islands of Pohnpei, Yap, Kosrae, and Palau by Cole et al. (1999). The maximum diameters of trees included in these equations were 132 cm for *Bruguiera gymnorrhiza* (L.) Lamk, 323 cm for *Sonneratia alba* J.E. Smith, and 60 cm for *Rhizophora apiculata* Bl. The total number of trees included in these equations were 327, 346, and 191, respectively (Cole et al. 1999). Most previous published equations are limited by smaller sample sizes (<104) and a maximum diameter of 49 cm (Komiyama et al. 2008). Prop root biomass for *Rhizophora apiculata,* and leaf biomass for all species were calculated from published equations (Table 1, Clough and Scott 1989).

The effects of the typhoon and the response of each individual tree in each plot were recorded. Methods of ascertaining tree damage were similar to those of Franklin et al. (2004). We first recorded if the tree was alive or dead. We also examined each tree for the following categorical (yes/no) types of damage: (1) crown damage (loss of leaves and fine stems); (2) snapped (main stems broken off by the typhoon and the height at which they were broken); (3) wind-thrown—either uprooted by the typhoon or leaning (when the tree was uprooted but leaning on other trees); and (4) no discernable damage to the tree. Tree responses included: (1) crown refoliated (tree canopy has produced new foliage); (2) epicormic sprouts (new stems and

Table 1 Equations to determine components of total above-ground biomass (TAGB) of mangrove forests in Yap, Federated States of Micronesia

Species and plant part	Equation
Live wood volume (m^3)[a]	
Bruguiera gymnorrhiza	V_{wood}=0.0000754(D)$^{2.50}$ (R^2=0.84)
Sonneratia alba	V_{wood}=0.0003841(D)$^{2.10}$ (R^2=0.78)
Rhizophora spp.	V_{wood}=0.0000695(D)$^{2.64}$ (R^2=0.96)
Live wood biomass (kg)	$AGB_{wood}=V_{wood}\times Sg\times 1000$[b]
Leaf biomass (kg)[c]	
Bruguiera gymnorrhiza[d]	$AGB_{leaf} = 10^{(-1.1679+1.4914\times\log(D))}$
Rhizophora spp.	$AGB_{leaf} = 10^{(-1.8571+2.1072\times\log(D))}$
Prop root biomass (kg)[e]	
D≤5.0 cm	$AGB_{p.root}=AGB_{wood}$ * 0.101
D>5.0≤10 cm	$AGB_{p.root}=AGB_{wood}$ * 0.204
D>10≤15.0 cm	$AGB_{p.root}=AGB_{wood}$ * 0.356
D>15≤20.0 cm	$AGB_{p.root}=AGB_{wood}$ * 0.273
D>20 cm	$AGB_{p.root}=AGB_{wood}$ * 0.210
Wood debris biomass (Mg)	
≥7.6 cm diameter	$Sg*100\left(\left(\pi^2\sum D^2\right)/(8L_t)\right)$
>2.55–7.5 cm diameter	Sg * 100((π^2NQMD^2)/(8L))
>0.65–2.54 cm diameter	Sg * 100((π^2NQMD^2)/(8L))
≤0.64 cm diameter	Sg * 100((π^2NQMD^2)/(8L))

Definitions for symbols used in the equations are: V_{wood}=live wood volume (m^3), AGB=aboveground biomass, Sg=specific gravity (g/cm^3), D=diameter of downed wood particles (cm), *N*=number of pieces of wood present along the transect, QMD=quadratic mean diameter of the downed wood particle size class (cm) and L=the transect length (cm)

[a] Wood volume equations developed for this study were a reanalysis of data from Cole et al. (1999)

[b] Specific gravities to convert volume to wood biomass are from Hidayat and Simpson (1994), Simpson (1996). Sg (g/cm^3) by species are: *Bruguiera*=0.84, *Sonneratia* = 0.78, and *Rhizophora* = 0.96

[c] Equations are from Clough and Scott (1989)

[d] Equation also used for *Sonneratia*

[e] *Rhizophora* prop root biomass ($AGB_{p.\ root}$) as a percentage of AGB_{wood}, were derived from Clough and Scott, (1989)

branches being produced from dormant meristematic tissues on trunks and mainstems); (3) basal sprouting (new branches arising from below-ground tissues or those at the base of the tree); and (4) no response. Overall tree mortality was calculated for each site and the mortality by species with all sites combined was also determined. For each species we also calculated the type and extent of damage, and their post-typhoon response.

