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Factors limiting the intertidal distribution of the mangrove species *Xylocarpus granatum*

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Abstract The tree species *Xylocarpus granatum* is commonly described as occurring in the upper intertidal zone of mangrove forests, but mature trees are occasionally found at lower elevations. In the Utwe River basin, on the Pacific island of Kosrae, we investigated the relative importance of several biotic and abiotic factors that may control the intertidal distribution of *X. granatum*. Factors we evaluated included differential seed predation across the lower, mid, and upper intertidal zones and seedling responses to salinity, tidal flooding, and shade. Seed predation was 22.4% over the first 34 days and varied little among zones or in gaps versus under the forest canopy. By day 161, there were still no differences in seed mortality, but a significant difference was found in seedling establishment, with much greater establishment in the upper intertidal plots. *X. granatum* seedlings in a greenhouse experiment exhibited greater growth in freshwater than seedlings in 23 ppt salinity, which is typical of salinity levels found in the mid intertidal zone in our field study sites in Micronesia, where mature *X. granatum* trees are generally absent. Seedlings grown in 23 ppt salinity, however, exhibited few visible signs of stress associated with patterns in growth. Seedlings grown in a simulated tidal flooding treatment (with 23 ppt salinity) also showed few signs of stress. Growth declined dramatically under 80% shade cloths, but there were few interactions of shading with either 23 ppt salinity or simulated tidal flooding. Differential seed predation is not likely to be the primary factor responsible for the intertidal distribution of *X. granatum* on Kosrae. However, seedling tolerance of flooding or salinity may be more important, especially relative to a potential contribution to secondary stress mortality. Other factors may ultimately prove to be more critical, such as physiological effects of salinity on seed germination, effects of tides on seed dispersal and rooting, or differential herbivory on seedlings.

Keywords Kosrae · Federated States of Micronesia · Seed predation · Salinity tolerance · Flood tolerance

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Introduction

Patterns of mangrove tree species zonation have been the subject of scientific interest for many decades (Watson 1928; Davis 1940; Egler 1950; Macnae 1968; Chapman 1976). Numerous factors influencing species zonation patterns have been proposed, including physiological adaptations to flooding and salinity, differential propagule dispersal, differential propagule predation, interspecific competition, forest succession following land building, and responses to geomorphological processes (Louda 1989; Smith 1992). The relative importance of these factors, however, has been examined systematically for only a few species (Smith 1992; Clarke and Myerscough 1993; McKee 1993; McGuinness 1997a).

One of the proposed factors that has been the subject of considerable recent attention is seed or propagule predation and particularly how it varies across the intertidal zone, in gaps versus the forest canopy, and in relation to the dominant tree species in the forest canopy (Smith 1987a; Smith et al. 1989; Osborne and Smith 1990; McKee 1995; McGuinness 1997a, 1997b; Patterson et al. 1997; Sousa and Mitchell 1999). Most mangrove species produce propagules that are effective at dispersing at least locally, so predation might be regarded as the first potentially critical post-dispersal factor affecting the ability of a species to establish itself across the whole intertidal range of a given river basin or estuary. Assuming that a species can disperse its propagules effectively across the whole intertidal zone and that

predation across that range is <100%, the next factors affecting a species' ability to establish across the entire intertidal zone would be the species' physiological tolerance to the range of tidal flooding, salinity, and light conditions encountered.

In this study, we examined the importance of these potential factors: differential seed predation and tolerance of flooding, salinity, and shade, as they affected the intertidal distribution of *Xylocarpus granatum* König, a mangrove species ranging from East Africa to islands in the central Pacific Ocean (Mabberley et al. 1995). Specifically, our objectives were to determine: (1) the level of seed predation on *X. granatum* across a range of intertidal positions and light levels, and (2) the survival and growth responses of *X. granatum* seedlings to combinations of tidal flooding, salinity, and shade.

Our interest in *X. granatum* stems from our experience working in the Federated States of Micronesia. The species is of considerable economic importance on some Micronesian islands, where it is commonly used for wood carvings and occasionally used for furniture and interior construction. Also, although the species is often described as occurring on the landward edge, or upper intertidal zone, of mangrove forests (Macnae 1969; Percival and Womersley 1975; Wells 1982), there are a number of intriguing situations in Micronesia and elsewhere (e.g., Chapman 1976; Bunt et al. 1982; Wells 1982) where mature trees of this species are found growing at lower elevations or at higher salinities than might be expected of a landward edge species. These types of observations suggest that the distribution of *X. granatum* cannot be explained simply by physiological limitations such as tolerance of tidal flooding or salinity.

