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Global Patterns of Pre-Dispersal Propagule Predation in Mangrove Forests[1]

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ABSTRACT

Mangroves in disparate families produce viviparous seedlings (propagules) that are attacked by many crab and insect predators both before and after dispersal. While post-dispersal predation is viewed as an important factor in structuring many mangrove communities, pre-dispersal predation rates and agents have been characterized for few species. Ten species of mangrove and 3299 propagules were surveyed for pre-dispersal propagule predation at 42 sites around the world. Pre-dispersal predation rates were variable among sites and species, ranging from 0 to 93 percent within stands, with a global total predation rate of 23.3 percent (across all propagules examined) and a mean level of 28.3 percent across sites. Grapsid crabs, Coleoptera and Lepidoptera were the primary predators identified. Forests near human population centers and stands occurring at high intertidal sites exhibited higher levels of propagule predation than those in unpopulated or low-intertidal sites. Predation rates on a species were weakly, negatively correlated with conspecific seedling density at a site. To explore temporal variation in, and ramifications of pre-dispersal predation for propagule growth and abscission dynamics, *Rhizophora mangle* propagules were monitored over two years at three sites in Belize, Central America. Predation did not significantly reduce hypocotylar growth of germinated propagules on the parent tree, but nearly doubled the abscission rate of premature propagules. Pre-dispersal propagule predation is a ubiquitous feature of mangrove forests world-wide, and must be accounted for in estimates of reproductive output, stand health, and propagule availability for forestry and restoration efforts.

Key words: Avicennia; *biogeography*; Bruguiera; Ceriops; *coleoptera*; *crabs*; *herbivory*; *Lepidoptera*; *mangroves*; Rhizophora.

MANGROVES EXHIBIT SEVERAL UNUSUAL PHYSIOLOGICAL FEATURES that enable them to colonize coastal habitats throughout the tropics. Vivipary, the precocious growth of embryos while still attached to the parent tree, is one such trait that has arisen evolutionarily in several disparate mangrove families (Tomlinson 1986). The advantages of vivipary in stressful coastal environments have been well articulated (Guppy 1906, Joshi 1933, Rabinowitz 1978a, Saenger 1982). However, the potential costs of producing numerous seedlings on the parent tree where they are vulnerable to predation are high.

Seed predation studies on other, non-viviparous tree species suggest that concentrating progeny close to the maternal tree encourages predation (*e.g.*, Janzen 1971). Limited physiological studies indicate that growing mangrove propagules receive substantial maternal carbon (Pannier 1962, Pannier & Pannier 1975). Such well-provisioned seedlings are a highly apparent (*sensu* Feeny 1976) and concentrated resource for herbivores. In general, seasonal and genotypic variability in phenology, and strategies such as masting may confound or satiate predators (*e.g.*, De Steven 1981, Auld 1986, Solbreck & Sillén-Tullberg 1986). Studies on phenological differences among individual mangroves or stands (*e.g.*, Duke *et al.* 1984, Steinke 1988, Clarke & Myerscough 1991) have not explicitly addressed links with predation patterns. Alternatively, seeds may contain high levels of protective anti-herbivore compounds. Smith (1987a) has documented tannin levels in mangrove propagules characteristic of, and exceeding those of leaves of "persistent" (long-lived non-pioneer) tropical trees, *sensu* Coley (1983): this high level of quantitative herbivore defense would be predicted for highly apparent species growing in low-resource environments (Feeny 1976).

Though mangrove propagules are tough, buoyant, and readily water-dispersed (Rabinowitz 1978b), they are preyed upon intensively by a host of decapod and insect predators once they have abscised (Smith 1987a, b, Wilson 1989, Robertson

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et al. 1990). Comparative studies of post-dispersal predation reveal damage on the majority of mangrove propagules. Post-dispersal propagule predation is a significant factor structuring mangrove communities throughout the world (Smith 1988, Smith *et al.* 1989). However, post-dispersal surveys on already fallen mature propagules may underestimate the number of propagules damaged or aborted owing to heavy predation levels on the parent tree.

Pre-dispersal predation has received less attention in mangrove studies. Burrowing beetles, moth larvae, and crabs are known to attack immature propagules prior to release (Gill & Tomlinson 1971, Lugo & Snedaker 1975, Christensen & Wium-Andersen 1977, Onuf *et al.* 1977, Rabinowitz 1977, Clarke 1992). Burrowing insects commonly destroy aerenchyma and vascular tissue in the developing hypocotyls of mangrove species in the Rhizophoraceae and in the cotyledons of *Avicennia* species. Although these organisms do not always kill the propagule outright, we broadly refer to their damaging activity as "propagule predation," paralleling the terminology of the literature on the comparable phenomenon of "seed predation." The magnitude of this damage and the implications for subsequent seedling establishment vary among species (Robertson *et al.* 1990, Rabinowitz 1977). In some areas, predators may potentially reduce the number of seedlings available for both natural regeneration and planting for agroforestry, but the magnitude of their impact on forest regeneration is little known.

This study documents levels of pre-dispersal mangrove propagule predation for 10 species of mangrove from 42 sites around the world. Data like these, collected during a global expedition to characterize and compare plant-animal interactions in many mangrove forests, can provide useful insight into levels, site-related trends, and interspecific differences in the global occurrence of propagule predation. Our static survey has limitations: it is restricted to the species that are reproducing at the time, and it does not capture temporal variability in predation rates. To complement these data, we present long-term field observations on *Rhizophora mangle* L. from Belize, Central America, that permit us to examine the ramifications of pre-dispersal predation for propagule growth and seedling availability in detail for one mangrove species.