Biomass of dead and downed wood was non-destructively sampled using the planar intercept technique (Van Wagner 1968, Brown and Roussopoulous 1974, Kauffman et al. 1998). In each of the first four plots we established four transects in directions that were 45° off the main transect (n=16 transects per site).

We partitioned the downed wood into size classes based on their diameter. The diameter classes and equations used to partition woody debris were the same as those of Kauffman et al. (1995) and Guild et al. (1998) for determination of woody debris in upland tropical forests: 0–0.64 cm diam., 0.65–2.54 cm diam., 2.55–7.5 cm diam. and ≥7.6 cm diam. For wood particles >7.5 cm diam. we further separated them into sound and rotten classes. Lengths of the sampling plane varied among the woody debris size classes: 2 m for wood particles ≤0.64 cm diam., 5 m for woody debris 0.65 to 2.54 cm diam., 10 m for woody debris 2.55–7.5 cm diam., and 12 m for the coarse wood (i.e., logs ≥7.6 cm diam.). We measured the diameter of each particle of coarse woody debris intercepting the plane to the nearest 0.5 cm. For biomass equations of the three woody debris size classes <7.6 cm diam, a quadratic mean diameter was calculated through measurement to the nearest 1 mm of 50 randomly encountered particles of each size class (Table 1). Thereafter, for these classes we counted the number of particles that intersected the sampling plane. Thirty-one to 117 randomly collected samples of each size class were measured to determine specific gravity (wood density) using the water displacement method. Specific gravity was determined as the oven dried weight of a wood sample divided by its volume. Few rotten wood samples were found and specific gravity was not calculated for the class.

Differences in site means of basal area, tree density, tree biomass, and wood biomass were analyzed using analysis of variance and Fisher's least significant difference test. Differences in total above-ground biomass (TAGB) and tree mortality between windward and leeward sites were compared using the non-parametric Wilcoxon rank sum test. Statistical analyses were generated using SAS/STAT software, Version 9.2 of the SAS System for Windows.

Results

Mangrove Composition and Structure

The six mangrove stands were dominated by three tree species; *Bruguiera gymnorrhiza, Sonneratia alba,* and *Rhizophora apiculata*. However, overstory dominance differed among sites (Table 2). *Sonneratia* was dominant at the Maaq, Qatliw, Ruunuw, and Qamun sites. *Rhizophora* was the overstory dominant at the Tabinifiy and Qaaf sites. Even though it was present at all sites, *Bruguiera* was secondary in importance compared to *Sonneratia* and *Rhizophora*.

While the plant species richness of the mangroves was quite low, the structure of the sampled forests was quite variable. For example, total tree density ranged from 690 to 1910 trees ha^{-1} (Table 2). Similarly, there was a four-fold difference in basal area ranging from 21 to 93 m^2 ha^{-1}

Table 2 Density (numbers ha^{-1}), basal area (m^2 ha^{-1}), and aboveground tree biomass (Mg ha^{-1}) of live and dead mangrove stems in six sampled sites on Yap, Federated States of Micronesia. Data are mean±SE for all trees combined (Total) as well as by species which includes *Bruguiera gymnorrhiza*, *Rhizophora apiculata* and *Sonneratia alba*. Different superscripted letters for the totals indicate significant differences between sites (Fisher's LSD, $P \leq 0.10$) and different superscripted numbers for totals indicate a significant difference comparing leeward and windward sites combined (Wilcoxon rank sum test $P \leq 0.05$)