Materials and methods

Study site

The field portion of this study was conducted on the island of Kosrae (5°19'N, 163°00'E) in the Federated States of Micronesia. Kosrae is a small (112 km^2) volcanic island, with relatively evenly distributed annual rainfall of 5,000–6,000 mm. Typhoons and other large-scale natural disturbances are rare in the region (Ray 1999; Allen et al. 2001). The high rainfall and flat topography of Kosrae's coastal plain allow for the development of extensive mangrove forests, which cover approximately 14% of the land area and two-thirds of the coastline (Whitesell et al. 1986). Eleven mangrove tree species, including one hybrid, are present on the island (Duke 1999), of which *Sonneratia alba* J. Smith, *Bruguiera gymnorrhiza* (L.) Lamk, and *Rhizophora apiculata* BL are the most common (MacLean et al. 1988; Ewel et al. 1998a). All of the field work was conducted within the Utwe River Basin, located on the southern end of the island. The Utwe River is about 2 km long and drains an area of 600 ha; the intertidal zone containing mangroves is approximately 500 m wide from the landward edge to the bay. The tidal regime in the area is semidiurnal, with an average range of approximately 1 m (Nautical Software 1996). Large *X. granatum* trees and saplings are common in the upper reaches of the intertidal zone, and seedlings are occasionally encountered at lower elevations within the basin.

Seed predation experiment

Seed predation was examined experimentally using methods similar to those originally employed for mangroves by Smith (1987a). Mature fruits were collected directly from trees in April 1999 and air-dried until the pericarps began to split open. Seeds were then extracted and inspected for insect or other damage. Apparently undamaged seeds were selected and weighed to the nearest 0.1 g. Individual seeds were tethered with a 1/0 fishhook to 1-m lengths of line consisting of a 30-cm wire leader, 70 cm of nylon twine, and a plastic numbered tag. The lines were tied to prop roots, pneumatophores, or seedlings. Fifteen seeds were tethered in each of 18 plots, with six plots each in the lower, mid, and upper intertidal zones. Within each zone, three of the plots were located under the forest canopy and three were located in adjacent forest gaps (≥98 m^2 in area). Seeds were laid out in three rows, with 2-m spacing between rows and 1.5 m between seeds within rows to minimize entanglement of the lines. The canopy coverage in all plots was estimated by taking four spherical densiometer readings, facing in cardinal directions from the plot center. *Xylocarpus granatum* seeds and seedlings already present in the plots were subsampled with 1-m^2 quadrants, and the length and width of the gap plots were measured. Seeds were monitored 5 times over the first 34 days, and any damage, mortality, and root or shoot development were noted. Seeds were considered dead if >25% of their biomass was removed. Although other studies have used 50% removal as criteria for mortality in dealing with propagules (cf., Smith et al. 1989), 25% seemed to be a better criterion for *X. granatum* seeds. On not a single occasion did a seed with >25% damage during the first 34 days become established by the end of the experiment. Seeds were monitored twice more, at 73 and 161 days after tethering, to check for seed survival and evidence of seedling establishment.

Mean amounts of predation, expressed as percentages, were analyzed following a square root transformation using a split-plot ANOVA with a nested error structure. Intertidal zone served as the main plot while light level served as the subplot effect; the error structure included light level nested within intertidal position. Since predation was low throughout and most of the percent data fell at a range <20%, it was appropriate to use a square root transformation as opposed to an arc sine transformation (Lantican and Baldwin 1994). Results, however, differed little regardless of transformation used.

Seed chemical composition was evaluated for a sample of ten *X. granatum* seeds selected from the same batch used in the predation experiment. The seeds were dried at 70°C to a constant mass and submitted to the University of Hawaii's Agricultural Diagnostics Laboratory for analysis of ash, crude protein, crude fat, crude fiber, and total carbohydrates. A second batch of eight seeds were collected in September 1999 and submitted to the same laboratory for the same analyses, with the exception that the tough, fibrous seed coat was first removed and discarded.

Greenhouse experiment

Mature *X. granatum* fruits were collected directly from trees on Kosrae in April 1998 and transported to a greenhouse facility in Waimanalo, Hawaii. Fruits were air-dried until the pericarps began to split open; seeds were extracted, inspected for insect or other damage, treated with powdered Sevin (Carbaryl), and sown directly into 2.8-l plastic pots (Tall One, Stuewe and Son, Corvallis, Ore.) containing a commercial potting mix (Sunshine 1 Mix, SunGro Horticulture, Bellevue, Wash.). Many seeds germinated quickly and were maintained for approximately 8 weeks after sowing in a greenhouse with screened sides and a roof of translucent fiberglass, which allowed transmittance of approximately one-third of full sunlight. Seedlings were maintained in the same greenhouse throughout the pre-experimental as well as the experimental growth phases.

Seedlings were fertilized initially with 3.6 g l^{-1} pot volume of a controlled-release 14-14-14 NPK fertilizer (Graviota, Brewer

Environmental Industries, Honolulu, Hi.), and starting 46 days after the experiment began, seedlings were fertilized approximately every 15 days with a water-soluble 20-20-20 NPK fertilizer with micronutrients (Peters Professional, United Industries, St. Louis, Mo.) at an average rate of 0.13 g l^{-1} pot volume. Both before and after initiation of the treatments, the seedlings were periodically sprayed with Dursban 50 W (Chlorpyrifos) and treated with Marathon (Imidacloprid; a systemic granular) to control insect infestations, particularly by black twig borers (*Xylosandrus compactus*), a common greenhouse, nursery, and orchard pest in Hawaii (cf., Solomon 1995).