METHODS

GLOBAL MANGROVE PROPAGULE PREDATOR SURVEY.—From 13 October 1994 to 30 May 1995, we visited 42 mangrove swamps in 16 countries. At each site, we located reproductive mangrove trees bearing propagules > 1 cm long (excluding the fruit structure in the Rhizophoraceae) and inspected an accessible subset of propagules for pre-dispersal predation. We non-destructively examined as many propagules as we could see from the ground for which we could reliably identify damage, including propagules growing on the outer and interior branches from the base of the tree to 4 m high. Where possible, we climbed trees to find propagules. Ten species in the genera *Rhizophora, Bruguiera, Ceriops* (Rhizophoraceae) and *Avicennia* (Avicenniaceae) were examined. We recorded the percent of propagules bearing signs of pre-dispersal predation, and identified the likely predator when possible. The sample sizes we report here reflect the numbers of accessible propagules still on trees for which we could identify damage types. Propagule availability, in turn, resulted from regional and species differences in phenological patterns. At each site, we sliced open a subset of 1–5 propagules bearing representative damage types to determine predator identity. The difficult logistics of transporting invertebrate specimens through multiple countries precluded us from collecting and preparing vouchers of field samples. Plausible identifications of propagule predators were made based on inspection of local collections, use of local taxonomic experts, and comparisons of field descriptions with existing literature on the major mangrove herbivores for each region.

PROPAGULE GROWTH, PREDATION AND ABSCISSION DYNAMICS.—To assess differences in propagule growth rates and levels of predation among mangrove stands, we followed propagule fates for two years on two cays in Belize, Central America, from 27 December 1991 to 24 December 1993. Wee Wee Cay (16°46'N, 88°08'W) is a 2 ha coral cay with a ≈ 40 yr-old stand of 10–15 m tall *Rhizophora mangle* L. predominating on the seaward fringe (Stoddart *et al.* 1982). Mature trees of *Rhizophora mangle* on the leeward (northwest) coast are tidally submerged to 30 cm at salinity ≈ 30 parts per thousand. Twin Cays (16°48′ N, 88°05′ W) comprises a complex of 4 small islands bisected by a 30 m side channel. Two separate populations of propagules were monitored at Twin Cays. The first was a monospecific stand of dwarf (*sensu* Lugo & Snedaker 1974) 1–1.5 m tall *R. mangle* trees in a hypersaline (soil interstitial water ≈ 51‰) interior lake known as West Pond (Rützler *et al.* 1993). The second population was observed on a mature interior stand at highest high water on the northwest side of Twin Cays (salinity 35 ‰), dominated by 7–10 m tall *R. mangle* with an understory of *Batis maritima* L., hereafter referred to as the "Batis stand."

At least 6 reproductive trees (from the edge of the fringing Wee Wee stand, and from the interior of the West Pond and Batis stands) were haphazardly chosen for monitoring in December 1991. At least 6, undamaged, newly germinated propagules were identified on each tree based on their accessibility to repeated censusing, from 1–3 m high inner and outer branches (final sample sizes reflected propagule availability). Propagules were labeled with a numbered plastic parakeet band (National Band & Tag Company, Lexington, Kentucky) fixed loosely around the pedicel. All 1991 propagules had abscised by December 1992. To compare reproductive dynamics across years, a second cohort was labelled in December 1992 and followed through abscission in December 1993. In 1991, propagule sample sizes were 100 (Wee Wee Cay), 45 (West Pond), and 70 (Batis stand). In 1992, very few trees at West Pond produced fruits, so propagules were observed only at Wee Wee Cay ($N = 93$) and the Batis stand ($N = 88$). On each sampling date, the length of germinated hypocotyl (± 1 mm), occurrence and identity of herbivore activity, and abscission status were noted for each propagule.

RESULTS

COMMON TYPES OF PROPAGULE PREDATORS.—Propagule predators fell into three major classes: burrowing beetle larvae, grapsid crabs, and lepidopteran larvae (Fig. 1). A small proportion of propagules exhibited epidermal mines, probably excavated by gracilariid lepidopteran miners (Feller 1995). This low-frequency miner damage was observed only in the Caribbean region (Belize and Venezuela). Because miners did not pierce the propagule below the epidermis, it is unlikely that gracilariids were a major source of seedling mortality in these neotropical sites.

Most damaging were the insect larvae and adults that excavated 1–3 mm wide burrows through the center of the elongating hypocotyl of Rhizophoraceae propagules, and that consumed cotyledons inside *Avicennia* pericarps. Both adults and larvae of beetles were found in Rhizophoraceae propagules, occupying galleries, and propagules were frequently riddled with their exit holes (Fig. 1b). These insects likely belonged to the cosmopolitan ambrosia beetle family (Coleoptera: Scolytidae), with *Poecilips* spp. (synonymous with *Coccotrypes*; Murphy 1990) predominating in the Caribbean and South American regions (Onuf *et al.* 1977, Rabinowitz 1977, Atkinson *et al.* 1991). *Poecilips* spp. have been reported previously in Hawaii, the Caroline Islands, India, Queensland, Madagascar, and Africa (Browne 1973), and *Coccotrypes* spp. have been found in Malaysian and Singaporan *Bruguiera* and *Rhizophora* propagules (Murphy 1990). Curculionid beetles occur on *Bruguiera* and *Rhizophora* spp. in Queensland (Robertson *et al.* 1990). An anthribid beetle also has been bred from the young propagules of *Avicennia marina* in Queensland (Hockey & De Baar 1988). The lepidopteran larvae we identified on *Rhizophora* and *Bruguiera* throughout Australasia likely belonged to the Tortricidae; tortricid moths are widely reported from mangroves of peninsular Malaysia, Singapore (Murphy 1990), and Borneo (Robinson & Tuck 1993). A phycitine moth larva characteristically infested *Avicennia* propagules in Asia (Murphy 1990) and Australia (Clarke 1992). We likewise observed a probable phycitine on *Avicennia marina* in Madagascar and South Africa (Fig. 1a).

Grapsid and sesarmid crabs have been widely reported as agents of post-abscission propagule damage. *Sesarma* and *Metapograpsus* spp. reportedly feed on fallen Rhizophoraceae, and *Sesarma* and *Neosamartium* spp. attack *Avicennia* propagules (Wium-Andersen 1981, Smith 1987a, Smith *et al.* 1989, Robertson *et al.* 1990), while *Aratus pisonii* (Milne Edwards) and *Goniopsis cruentata* (Latreille) consume many abscised *Rhizophora mangle* propagules throughout the Caribbean (Warner 1969, Wilson 1989, EJF pers. obs.). We observed frequent evidence of their feeding on propagules still attached to the tree, 1–3 m above the ground (Fig. 1c, 1d). In neotropical regions, mangrove tree crabs (*A. pisonii*) were seen perching on the pedicels of propagules and consuming both the fruit wall and the seedling hypocotyl of Rhizophoraceae species, gouging out *ca* 1 cm^2 craters in the epidermis (Fig. 1c). Where holes were excavated in the fruit wall, the seedling apical meristem was often damaged; occasionally the germinating hypocotyl emerged through the hole, markedly distorting seedling growth.