Species	Maaq	Qatliw	Ruunuw	Leeward Sites Combined	Tabinifiy	Qamum	Qaaf	Windward Sites Combined	All Sites
Density									
Total	778±123^{b}	1026±117^{b}	884±97^{b}	896±72^{1}	690±184^{b}	1910±251^{a}	1910±378^{a}	1503±407^{2}	1200 ±229
B. gymnorrhiza	159±59	301±91	637±182	367 ±142	35±35	18±18	106±65	53±27	209±95
R. apiculata	159±99	230±91	–	130±68	654±160	796±309	1680±368	1043±321	587±252
S. alba	460±94	495±72	248±120	401±77	–	1096±317	124±87	406±347	404±159
Basal area									
Total	82±24^{ab}	51±10^{bc}	93±28^{a}	75±13^{1}	21±4^{c}	37±6^{c}	43±6^{c}	34±7^{2}	54±11
B. gymnorrhiza	28±14	14±8	35±7	26±6	0.01±0.01	0.05±0.05	6±3	2±2	14±6
R. apiculata	1.2±0.9	9±4	–	3±3	21±4	7±3	28±5	19±6	11±5
S. alba	53±12	28±5	57±31	46±9	–	30±7	9±6	13±9	30±9
Biomass									
Total	487±151^{ab}	298±63^{abc}	517±179^{a}	434±69^{1}	169±39^{c}	200±33^{c}	257±34^{bc}	208±26^{2}	321±60
B. gymnorrhiza	172±89	66±44	171±28	136±35	0.02±0.02	0.1±0.1	31±15	10±10	73±33
R. apiculata	7 ± 6	76±34	–	28±24	169±39	40±21	179±32	129±45	78±32
S. alba	308±72	156±30	346±190	270±58	–	161±36	48±31	70±48	170±56

(Table 2). Sites with the largest basal area were those in which large *Sonneratia* individuals were a prevalent feature of the stands.

Total aboveground tree biomass greatly differed among the sites ranging from 169 Mg ha^{-1} at the *Rhizophora*-dominated Tabinifiy site to 517 Mg ha^{-1} at the *Sonneratia*-dominated Ruunuw site (Table 2). Tree biomass, basal area, and density were significantly larger on the leeward side of the islands (Maaq, Qatliw, and Ruunuw) than on the windward site of the islands (Tabinifiy, Qamum, and Qaaf).

Mass of Downed Wood Following Typhoon Sudal

To calculate the mass of downed wood required collection of the mean specific gravity of the downed wood in the mangroves as well as the diameter and quadratic mean diameters for the wood size classes <7.6 cm diam. (Table 3).

Wood mass ranged from 23 to 57 Mg ha^{-1} (Table 4). At all sites the wood size class that comprised the largest quantity of mass was the sound wood ≥7.6 cm diam. Rotten wood was scarce and only exceeded 1 Mg ha^{-1} at one site (1.8 Mg ha^{-1}). This suggests that most of the downed wood originated from the typhoon.

We observed no evidence of wood extraction or harvest on the sites that we sampled. Differences in the quantity of downed wood between the sites appeared to be reflective of a combination of species composition, typhoon severity, and landscape position. The mass of downed wood was highest at Ruunuw site (57 Mg ha^{-1}), which also had the second-lowest mortality of the sampled forests (Fig. 1). This high mass of downed wood was likely related to the high basal area of this forest (93 m^2 ha^{-1}) and its dominance by the stiffly branched *Sonneratia* which was subject to breakage. High quantities of downed wood were also

Table 3 The specific gravity, mean diameter, and quadratic mean diameter of the downed wood size classes used to determine wood mass in mangrove forests. Data were sampled 4 mo following typhoon Sudal, Yap Federated States of Micronesia. The diameter of all wood particles ≥7.6 cm diameter were measured in the field, therefore the mean and quadratic mean diameter are not required to calculate mass