Seedlings were then randomly assigned to one of six treatment combinations of light and tidal flooding/salinity as follows: (1) unshaded, <0.5 ppt salinity; (2) unshaded, 23 ppt salinity; (3) unshaded, 23 ppt salinity plus tidal simulation; (4) 80% shade, <0.5 ppt salinity; (5) 80% shade, 23 ppt salinity; and (6) 80% shade, 23 ppt salinity plus tidal simulation. The salinity level of 23 ppt was chosen to approximate the mean salinity levels found in the interior and riverine mangroves (i.e., lower and middle intertidal zones) of Kosrae (Krauss and Allen, in press; Ewel et al. 1998a).

Salinity treatments were created with a commercial seawater mix that closely approximates the true ionic composition of seawater (Forty Fathoms Marine Mix, Marine Enterprises, Baltimore, Md.). Seedlings were acclimated to the 23 ppt salinity treatments gradually with an initial 3-day freshwater (<0.5 ppt) flood, followed by a rise in salinity to 5 ppt for 4 days, a rise in salinity to 13 ppt for 11 days, and, finally, a rise in salinity to 23 ppt. Pots were flooded to 14 cm below the soil surface, which, due to capillary movement of water, ensured that the entire soil volume remained saturated. In the tidal simulation treatment, water levels were maintained to simulate a semidiurnal tide, which is common throughout Micronesia. Each flood cycle was approximately 2 h in duration with flow simulations taking approximately 5 min to reach maximum tidal heights and ebb simulations taking approximately 15 min to drain tanks. At high tide, seedlings were flooded to approximately 4 cm above the soil surface and were drained to approximately 28 cm below the soil surface at low tide. Flooding regimes were not of sufficient duration to induce permanent anaerobic conditions to any of the hydrologic treatments. Average pH-unadjusted redox potential of the soil matrices across all three hydrologic treatments at 7 cm below the surface was +316 mV.

Shading was created artificially using 80% neutral density, black knitted shade cloths (DeWitt Company, Sikeston, Mo.). Photosynthetic photon flux density (PPFD) in the unshaded treatments within the greenhouse attained maximum levels between 700 and 800 μmol m^{-2} s^{-1}, whereas shaded treatments attained maximum levels around 100 μmol m^{-2} s^{-1}. Measurements of maximum midday PPFD from an open site on Kosrae indicated a light level of 2,223±221 (SE) μmol m^{-2} s^{-1}. Assuming that 1.8–3.4% above canopy light reaches the mangrove understory (c.f., Sherman et al. 2001), approximately 40–76 μmol m^{-2} s^{-1} of light would be expected for Kosrae. Smith (1987b), on the other hand, reported 100–350 μmol m^{-2} s^{-1} of light under an Australian mangrove canopy, which may be more representative of sites in Kosrae owing to similar species assemblages. The temperature of the water in the unshaded and shade treatments averaged 25.3°C and 25.5°C, respectively, and did not differ significantly (P=0.7731).

Each individual treatment combination was imposed in a separate 378-l tank with a small submersible pump (circulation rate of 44 l min^{-1}) on the bottom to keep the water well-mixed, though not aerated. Each treatment combination was replicated 3 times, with replicates consisting of a total of 54 seedlings – nine per salinity/shade combination. In all, we evaluated the growth response of a total of 162 seedlings.

Height and diameter measurements were taken at the beginning of the experiment and at approximately bimonthly intervals. Numbers of leaves were also counted and observations were recorded on leaf condition and the presence of black twig borer damage at each measurement interval. After a treatment period of approximately 25 weeks, lengths of the top five nodes of each seedling were measured, and seedlings were harvested and separated into roots, stems, and leaves. Total leaf area was measured for each seedling using a Li-Cor Model 3100 leaf area meter (Li-Cor, Lincoln, Neb.), after which roots, stems, and leaves were dried at approximately 70°C to a constant mass and weighed on an analytical balance. Several additional variables were calculated from harvest data, including individual leaf area (cm^2), specific leaf area (cm^2 g^{-1}), leaf weight ratio, stem weight ratio, and root:stem ratio. Leaf and stem weight ratios were calculated as the biomass proportion of either leaves or stem to the biomass of the entire seedling.

After biomass was determined, all leaves from one seedling in each treatment combination and replication (n=18) were submitted to the University of Hawaii's Agricultural Diagnostics Laboratory for foliar nutrient analysis. There, macronutrient concentrations of N, P, K, Ca, Mg, and Na as well as micronutrient concentrations of Mn, Fe, Cu, Zn, and B were determined.