Most guilds of propagule predators (with the exception of the gracilariids, which occurred only on *Rhizophora mangle*, and the apparently *Avicennia*-specific phycitine moths) were polyphagous generalists, feeding on a variety of hosts within and among sites. Because few specimens could be iden-

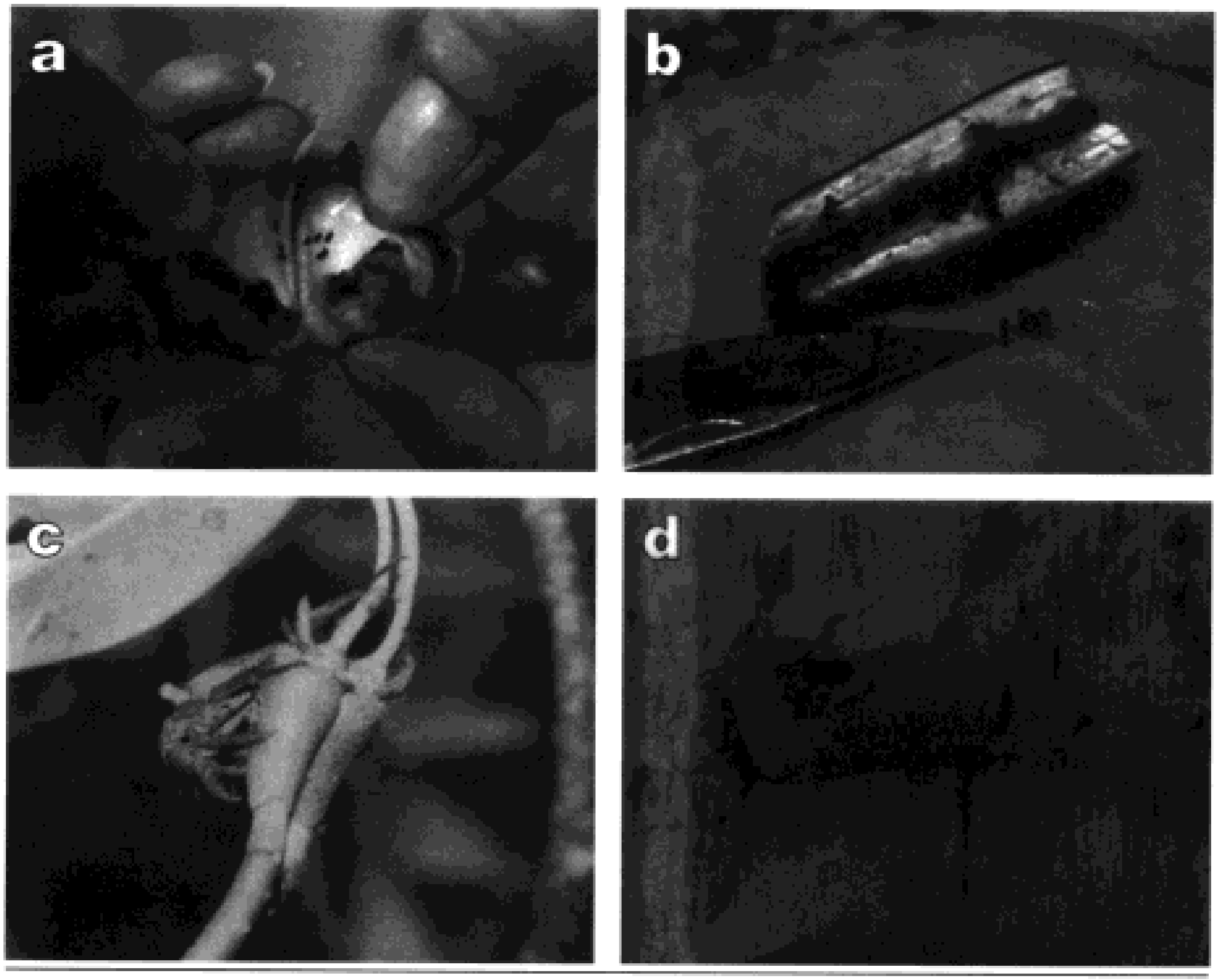

FIGURE 1. Characteristic propagule damage by the three most important groups of mangrove propagule predators found. (a) a phycitine moth larva in a propagule of *Avicennia marina*, showing frass and damage to cotyledons, Nosy Be, Madagascar; (b) a 4 cm-long segment of a *Rhizophora mucronata* propagule bearing galleries and larvae of a scolytid beetle, with knife blade pointing out an adult, Sunderbans, India; (c) the grapsid crab (*Aratus pisonii*) consuming the fruit wall of *Rhizophora mangle*, Wee Wee Cay, Belize; (d) typical crab hole in *Rhizophora mangle*, Wee Wee Cay, Belize.

tified precisely to species, associations of predators on hosts could be resolved only coarsely. Crabs, scolytid beetles and tortricid moths fed on all Rhizophoraceae mangrove species examined, with variable frequency. We did not see scolytids or crab damage on *Avicennia*. There was little overlap among predators on a given propagule: scolytid burrows together with low levels of crab damage were scored together on only 0.8 percent of all propagules surveyed. Crab damage was recorded in 33 sites (52%) on 47 percent of all propagules, scolytid holes in 25 sites (30%) and 34 percent of all propagules; Lepidoptera including miners occurred at 9 sites (14%) and 5 percent of all propagules (Table 1).