Size classes (diameter, cm)	Specific gravity (g cm^{-3})±SE	Sample size	Diameter (cm)	Quadratic mean diameter (cm)	Sample size
≦0.64	0.48±0.01	117	0.43±0.15	0.43	50
0.65–2.54	0.64±0.02	31	1.33±0.78	1.47	48
2.55–7.5	0.71±0.01	69	4.30±0.18	4.52	52
≥7.6	0.69±0.02	61	–	–	–

Table 4 Downed wood mass (Mg ha^{-1}) by size class (diameter in cm) and condition in mangrove forests following Typhoon Sudal, Yap FSM. Data are mean±SE. Different superscripted letters indicate significant differences in total mass between all six sites (Fisher's LSD, $P \leq 0.10$)

Site	≥7.6 cm sound	≥7.6 cm rotten	2.55–7.5 cm	0.65–2.54 cm	≤0.64 cm	Total mass
Leeward sites						
Maaq	9.8±5.2	0.3±0.3	7.9±0.4	6.0±1.0	0.1±0.03	24.1±5.8^{b}
Qatliw	14.0±2.1	0.0±0.0	9.0±1.1	8.7±0.4	0.6±0.1	32.3±2.8^{b}
Ruunuw	42.5±17.2	0.0±0.0	8.0±1.5	5.5±0.8	0.5±0.1	56.5±15.8^{a}
Windward Sites						
Tabinifiy	23.3±6.4	1.8±1.8	9.8±0.3	6.7±0.9	0.2±0.03	41.7±6.8^{ab}
Qamum	14.1±10.1	0.0±0.0	5.9±1.1	3.1±0.9	0.2±0.1	23.2±10.3^{b}
Qaaf	13.9±3.1	0.3±0.3	7.5±1.2	9.0±1.0	0.4±0.1	31.1±4.2^{b}
All Sites Combined	19.6±5.2	0.4±0.3	8.0±0.5	6.5±0.9	0.3±0.1	34.8±5.1

present at the Tabinifiy site where we measured the highest mortality of trees. The high quantity of downed wood at the site was notable as the basal area of the site (21 m^2 ha^{-1}) was the lowest of the six mangrove forests sampled (Table 2).

Total Above-Ground Biomass

The mean (±SE) total above-ground biomass (TAGB= downed wood+standing trees) for the mangroves in this study was 356±62 Mg ha^{-1} ranging from 211 Mg ha^{-1} to 573 Mg ha^{-1} (Fig. 2). Standing trees comprised 80% to 95% of the TAGB. The mean TAGB of the leeward mangrove sites was significantly greater (P=0.04) than the mean of the windward sites (471±73 Mg ha^{-1} vs. 241±21 Mg ha^{-1}).

Typhoon Effects on Mangrove Trees

Mortality of the trees at the six sites was relatively high but variable (Fig. 1). Site mortality ranged from 3% to 8% at the leeward sites. In contrast, mortality exceeded 27% at windward Qaaf and Tabinifiy sites. Since we have no pre-typhoon data we cannot be sure that mortality presented here is completely due to the typhoon. However, in this analysis only dead trees that appeared to have been killed due to typhoon effects were included.

Composition was likely an important factor influencing site mortality or survival. Survival of *Sonneratia* and *Bruguiera* was 96% and 89%, respectively (Table 3). In contrast, survival of *Rhizophora* was 77%. Sites with the highest mortality were dominated by *Rhizophora* while sites with the lowest mortality were dominated by *Sonneratia*. In addition, there may be a relationship between composition and landscape position as the three