Data for growth parameters were analyzed using analysis of covariance, with a split-plot design (light level being the main plot treatment, and salinity or tidal flooding being the subplot). Initial height was used as the covariant except for final diameter and leaf count in which case their respective initial measurements were used. Significant relationships were found between measurements for all variables at harvest and assigned covariants, except for specific leaf area. ANOVA procedures were used for analysis of specific leaf area and foliar nutrient data. All growth data were first square-root transformed to improve homogeneity of variances. Salinity effects were evaluated by comparing the <0.5 ppt and 23 ppt soil water treatments only. Tidal flooding effects were evaluated by comparing the 23 ppt soil water salinity treatment and the tidal simulation treatment only, which also had water of 23 ppt.

Results

Seed predation

Plots established under the forest canopy were fairly well shaded, with an average of only 3.3% (±0.56% SE) open canopy across all intertidal locations. Gap plots were established within gaps ranging in size from 98.1 to 209.1 m^2, which corresponded to between 12.2 and 60.8% open canopy, depending upon not only gap area, but also stand height. Stand heights in the lower intertidal zones were shorter and therefore more sunlight could reach tethered seeds for a given gap size. Vegetation in the lower intertidal zone was dominated by short-statured *Rhizophora stylosa* Griff., *R. apiculata, B. gymnorrhiza*, and *S. alba*. In the mid and upper intertidal zones, the canopies were taller; therefore, gaps of comparable size allowed less light to reach the tethered seeds (21.1±2.9% open canopy vs. 43.7±12.6% for the lower intertidal). The mid intertidal zone was dominated mostly by *B. gymnorrhiza*, with some plots having *S. alba* and *R. apiculata* as a co-dominant. The species composition of the upper intertidal zone differed from the other two zones in that 26.9% was composed of *X. granatum* saplings or trees. Both *B. gymnorrhiza* and *S. alba* as well as the occasional *R. apiculata* and *Barringtonia racemosa* (L.) Spreng. composed the remainder of the upper intertidal forest. Only upper intertidal plots had mature *X. granatum* trees, seeds, or seedlings, though occasional seedlings were seen near our mid intertidal plots. The average number of *X. granatum* seeds and seedlings in upper intertidal zone plots was 0.5 and 1.8 m^{-2}, respectively.

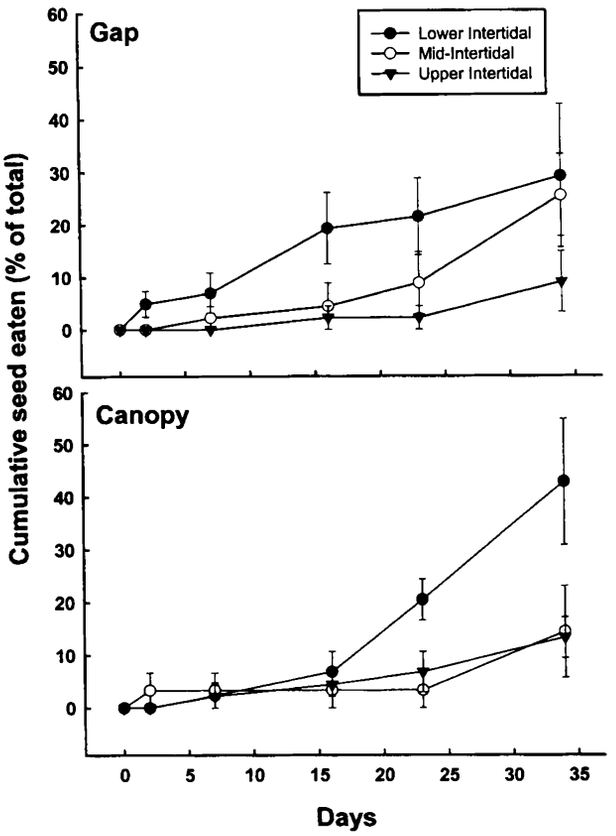

Fig. 1 Cumulative amount of *Xylocarpus granatum* seeds with 25% or more biomass consumed by crabs at several contrasting intertidal positions and two levels of canopy shading (full intact canopy vs. gap) in the Utwe River basin over the first 34 days

Virtually 100% of the seeds had some evidence of crab (91.0%) and/or insect (66.7%) damage after 34 days; however, the overall mean proportion of seeds killed by predators, defined as seeds at least 25% consumed, was only 22.4%. Differences in the proportion of seeds consumed at day 34 were not significant for intertidal zone ($F_{2,2}$=2.68; P=0.2721), gap versus canopy plots ($F_{1,2}$=0.06; P=0.8309), mean densiometer reading (r^2=0.042; P=0.4154), or gap size (r^2=0.235; P=0.1869). There was also no significant predictive relationship between seed mass and likelihood of predation (r^2=0.028; P=0.0090).