GLOBAL MANGROVE PROPAGULE PREDATOR SURVEY.— Propagule predation percentages ranged from 0 to 93 percent (Table 1), with a global total attack rate of 23 percent (*N* = 3,299 propagules surveyed), a global mean attack rate of 28 ± 3.5 percent (SE, *N* = 64, all species by site combinations) and a mean predation rate per site of 25 ± 3.4 percent (*N* = 42 sites, species pooled within site). *Avicennia marina* (Forsk.) Vierh. exhibited the highest mean levels of propagule predation (50.0 ± 40% [sd], *N* = 3 sites), followed by members of the Rhizophoraceae (*Rhizophora mucronata*: 33.7 ± 31.2%, *N* = 11; *Bruguiera gymnorrhiza*: 27.5 ± 35, *N* = 10; *R. mangle*: 26.9 ± 26.4, *N* = 12; *Ceriops tagal*: 24.9 ± 23.0, *N*=8; *R. apiculata*: 24.5 ± 27.9, *N* = 7; *R. stylosa* 17.7 ± 7.9, *N* = 9; *R. samoensis*: 10 ± 14.6, *N*=3). Mean predation rates were uncorrelated with sample sizes ($r^2 = 0.022$, $P = 0.26$), suggesting little sampling bias.

Predation rates were highly variable throughout

TABLE 1. *Percentages of mangrove propagules attacked by predators in 42 sites throughout the world. Listed are the sites surveyed, site coordinates, dates of surveys, mangrove species surveyed, numbers of propagules examined, percent of propagules attacked, and the probable predators. Location coordinates were determined primarily using a portable global positioning system (Trimble Instruments, Torrance, California). Mangrove species are abbreviated as in Table 1. Key to mangrove species: Am =* Avicennia marina *(Forsk.) Vierh.; Bg =* Bruguiera gymnorrhiza *L. (Lamk.); Cd =* Ceriops decandra *(Griff.) Ding Hou; CT =* Ceriops tagal *(Perr.) C. B. Robinson; Cta =* Ceriops tagal *var.* australis; *Ra =* Rhizophora apiculata *Bl.; Rl =* Rhizophora lamarckii *Montr; Rma =* Rhizophora mangle *L.; Rmu =* Rhizophora mucronata *Lamk., Rsa =* Rhizophora samoensis *(Hockr.) Salvoza; Rst =* Rhizophora stylosa *Griff. (nomenclature follows Tomlinson 1986). Propagule predators are abbreviated: B = beetle; L = lepidopteran; C = crab; M = miner and listed in decreasing order of importance as herbivores. "AIMS" refers to the Australian Institute of Marine Science, Townsville, Australia.*

Site	Coordinates	Date	Species	# Propagules	% Attacked	Predators
Bahia Cartago, Galápagos Ils, Ecuador	0°36′49″S 90°54′27″W	19 October 1994	Rma	14	92.9	B, C
Villamil, Galápagos Ils, Ecuador	0°58′13″S 90°57′37″W	20 October 1994	Rma	284	47.9	B, C
Floreana, Galápagos Ils, Ecuador	1°13′45″S 90°26′33″W	21 October 1994	Rma	40	55.0	B, C
Morrocoy National Park, Venezuela Cayo Muerto	10°55′50″N 68°16′34″W	2 November 1994	Rma	50	10.0	B
La Restinga west, Isla Margarita, Venezuela	10°58′02″N 64°07′21″W	6 November 1994	Rma	23	34.8	B, C
La Restinga east, Isla Margarita, Venezuela	11°01′06″N 64°10′44″W	7 November 1994	Rma	157	21	M, C
La Gaviota, Isla Margarita, Venezuela	10°59′16″N 64°07′21″W	7 November 1994	Rma	151	21.2	C, B, M
Pearl Harbor, Oahu, Hawaii	22°N 158°W	13 November 1994	Rma	137	2.9	B, C
Chinaman's Hat State Park, Oahu, Hawaii	21°30′27″N 157°50′35″W	13 November 1994	Rma	49	2.1	C
Utwe River, Walung, Kosrae, Federated States of Micronesia	5°17′07″N 162°54′44″E	15 November 1994	Bg, Ra	21, 25	71.4, 0.0	B, C
Southwest Pohnpei Island, Federated States of Micronesia	6°48′35″N 158°11′53″E	18 November 1994	Rmu	74	0.0	—
Temwen Islet, Pohnpei, Federated States of Micronesia	6°50′34″N 158°18′49″E	18 November 1994	Rmu, Bg	20, 16	0.0, 25.0	B
Gurong Village, Yap, Federated States of Micronesia	9°33′33″N 138°06′13″E	23 November 1994	Rmu, Bg	59, 26	66.1, 80.8	B, C
Colonia, Yap, Federated States of Micronesia	9°34′10″N 138°09′19″E	24 November 1994	Rmu	52	19.2	C, B
Babeldaob Causeway, Koror, Republic of Palau	7°21′19″N 134°29′51″E	25 November 1994	Ct	18	0.0	—
Rock Islands, Republic of Palau	7°09′53″N 134°22′31″E	26 November 1994	Bg	20	0.0	—
Faloha, Tongatapu, Kingdom of Tonga	21°10′08″S 175°11′54″W	1 December 1994	Rsa	41	26.8	C, L
Nuku'alofa Bay, Tongatapu, Kingdom of Tonga	21°09′13″S 175°12′52″W	1 December 1994	Rsa	31	3.2	B
North of Nadi, Fiji	17°41′28″S 177°25′09″E	3 December 1994	Rsa	55	0.0	—
Vila Chaumierès, Port Vila Lagoon, Efate Island, Vanuatu	17°44′26″S 168°20′28″E	4 December 1994	Rst	139	20.1	C, B