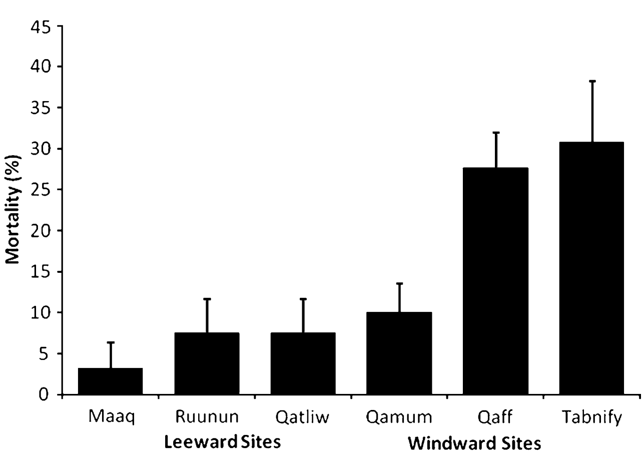

Fig 1 Mortality (%) of mangrove trees attributed to typhoon effects in six sampled mangrove forests, four months following Typhoon Sudal, Yap Federated States of Micronesia

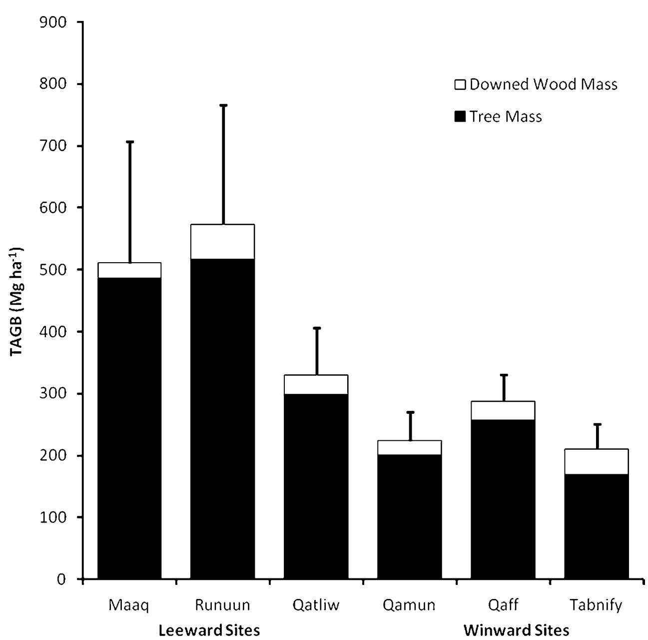

Fig. 2 Total above-ground biomass (Mg/ha^{-1}) of six mangrove forest sites sampled four months following typhoon Sudal, Yap Federated States of Micronesia

sites on the eastern-windward side of the island were dominated or co-dominated by *Rhizophora* while those on the western-leeward side were dominated by *Sonneratia*. *Bruguiera* was most abundant at the sites sampled on the leeward side of the islands.

In addition to differences in survival and mortality, the three mangrove tree species had variable adaptations to survive the typhoon. *Sonneratia* was the largest of the species in terms of both height and trunk diameter. The largest trees that were sampled had a dbh exceeding 100 cm. *Bruguiera* was second in size with the largest trees being 59–67 cm in dbh. In contrast, the largest *Rhizophora* were 30–35 cm in dbh. The mean dbh of all trees sampled was 30.9±4.5, 20.5±6.2 and 14.0±3.0 cm (mean±SE) for *Sonneratia, Bruguiera*, and *Rhizophora*, respectively. In addition to size, there were differences in trunk characteristics, with the most obvious being the well-developed prop roots on *Rhizophora* (Table 5). Branching characteristics also differed. Mainstems of *Sonneratia* were relatively stiff compared to the other species. This was apparent by the differences in the number of the trees with snapped mainstems (26% of *Sonneratia*, and <15% for the other species). However, the stiff branches subject to breakage may compensate in lowering the degree of individuals that were wind-thrown; none of the *Sonneratia* was observed to have been uprooted or leaning (wind-thrown). In contrast, >3% of the *Bruguiera* and >7% of the *Rhizophora* were wind-thrown. Crown damage (apparent damage to the foliage) exceeded 75% for all species (Table 5).