On most of the plots, the proportion of seeds consumed increased relatively steadily throughout the entire 34-day period (Fig. 1). Although overall seed deterioration precluded the collection of additional data on crab or insect damage at days 73 and 161, evidence of fresh damage was noted for some seeds at both times, suggesting that *X. granatum* seeds are subject to predation for an extended time period.

By day 73, and especially by day 161, potentially important differences in seedling establishment among the intertidal zones were apparent (Fig. 2). Although the amount of seed mortality was not significantly different among the three zones for day 73 ($F_{2,2}$=11.96; P=0.0771) or day 161 ($F_{2,2}$=8.05; P=0.1105), a significantly greater proportion of the surviving seeds had successfully anchored their roots into the soil and developed shoots in the upper intertidal plots by day 161 ($F_{2,2}$=21.68; P=0.0441). No statistical differences were found for either seed mortality or seedling establishment in gap versus canopy plots on days 73 and 161.

Seed chemical composition

Mean seed mass and crude chemical composition of ten *X. granatum* seeds selected from the same batch used in the predation experiment were contrasted with published data on eight other mangrove species (Table 1). *X. granatum* seeds are highly variable in mass but are generally larger than propagules of the other species. Crude chemical composition also differed from the other species, particularly in crude fiber content. Although a substantial portion of the crude fiber is in the tough seed coat, a smaller sample of seeds submitted for analysis with their seed coats removed also had a high crude fiber content (Table 1).

Table 1 Properties of mangrove propagules used in past predation studies as well as in the current study

Species	Cumulative predation (%, ±SE)	Physical and chemical properties (%, ±SD)						Source
		Fresh mass (g)	Ash	Crude protein	Crude fat	Crude fiber	Total carbohydrates	
Avicennia germinans[a]	60.0±8.0	1.0±0.2	4.7±0.7	–	–	–	–	McKee (1995)
Rhizophora mangle[a]	18.0±5.0	10.1±2.4	3.8±0.4	–	–	–	–	McKee (1995)
Laguncularia racemosa[a]	28.0±9.0	0.3±0.1	8.6±2.1	–	–	–	–	McKee (1995)
Avicennia marina[a]	96.0±1.8	3.4±0.9	–	2.4±0.3	8.0±1.5	1.6±1.7	61.5±4.2	Smith (1987a)
Bruguiera exaristata[a]	73.7±5.9	3.0±0.6	–	6.1±1.4	18.2±3.0	5.2±0.8	44.6±3.5	Smith (1987a)
Bruguiera gymnorrhiza[a]	59.0±6.4	19.8±9.5	–	6.5±1.1	9.5±1.6	11.0±1.8	31.2±3.1	Smith (1987a)
Ceriops tagal[a]	71.7±4.3	1.4±0.3	–	5.6±1.1	7.7±2.3	19.4±6.5	22.8±4.3	Smith (1987a)
Rhizophora stylosa[a]	50.4±10.9	30.3±10.4	–	5.3±0.5	5.3±1.3	21.4±2.0	38.2±3.8	Smith (1987a)
Xylocarpus granatum (entire seed)	22.4±8.6	40.7±21.8	2.8±0.6	3.4±0.6	2.0±0.4	55.1±9.9	36.6±10.6	Present study
X. granatum (cotyledon only)	–	–	3.0±0.8	5.1±0.7	4.1±0.9	42.9 ±5.1	45.0±6.6	Present study