TABLE 1. *Continued.*

Site	Coordinates	Date	Species	# Propagules	% Attacked	Predators
Lakatoro, Malekula Island, Vanuatu	16°06′13″S 167°25′73″E	8 December 1994	Rst, Ct	39, 66	15.4, 3.0	C, B
Litslits Village, Malekula Island, Vanuatu	16°06′54″S 167°26′39″E	8 December 1994	Rst, Ra	12, 14	8.3, 14.3	C, B
Townsville City Environmental Park, Queensland, Australia	19°12′27″S 146°19′04″E	13 December 1994	Ct	107	29.9	B, C
Gentle Annie Creek, Lucinda, Queensland, Australia	19°12′27″S 146°19′04″E	14 December 1994	Cta, Rst	44, 53	29.5, 30.2	B, C
Dungeness Creek, Lucinda, Queensland, Australia	18°32′35″S 146°99′47″E	14 December 1994	Cta, Bg	39, 24	35.9, 0.0	C, B
AIMS North site, Queensland, Australia	19°17′29″S 147°02′30″E	15 December 1994	Rst	93	15.1	C
AIMS Dock, Queensland, Australia	19°16′S 147°02′E	15 December 1994	Rst	68	4.4	C
Magnetic Island, Queensland, Australia	19°10′23″S 146°49′39″E	16 December 1994	Cta, Ra, Rst	27, 37, 22	25.9, 0.0, 22.7	C
Sungei Sementa Kecil, Peninsular Malaysia	3°04′18″N 101°22′35″E	10 January 1995	Rmu, Ra, Ct	15, 7, 38	73.3, 71.4, 71.1	C, B, L
Potwell/Matang 30-yr rotation stand, Peninsula Malaysia	4°50′23″N 100°37′10″E	13 January 1995	Ra	9	55.6	B, C, L
Sibu Island northeast site, Malaysia	2°13′22″N 104°04′06″E	28 January 1995	Rst, Bg	66, 5	24.2, 20.0	C, B
Sibu Island south site, Malaysia	2°13′N 104°04″E	28 January 1995	Rst, Rmu	135, 35	20.0, 25.7	C, B
Wandoor, Andaman Islands, India	11°37′15″N 92°37′02″E	6 February 1995	Rmu	7	57.1	C
Sunderbans Tiger Reserve, India	22°05′N 88°50′E	10 February 1995	Ra, Bg, Cd, Ct, Rmu	33, 9, 22, 25, 72	18.2, 77.8, 81.8, 4.0, 9.7	B, C
Androadroate, Nosy Be, Madagascar	13°22′38″S 48°11′39″E	14 February 1995	Ra	17	11.8	C
Lokobe, Nosy Be, Madagascar	13°22′14″S 48°19′19″E	14 February 1995	Rmu, Am	8, 30	37.5, 50.0	C, L
St. Lucia Estuary, South Africa	28°12′36″S 32°24′19″E	20 February 1995	Bg, Am	60, 50	0.0, 10.0	L
Beechwood Reserve, Durban, South Africa	29°48′23″S 31°02′28″E	21 February 1995	Rmu, Bg, Am	7, 25, 30	0.0, 0.0, 90.0	L
Durban Bay Head, Durban, South Africa	29°53′18″S 31°00′44″E	21 February 1995	Rmu, Bg	22, 65	81.8, 0.0	B, C
Wee Wee Cay, Belize	16°42′58″N 88°09′57″W	27 May 1995	Rma	160	20.6	C, M
Spruce Cay, Belize	16°43′27″N 88°09′19″W	28 May 1995	Rma	100	9.0	C
Sittee River, Belize	16°42′N 88°08′W	29 May 1995	Rma	100	6.0	C

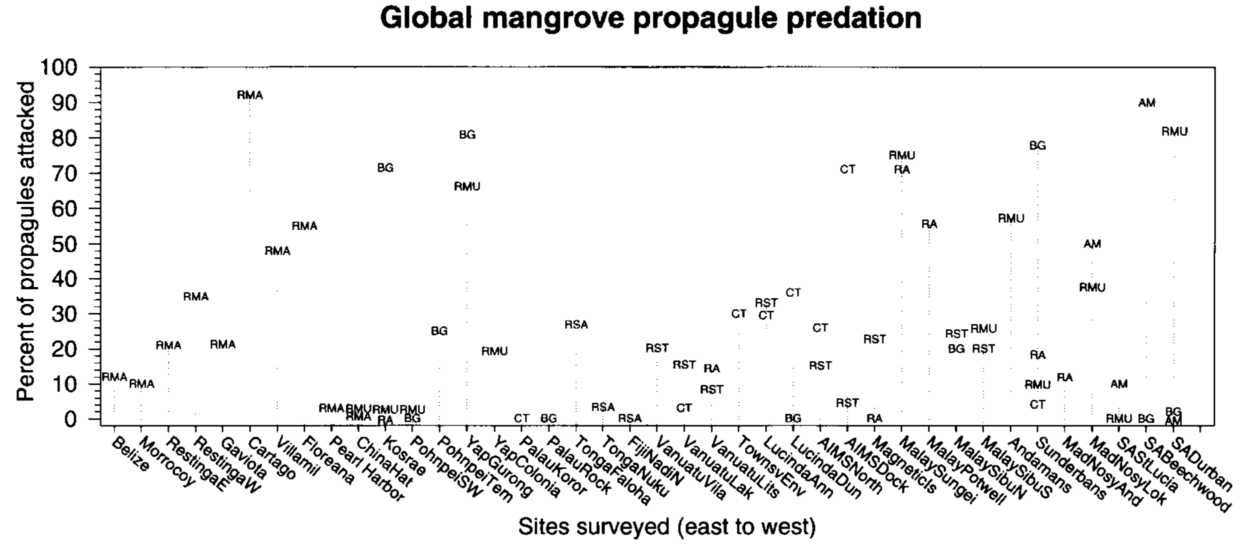

FIGURE 2. Levels of propagule predation for the eight most common mangrove species. Species abbreviation points indicate the percentage of propagules attacked by herbivores at each site where the species was surveyed, proceeding east to west. Census sample sizes are given in Table 1. Species symbols with overlapping predation values are jittered (separated vertically) for clarity. Abbreviations for species as in Table 1.

the world, and biogeographic trends were not readily discernible. There were no apparent longitudinal trends in predation rates: neotropical and paleotropical species exhibited similarly variable levels of pre-dispersal damage (Fig. 2). Mangroves of the north and south Pacific Islands, from Hawaii to Vanuatu (with the exception of *Bruguiera gymnorrhiza* on Kosrae and Yap, Federated States of Micronesia), exhibited slightly lower percent damage levels than Asian and African sites (Fig. 2; mean Pacific islands = 14.4 ± 5.1% [SE]; mean Australasia/Madagascar/Africa = 30.2 ± 4.9%; t-test $t = 2.3$; $P = 0.03$; df = 30). Sites were also coded for the rough tidal height at which they occurred (determined from site maps and personal communication): 0 for censused trees below mean water (inundated by tides to ≥ 30 cm for at least 6 h daily), 1 for trees above mean water (inundated to < 10 cm for < 6 h daily, excluding storm tides). Propagules on trees in the higher tidal zones received approximately twice the level of predation ($x = 32.9 \pm 3.8\%$ [SE] of propagules attacked, $N = 21$ sites) as propagules growing on trees in lower tidal zones ($x = 16.2 \pm 2.6\%$, $N = 21$ sites). Attack rates were significantly different by t-test ($t = 2.6$; $P = 0.01$; df = 40).