Crown refoliation (i.e., the regeneration of leaves from surviving apical mainstems located on small branches) was common in all species and the only observed refoliation response for *Rhizophora* (Table 5). In terms of response, *Sonneratia* was the only species to produce abundant basal and epicormic sprouts in response to the typhoon. We did not observe any of the *Bruguiera* or *Rhizophora* to produce basal sprouts (those originating from meristematic tissues located at the base of the trunk or roots), while 55% of the sampled *Sonneratia* produced basal sprouts. Similarly 80% of all individuals of *Sonneratia* vigorously sprouted from epicormic tissues (i.e., dormant meristematic tissues on trunks and mainstems). Epicormic sprouting was not observed in *Rhizophora*, and only rarely in *Bruguiera* (Table 5).

Finally, we report that 36% of the *Rhizophora*, 18% of the *Bruguiera,* and 5% of the *Sonneratia* exhibited no refoliation responses. This observation includes those individuals that were already dead as well as those that were still alive with a few damaged leaves, but not refoliating by any means. This suggests that typhoon-caused mortality may ultimately be higher that what we measured four months following the typhoon.

Table 5 Response characteristics of the dominant mangrove trees by species following Typhoon Sudal, Yap Federated States of Micronesia

Species (number sampled)	Trunk characteristics	Branching characteristics	Tree survival (%)	Stem damage			Stem response		
				Crown damage (%)	Main stems snapped (%)	Uprooted/ leaning (%)	Sprouting (%)	Crown refoliation (%)	No refoliation response (%)
Bruguiera gymnorrhiza (70)	Buttressed	Flexible- rapid refoliation	89	87	13	1.4/1.4	3% epicormic 0% basal	82	7
Rhizophora apiculata (199)	Prop roots	Flexible- rapid refoliation	77	78	15	3.0/4.0	0% epicormic 0% basal	64	13
Sonneratia alba (56)	Columnar	Stiff- subject to shear	96	75	26	0/0	80% epicormic 55% basal	62	1

Discussion

Total above-ground biomass in the mangrove forests of this study, particularly those of the Ruunuw and Maaq sites is quite large relative to other tropical forest ecosystems (Fig. 2). In a review of the total above-ground biomass of tropical forests, Kauffman et al. (2009) reported that TAGB of tropical forests range from <6 to >600 Mg ha^{-1}. Reviews by Putz and Chan (1986), Saenger and Snedaker (1993), and Komiyama et al. (2008) report tremendous variation in the structure of mangroves with a range in TAGB of seven to 460 Mg ha^{-1}. The average TAGB of the Yap mangroves of 356 Mg ha^{-1} occurs at the high end of this range while the TAGB of the Ruunuw (573 Mg ha^{-1}) and Maaq (511 Mg ha^{-1}) sites exceeds all results presented in these reviews. Given their relatively large biomass, it is clear that mangroves function as important C sinks.

Few studies have quantified the mass of downed wood in mangrove forests (Allen et al. 2000, Krauss et al. 2005). Krauss et al. (2005) reported that mangrove wood volumes in Florida mangrove forests 9–10 years after a major hurricane ranged from 16 to 98 m^3 ha^{-1} (a mean of 67 m^3 ha^{-1}). Allen et al. (2000) reported that the volume of mangrove forests in Yap was 35 m^3 ha^{-1}. The mean total volume of woody debris in our study was 51 m^3 ha^{-1} (range=34–83 m^3 ha^{-1}) and the mass was at least two-fold greater than that reported by Allen et al. (2000). In our study, conducted only 4 months after Typhoon Sudal, almost all wood originated from trees that were alive prior to the typhoon. In contrast, almost half of the wood debris measured by Allen et al. (2000) consisted of rotten wood. The differences in mass can be explained by the differences in wood composition (i.e., sound as compared to rotten wood).