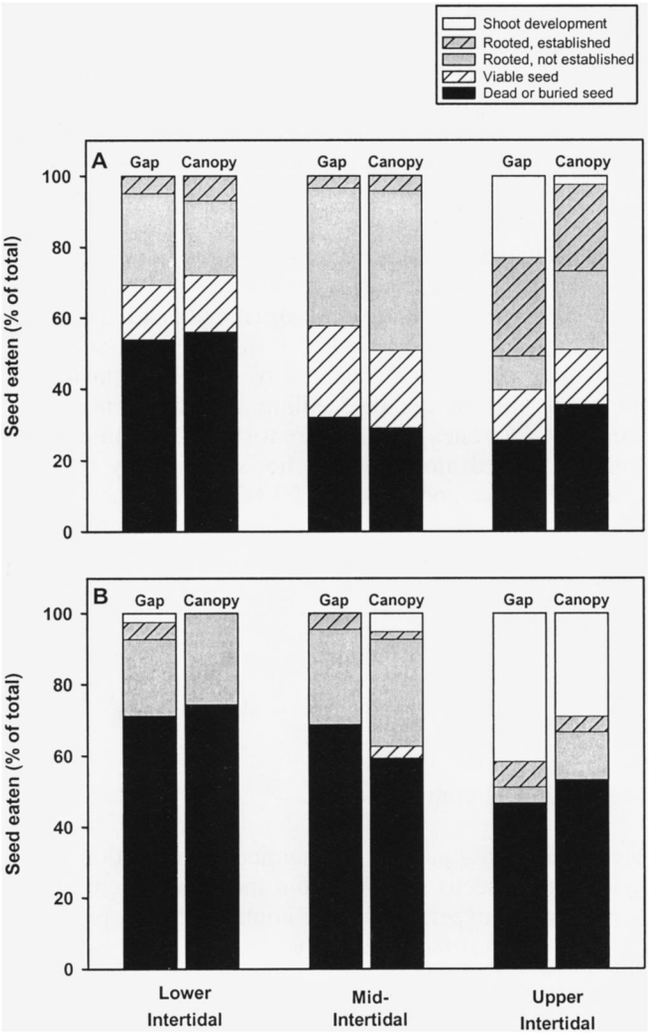

Fig. 2 Condition of *X. granatum* seeds tethered in the Utwe River basin after **A** 73 days and **B** 161 days. Seedlings with shoot development and rooted were considered to be successfully established within the respective intertidal and/or canopy locations

Seedling responses to salinity, tidal flooding, and shade

Survival of *X. granatum* seedlings subjected to the salinity/flooding regime and shade treatments in the greenhouse for 25 weeks was 93%. Virtually all of the 11 seedlings that died are believed to have been killed by black twig borers rather than by the effects of the treatments themselves. Seedlings killed by the black twig borer all had similar patterns of decline, characterized by rapid wilting of the leaves and the presence of bore holes on the stem. Approximately 28% of the surviving seedlings showed some evidence of attack by black twig borers; mainly, the presence of dried sap around a borehole indicated a successfully repelled attack. The growth of surviving seedlings appeared to be relatively unaffected, with some of the largest seedlings in the experiment being among those with signs of black twig borer attack.

Table 2 Means for growth response variables (±SE) measured for *Xylocarpus granatum* seedlings subjected to different combinations of sunlight, salinity, and tidal flooding. *FS* Freshwater saturation, *SS* saltwater saturation, *TS* tidal simulation, *wt* weight

Variable	Unshaded				80% Shade			
	FS	SS	TS	Mean	FS	SS	TS	Mean
Height (cm)	93.1±4.5	86.1±4.1	89.0±4.7	89.4±2.5	55.6±3.1	58.3±3.5	62.2±3.0	58.6±1.8
Diameter (mm)	12.3±0.6	10.5±0.5	11.7±0.5	11.5±0.3	6.2±0.2	6.2±0.3	6.8±0.3	6.4±0.1
Leaves (no.)	53.4±4.1	46.7±3.2	50.4±5.3	50.1±2.4	18.3±1.8	18.5±1.7	18.6±2.2	18.5±1.1
Leaf biomass (g dry wt)	20.5±1.8	16.4±1.2	18.4±2.2	18.4±1.0	4.9±0.6	5.0±0.6	5.2±0.7	5.0±0.4
Stem biomass (g dry wt)	23.3±3.0	15.7±1.9	16.4±2.1	18.5±1.4	3.1±0.3	3.6±0.5	4.5±0.5	3.7±0.3
Root biomass (g dry wt)	15.0±2.1	9.3±1.1	9.1±1.0	11.1±0.9	2.4±0.2	2.9±0.3	3.4±0.4	2.9±0.2
Total biomass (g dry wt)	58.9±6.7	41.4±4.0	43.9±5.2	48.0±3.2	10.3±1.1	11.5±1.4	13.1±1.5	11.6±0.8
Leaf area (cm^2)	2,111.5±173.8	1,780.4±122.7	2,063.1±260.0	1,981.2±109.8	679.7±94.7	646.7±79.1	657.6±86.3	661.6±49.7
Individual leaf area (cm^2)	40.2±1.9	38.3±1.4	39.4±1.5	39.3±0.9	34.5±1.9	33.4±1.6	34.8±1.8	34.2±1.0
Mean internode length (mm)	34.0±2.8	41.8±3.3	34.6±2.4	36.8±1.7	16.7±1.0	14.5±1.3	17.5±1.4	16.2±0.7
Specific leaf area ($cm^2\ g^{-1}$)	104.7±1.9	110.7±2.8	110.9±2.2	108.8±1.4	137.6±3.3	128.6±3.0	124.6±3.6	130.4±2.0
Leaf weight ratio	0.37±0.01	0.42±0.02	0.42±0.01	0.40±0.01	0.44±0.01	0.44±0.01	0.39±0.01	0.43±0.01
Stem weight ratio	0.38±0.01	0.36±0.01	0.37±0.01	0.37±0.01	0.30±0.01	0.30±0.01	0.34±0.01	0.31±0.00
Root:stem ratio	0.65±0.02	0.61±0.02	0.58±0.02	0.61±0.01	0.84±0.03	0.91±0.04	0.77±0.03	0.84±0.02