We also investigated whether mean attack rates varied predictably with the richness of propagule-producing mangrove host species present at a site. Where only one fruiting species was present, mean attack rates were 21.8 ± 4.9 % ($N = 25$). Where two simultaneously fruiting species occurred in close proximity, attack levels were 26.5 ± 5.2 percent ($N = 13$); with 3-species assemblages, 39.4 ± 16.7 percent ($N = 3$). Despite this increasing trend, the regression of attack rate on species richness was not significant ($r^2 = 0.04$; $P = 0.23$).

Propagule predation level on a given species at a site was weakly and negatively correlated with density of conspecific seedlings occurring beneath the canopy (Fig. 3; $F = 5.14$, $r^2 = 0.08$, $P = 0.03$, $N = 64$ sites). Both linear and hyperbolic functions explained less than 10 percent of the variance in the model, however, indicating that pre-dispersal propagule predation was a relatively unimportant factor explaining subsequent seedling establishment (as reflected in understory density).

PROPAGULE GROWTH, PREDATION AND ABSCISSION DYNAMICS.—Our single static survey yielded little information (other than the above weak correlation) on the impacts of pre-dispersal predation on subsequent survivorship of seedlings. Thus, we examined the hypothesis that pre-dispersal propagule predation damages growth and survivorship of propagules by collecting long-term data on propagule cohorts from multiple mangrove populations in Belize, Central America. *Rhizophora mangle* propagule growth patterns differed significantly between sites within years (repeated measures ANOVA, $F = 8.05$, $P = 0.001$ for year 1 cohort; $F = 13.21$, $P = 0.001$ for first 4 sampling dates of year 2). In both years, Wee Wee cay cohorts grew to greater final lengths before abscising than propagules at the

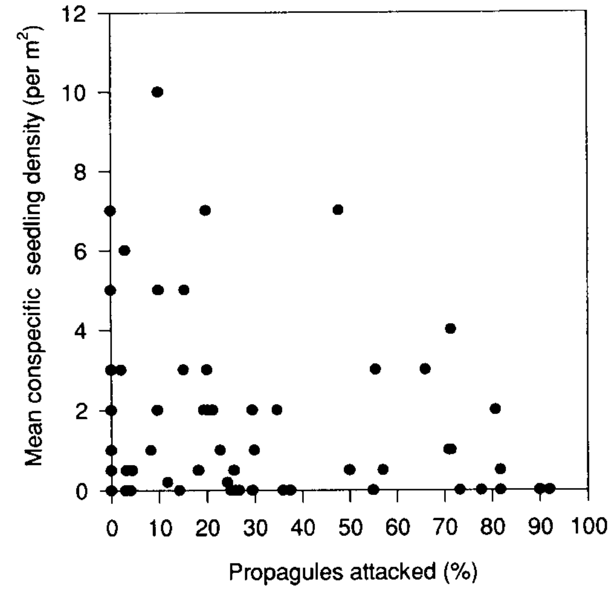

FIGURE 3. Relationship between the percent of propagules attacked by predators and the understory density of mangrove seedlings of the same species observed at a given site. Mangrove "seedlings" were identified as rooted individuals < 30 cm tall, with < 20 leaves and without aerial roots. Seedling densities below the canopy was measured where possible (Ecuador, Venezuela and Malaysia) with a series ($N \geq 5$) of 1 m^2 quadrats laid along a belt transect through the stands. Where such sampling was not feasible, seedling densities were recorded for $N \geq 5$ haphazard 1 m^2 areas on the forest floor.

other two sites, reaching a mean final length of over 20 cm (Fig. 4). West Pond and Batis stand propagules grew at similar rates and reached similar final sizes despite differences in tree morphology and salinity between the sites. Propagule growth rates were similar between years at the Batis stand, but among the Wee Wee cohorts, year 2 propagules attained smaller final sizes than year 1 propagules. Nonetheless, Wee Wee propagules were significantly larger than Batis site propagules in year 2 (see above).

Abscission dynamics followed similar paths at all sites (Fig. 4), although the Wee Wee cohort of propagules abscised slightly sooner on average than the other populations. The Mantel-Haenszel log-rank test for censored survivorship data was used to discern differences in abscission dynamics among sites within years, and between years within sites (S-Plus for Windows, version 3.2, StatSci, Inc., Seattle, Washington). Propagule cohorts showed abscission dynamics that differed among sites in both the first year ($\chi^2 = 27.4$, $P < 0.0001$, 1 df) and the second year ($\chi^2 = 10.9$, $P = 0.0009$, 1 df). West Pond propagules were the slowest to abscise in year 1, while Wee Wee propagules dropped relatively quickly in both years. The Wee Wee cohorts of propagules showed similar abscission rates in both years ($\chi^2 = 3.5$, $P = 0.063$, 1 df), while the Batis stand cohort abscised relatively earlier in year 2 than in year 1 ($\chi^2 = 6.2$, $P = 0.013$, 1 df).