Traits of mangrove forest species that facilitate typhoon survival included main stem characteristics that reduce stem breakage and blow-down in high winds. These were buttressed stems for *Bruguiera* and prop roots for *Rhizophora*. These two species also possess flexible stems that tend to break off in lower percentages than the stiffly stemmed *Sonneratia* (Table 5). However, *Sonneratia* was unique among the three mangrove species in its prolific capacity to sprout. While the number of mainstems of *Sonneratia* that snapped by winds was double that of *Rhizophora*, the overall survival was higher due to the capacity to sprout from epicormic or basal meristematic tissues (Table 5). The capacity to sprout coupled with a mainstem that breaks rather than uprooting are traits that combined for a survival rate of 96% for *Sonneratia.*

Sprouting following disturbances tends to be more prevalent in upland forests compared to mangroves. For example, Sampaio et al. (1993) reported that 93% of all individuals in a Brazilian tropical dry forest sprouted following cutting and 10% to 43% sprouted following cutting and burning. Following the same methods used to quantify mangrove response, we also sampled three upland forests of Yap, during the same time period. We found that 68% of the trees sprouted from epicormic sprouts and 9% from basal sprouts (J.B. Kauffman unpubl. data). Average tree survival was 93% in uplands (N=279 trees) which is quite similar to mortality following cyclones in other tropical upland forests reported in other studies (Franklin et al. 2004).

Given their location at the land water interface where susceptibility to winds and storm surge damage is great, mangrove forests must be adapted to such relatively common disturbances in their environment. Sherman et al. (2001) reported a category-3 hurricane resulted in a mean mortality of 48% with a range of 14% to 100% for mangroves in the Dominican Republic. They measured a decrease in basal area of 9% to 100%. Similarly, Doyle et al. (1995) reported reductions in standing biomass of 50% to 100% of South Florida mangroves following a severe hurricane. Comparisons of mangrove mortality and cyclone effects are difficult given differences in landscape, storm parameters, and mangrove composition. In our study, standing trees composed 81% to 95% of the post-typhoon above-ground biomass at Yap suggesting a much lower decline in basal area than reported by Doyle et al. (1995) or Sherman et al. (2001). The mortality of mangrove trees averaging 14% with a range from 3% to 31% is also much lower than that reported in other studies. These great differences in mortality and post-cyclone structure suggest caution when making generalizations concerning impacts of tropical storms on mangroves.

In addition to composition differences, there are a number of other factors that could explain the variation in tree mortality of the sampled mangrove forests. External factors include the intensity and track of the typhoon, timing of tidal surges and landscape position. At the leeward sites, mortality was less than 8% while on the windward sites mortality was 10% to 31% (Fig. 1). Based upon observations of local inhabitants and relief workers, the severity of Typhoon Sudal was greatest on the windward side of the island.

In summary, Typhoon Sudal had a profound yet variable effect on the structure of the Yap mangrove forests. Practically all trees suffered canopy damage, and significant proportions of trees were snapped or wind thrown but this varied by species. Yet post-typhoon above-ground biomass of standing trees remained quite high particularly in comparison to results of other mangroves following tropical cyclones. The relative frequency of typhoons (about 35 years in Yap), coupled with a large standing forest mass immediately following this typhoon suggests a great deal of resistance and resilience to typhoons by mangrove spp. in Micronesia. This study was limited in that it only examined the short-term responses to a severe typhoon. Long term studies to examine mangrove recovery, reproduction and recruitment in periods following typhoon events would provide a larger picture of ecosystem response and how increasing typhoon severities associated with climate change may affect mangrove structure and persistence.

Acknowledgments Margie Falanruw provided valuable assistance in the field and with logistics. Mychal Tetteh assisted in the field, and Janice Haraguchi determined the specific gravity of the downed wood. We are grateful to the Yap Division of Agriculture and the people of Yap for their cooperation and assistance in allowing us to work in their forests and mangroves and providing us with valuable information on Typhoon Sudal. We are especially grateful to Pius Liyagel, Francis Ruegorong, Charlie Gilgaayan, Godfrey Chochol, Kevin Sog, Joe Fanafal, James Lukan, John Tun, Steven Mar, Raymond, John Libiy, and Tom Tamangmow. Without their wisdom and assistance in the field, this project would not have been possible. We thank Dan Donato for earlier reviews of this paper. The study was funded from the USDA Forest Service, PSW Research Station and the USDA Forest Service International Programs.

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