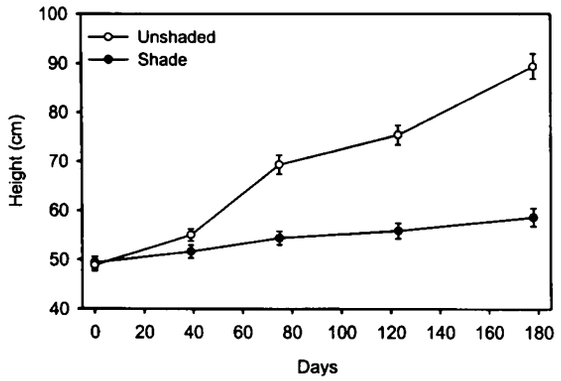

Fig. 3 Stem height growth (cm) of *X. granatum* seedlings subjected to different light environments for 25 weeks

Means for 14 response variables are presented by treatment in Table 2, and a summary of statistical differences is presented in Table 3. When seedlings were subjected to 23 ppt salinity, stem diameter and biomass, root biomass, and total biomass were reduced (Tables 2, 3) as compared with <0.5 ppt controls, but there were no significant effects on any other morphological variables measured. Compared to the 23 ppt salinity soil saturation treatment, seedlings in the tidal simulation treatment (i.e., periodic flooding with 23 ppt salinity water) differed by maintaining slightly greater mean root, stem, and total biomass as well as a higher mean stem weight ratio.

Shading had far greater effects on seedling growth and morphology than 23 ppt salinity or simulated tidal flooding. Unshaded seedlings were on average 52% taller, had 32 (171%) more leaves, and had >4 times as

Table 3 Significance values (*Pr>F*) from analysis of covariance for *X. granatum* seedlings subjected to different combinations of sunlight, salinity, and tidal flooding

Variable	Light	Salinity	Tidal flooding	Light×salinity	Light×tidal flooding
Height (cm)	**	NS	NS	NS	NS
Diameter (mm)	***	*	NS	NS	NS
Leaves (no.)	**	NS	NS	NS	NS
Leaf biomass (g dry wt)	***	NS	NS	NS	NS
Stem biomass (g dry wt)	***	*	*	NS	NS
Root biomass (g dry wt)	***	**	*	*	NS
Total biomass (g dry wt)	***	*	*	NS	NS
Leaf area (cm^2)	**	NS	NS	NS	NS
Individual leaf area (cm^2)	*	NS	NS	NS	NS
Mean internode length (cm)	**	NS	NS	*	*
Specific leaf area ($cm^2\ g^{-1}$)[a]	***	NS	NS	NS	NS
Leaf weight ratio	NS	NS	NS	NS	NS
Stem weight ratio	*	NS	*	NS	*
Root:stem ratio	***	NS	NS	**	NS
Significant variables (at α=0.05)	13	4	4	3	2

NS $P>0.05$, *$0.01<P<0.05$, **$0.001<P<0.01$, ***$P<0.001$

[a] ANOVA, instead of analysis of covariance, was used for specific leaf area

Table 4 Means for foliar micro- and macronutrient concentrations (±SE) of *X. granatum* seedlings subjected to different combinations of sunlight, salinity, and tidal flooding. For abbreviations, see Table 2

	Unshaded				80% shade			
	FS	SS	TS	Mean	FS	SS	TS	Mean
Macronutrient (%)								
N	1.32±0.37	2.16±0.16	2.53±0.02	2.01±0.21	2.46±0.26	2.69±0.18	2.35±0.13	2.50±0.11
P	0.17±0.02	0.13±0.02	0.16±0.01	0.15±0.01	0.18±0.04	0.17±0.02	0.19±0.02	0.18±0.01
K	1.73±0.13	1.47±0.24	1.61±0.14	1.60±0.10	1.77±0.13	2.31±0.19	2.40±0.30	2.16±0.15
Ca	3.53±0.31	3.28±0.11	3.37±0.17	3.39±0.11	3.87±0.11	3.65±0.30	3.65±0.18	3.72±0.11
Mg	0.33±0.03	0.20±0.04	0.24±0.01	0.26±0.02	0.42±0.08	0.35±0.02	0.33±0.04	0.37±0.03
Na	0.27±0.02	0.74±0.16	0.94±0.12	0.65±0.11	0.23±0.03	0.74±0.15	0.93±0.18	0.63±0.12
Micronutrient ($\mu g\ g^{-1}$)								
Mn	36.7±3.2	58.3±2.9	85.0±18.6	60.0±8.9	41.0±7.0	48.0±3.2	53.0±14.1	47.3±5.0
Fe	43.3±7.0	77.0±21.5	42.7±5.8	54.3±8.8	45.3±1.8	53.0±4.0	37.7±1.3	45.3±2.6
Cu	4.7±1.5	4.7±0.3	4.3±0.9	4.6±0.5	4.0±0.6	7.7±0.7	7.0±1.5	6.2±0.8
Zn	4.0±0.6	7.0±1.0	8.3±0.9	6.4±0.8	9.0±1.0	8.3±0.9	10.0±1.5	9.1±0.6
B	27.0±4.7	121.0±10.4	212.3±35.5	120.1±28.8	50.3±4.7	103.7±15.3	240.7±21.3	131.6±29.4
Ratio								
Na/K	0.16±0.02	0.54±0.14	0.61±0.13	0.43±0.09	0.13±0.01	0.33±0.07	0.39±0.05	0.28±0.05
Na/Ca	0.08±0.01	0.22±0.04	0.28±0.04	0.19±0.03	0.06±0.01	0.20±0.04	0.26±0.06	0.17±0.04