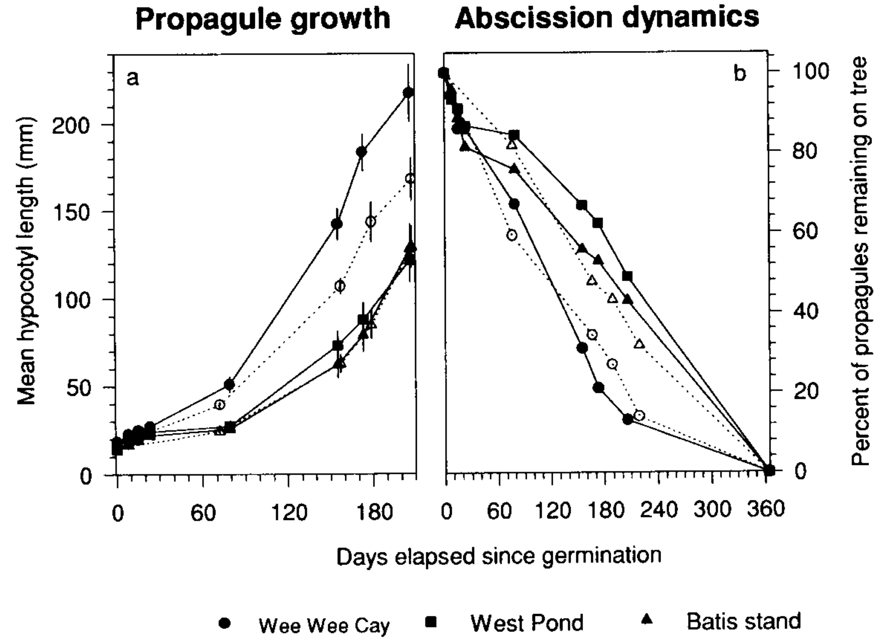

FIGURE 4. (a) Mean *Rhizophora mangle* propagule lengths (± SE.) and (b) percent of marked propagules remaining on trees at 3 sites in Belize. Filled symbols denote the 1991-92 cohort, open symbols denote the 1992–93 cohort.

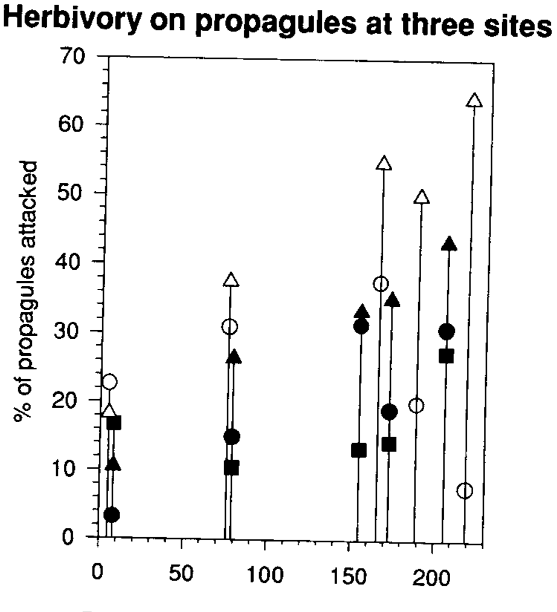

FIGURE 5. Propagule predation levels at 3 sites in Belize, on two cohorts of propagules still attached to parent tree, followed in 1991–92 (filled symbols) and 1992–93 (open symbols). Symbol shapes refer to sites as in Fig. 4. Apparent fluctuations in percent herbivory between sampling dates reflect the fact that previously attacked propagules often abscised early.

Predators attacked 3.2–64.3 percent of marked propagules at various times throughout the year (Fig. 5). The Batis stand consistently showed the highest percent attack, with the Wee Wee Cay population exhibiting intermediate levels of herbivory, and West Pond propagules the lowest. Most trees showed some proportion of propagules attacked. To investigate the putative impacts of propagule predation on pre-dispersal growth rate and propagule abscission, the behavior of 1992–1993 populations of damaged and undamaged propagules were examined separately. The mean relative growth rate ([length at 166 d − length at 76 d]/[length at 76 d]) of propagules eaten as of 11 March 1993 was compared between damaged and undamaged cohorts. Mean relative length increase of undamaged propagules (119 ± 120% [SD], $N = 105$) did not differ from that of damaged propagules (117 ± 110%, $N = 22$; $P = 0.95$ from independent-sample t-test). However, the proportion of damaged propagules that abscised prematurely by day 176 (40.5%) was nearly double that of undamaged propagules (27.6%).

DISCUSSION

Pre-dispersal propagule predation is a ubiquitous feature of mangrove forests throughout the world. More than a quarter of all propagules produced by these ten mangrove species on average are attacked while still on the parent tree. Levels of infestation are highly variable among regions and sites within regions, ranging from 0–93 percent of the propagule crop (Table 1). Our long-term data on the dynamics of propagule predation from Belize show comparable levels (3–64% of propagules attacked) with similar variability between sites and among years. Our static global survey, despite its inability to demonstrate temporal trends and interspecific differences within all sites, can confirm that pre-dispersal propagule predation reaches significant levels, and that similar types of predators operate throughout all mangrove forests. Three major guilds of polyphagous predators frequently attack propagules: scolytid beetles, lepidopteran larvae, and crabs. We have detected crabs and beetles in propagules throughout the world, while burrowing moth larvae are more common in the southern hemisphere (Table 1). Crabs damage the largest proportion of propagules in the widest array of sites; scolytids are the next most common propagule predator, and moths are a distant third.

Few biogeographic trends are apparent in either the type or frequency of propagule predation, although isolated Pacific Island stands exhibit slightly lower levels of damage than continental sites (Fig. 2). The full complement of propagule predator guilds are present on these islands, so lack of predator diversity or colonization does not appear to explain this pattern. Of interest is the fact that *Rhizophora* is a relatively recent introduction to some Pacific Islands, although the date and source of human introductions are definitively known only for Hawaii. *Rhizophora samoensis* may (McCoy and Heck 1976) or may not (Ricklefs and Latham 1993) be a recent introduction in Fiji, Samoa and Tonga. The relatively low attack rates at these sites (Table 1) could reflect a recent introduction if predators have had less time to colonize a new host. Our single survey is suggestive, but could not test this hypothesis directly. Other archipelagos, such as the Galápagos Islands, support high levels of propagule infestation.

Likewise, proximity of a site to high-density population centers or vulnerability to anthropogenic disturbance cannot be linked definitively to high predation rates within a region. Attack rates peak near the urban centers of Durban, South Africa; Sungei Sementa Kecil/Kuala Selangor, Malaysia; the densely settled Sunderbans region of India; and the village of Gurong, Yap Island. These stands show higher levels of attack than more isolated stands within the same region (Fig. 2: St. Lucia Estuary, South Africa; Sibu Island, Malaysia; Andaman Islands, India; and northwest Yap, respectively). However, the uninhabited Cartago mangrove stand in the Galápagos Islands also shows extensive propagule predation. Both disturbed and undisturbed stands show highly variable levels of herbivory, and commonalities among sites showing high infestation are difficult to detect from a single static survey.

In Belizean sites, where we have followed three populations of propagules over two production seasons, we notice that propagule herbivory patterns appear to parallel leaf herbivory trends comparing among trees growing in the low intertidal (Wee Wee Cay) and the high water interior (Batis stand). Propagules on low-intertidal trees exhibit lower levels of damage, a pattern also noted in leaves (Farnsworth & Ellison 1991). Comparing low-intertidal *versus* upland sites around the world (Table 1), we obtain the same result: propagules on fringing trees in the low tidal zones exhibit approximately half the pre-dispersal attack rates as high-water propagules. Similarly, Smith (1987a) found significantly higher crab predation rates on propagules of high-intertidal *Avicennia marina* in Australia. This pattern apparently does not result from differences in propagule availability among low and high tidal sites (in this survey, $n_{low} = 1733$, $n_{high} = 1566$ propagules surveyed). Rather, it may reflect foraging preferences of the major predators involved. Beetles, crabs and moths may have more opportunity to attack propagules on high and dry trees. In Belize, propagules from the hypersaline West Pond site exhibited the lowest levels of predation in year 1. Crab and insect densities may be lower in this site; for example, non-predator fiddler crabs (*Uca* spp.) predominate over grapsids (EJF, personal observation). Alternatively, salt content or other chemical constituents of the West Pond propagules may differ from those at less saline sites, deterring predators, especially tissue borers. A third possibility is that high temporal variability in reproduction at this site (trees did not reproduce in year 2) may confound predator populations (*e.g.*, Solbreck & Sillén-Tullberg 1986, De Steven 1981).

Within a site where multiple mangrove species are present, a single species of mangrove usually receives the majority of attacks. For example, *Bruguiera gymnorrhiza* exhibits high propagule damage in Kosrae and the Sunderbans, while predators are less concentrated on co-occurring *Rhizophora* and *Avicennia* species (Fig. 2). Herbivory rates are slightly, but not significantly, higher in multi-species mangrove stands. The Belize study demonstrates that most trees are eventually attacked to some degree; predators are evenly spread among reproductive host plants, even though reproduction itself is spatially patchy. Such a dispersion pattern implies that most propagules are highly apparent resources for predators, and thus should exhibit high levels of quantitative defenses such as phenolics (Coley 1983). Smith's (1987b) analyses confirm high tissue concentrations of tannins and other phenolics in propagules.

Though the major predators are generalists, some partitioning of hosts is apparent, possibly reflecting the many interspecific chemical and physical differences among propagules (Smith 1987b). Our survey was too coarse in many cases to distinguish individual predator species (especially insects, for which taxonomy is still under revision, Rau & Murphy 1990); herbivore species biogeography and evolution deserve their own study. For example, scolytid beetles, which may rear entire haplo-diploid generations inside propagules and utilize specialized pheromone signals (Raffa 1991), may potentially undergo rapid species radiation among hosts and sites.

What are the ramifications of pre-dispersal propagule predation for seedling establishment and stand structure in mangroves? Onuf *et al.* (1977), Robertson *et al.* (1990) and Clarke (1992) also found high levels of predation on mangrove propagules, suggesting that this highly apparent and concentrated resource attracts predators in high numbers. Although predators may damage a large proportion of propagules, their effects on propagule growth and eventual seedling establishment are less clear. Rabinowitz (1977) found that growth of individually planted *Rhizophora mangle* propagules was not impaired by low initial borer damage in the neotropics, while Onuf *et al.* (1977) observed impaired establishment at higher levels of infestation. However, Robertson *et al.* (1990) showed that insects can decrease survivorship of Australian *Xylocarpus* spp. and *Bruguiera parviflora* Wight and Arnold ex Griffith, and hinder growth of *Avicennia marina* and *Bruguiera exaristata* Ding Hou, but do not increase mortality of *Rhizophora stylosa* and *Bruguiera gymnorrhiza.* According to our global survey, crabs inflicted primarily superficial epidermal damage, and probably contributed less to individual propagule mortality, despite their higher frequency, than scolytids and moths that burrowed into and destroyed the interior of the hypocotyl.

Our data on marked propagules confirm that those that remain on the parent tree can compensate for minor damage, and do not show reduced growth rates. Importantly, though, we found higher abscission rates of damaged propagules relative to undamaged propagules (41% *vs.* 28%). Clarke (1992) also described higher fruit abortion rates associated with predation by phycitine moths in *Avicennia marina,* against a baseline of already high maternally-regulated abscission. Premature abscission removes a seedling population that cannot be accounted for in static post-dispersal predation surveys (Robertson *et al.* 1990). Maternal abortion may be one mechanism by which mangroves jettison both damaged propagules and predators.

If both pre- and post-dispersal predators consume a substantial proportion of the progeny of a particular species of mangroves in a given area, one might expect lower seedling recruitment of conspecifics in the understory. Smith *et al.* (1989) made a case for this hypothesis in a comparative survey of forests on three continents, and Bertness *et al.* (1987) suggested a similar scenario for temperate-zone salt marshes. Our data support the notion that mangrove seedling density is correlated negatively with the intensity of pre-dispersal propagule predation (Fig. 3). However, our low *r*-value indicates that much of the variation in seedling density remains to be explained by factors other than pre-dispersal herbivory. Propagule maturation rates as well as seedling growth and establishment vary among years and sites (Fig. 4) owing to multiple factors impinging on the maternal and edaphic environments (*e.g.,* Ellison & Farnsworth 1993). Post-dispersal predation may remove a further 75 percent of propagules from the seedling cohort in a given year (Smith 1987a). Likewise, predation rates and reproductive output both vary temporally, as our Belize data show (Fig. 5).

Our study, combining static and dynamic observations, demonstrates the ubiquitous presence, and ecological importance of pre-dispersal propagule predators on mangroves worldwide. The advantages of vivipary clearly entail costs. Estimates of the standing stock of mangrove propagules available for natural regeneration or assisted restoration must account for loss due to these very common agents.

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