Table 5 Significance values ($Pr>F$) from ANOVA comparisons for foliar nutrient concentrations of *Xylocarpus granatum* seedlings subjected to different combinations of sunlight, salinity, and tidal flooding

Variable	Light	Salinity	Tidal flooding	Light×salinity	Light×tidal flooding
N	NS	*	NS	NS	NS
P	NS	NS	NS	NS	NS
K	*	NS	NS	NS	NS
Ca	NS	NS	NS	NS	NS
Mg	NS	*	NS	NS	NS
Na	NS	**	NS	NS	NS
Mn	NS	*	NS	NS	NS
Fe	NS	NS	*	NS	NS
Cu	*	NS	NS	NS	NS
Zn	NS	NS	NS	NS	NS
B	NS	**	**	NS	NS
Na/K	**	*	NS	NS	NS
Na/Ca	NS	**	NS	NS	NS
Significant variables (at α=0.05)	3	7	2	0	0

NS $P>0.05$, *$0.01<P<0.05$, **$0.001<P<0.01$, ***$P<0.001$

much total biomass as shaded seedlings (Table 2). Differences in seedling size between the shaded and unshaded treatments continued to increase throughout the experiment (Fig. 3). Seedling morphology also differed, with shaded seedlings having a greater specific leaf area and unshaded seedlings having a greater mean internode length.

Shading resulted in significant increases in concentrations of K and Cu in leaves but had no significant effects on other nutrients (Tables 4, 5). Compared to the freshwater treatment, exposure to 23 ppt salinity resulted in significantly greater Na, Mn, and B concentrations and greater Na:K and Na:Ca ratios in leaf tissue. Mg concentrations decreased with exposure to salinity (Table 4). Tidal simulation had few effects on nutrient concentrations in leaf tissue when compared to the 23 ppt salinity treatment. Interaction between light level and salinity or light level and tidal flooding were not significant for any variable, although K concentrations tended to decrease in the unshaded, 23 ppt salinity treatments but increase for the same salinity in the shade (Table 4).

Discussion

Effects of seed predation

Xylocarpus granatum seed predation in the Utwe River basin over the first 34 days (hereafter referred to as the initial rate or period) was low, in general, compared to reports for most other mangrove species evaluated elsewhere over similar or shorter time periods (Table 6). The initial seed predation rate of 22.4%, with little variation across the intertidal zone, does not seem likely to be the main factor limiting the intertidal distribution of *X. granatum* on Kosrae.

Interspecific differences in seed predation have been reported (Table 6) and might be explained for mangroves at least in part by differences in chemical composition. Propagules of species such as *Avicennia marina* (Forsk.) Vierh. and *A. germinans* (L.) Stearn, for example, tend to be high in nutritive value and have relatively few chemical defenses (Smith 1987a; McKee 1995). Such species tend to exhibit a pattern of very rapid initial predation. In contrast, the tough seed coat and relatively high fiber content of *X. granatum* seed (Table 1) might effectively slow the rate that predators can gain entrance to and consume the seeds, resulting in a more gradual increase in cumulative predation. The time period over which mangrove propagule predation is monitored, therefore, might be at least as an important a consideration as other factors, such as length of the tether used to secure the seed (McGuinness 1997c).

The relative importance of crabs and insects as seed predators on *X. granatum* seeds at our Micronesia study site was substantially different than that found by Robertson et al. (1990) in Queensland, Australia. Although they reported a very similar incidence of insect damage, an overall mean of 61.9% compared to 66.7% in our study, Robertson et al. (1990) reported a dramatically lower incidence of crab damage (7.4% vs. our 91.0%). The possibility of a biased (low) estimate of crab predation, however, was acknowledged by Robertson et al. (1990), since their survey did not account for propagules completely consumed or taken down burrows.

We are only aware of one other published account of extensive damage of *X. granatum* seeds by crabs (Dahdouh-Guebas et al. 1998), though such damage has also reportedly occurred to seeds sown on at least one other Micronesian island (Island of Pohnpei; H. Anson, personal communication). Although we did not directly observe crabs feeding on our *X. granatum* seeds, the pattern of damage we attributed to crabs, which generally included the removal of a substantial portion of the seed coat and seed contents and also included a total of 13.7% that were taken belowground, differed markedly from the obvious boreholes, tunnels, and frass associated with most insect damage. Robertson et al. (1990) noted that *X. granatum* seeds with three or more boreholes in the

Table 6 A summary of studies investigating cumulative and presumed crab predation on mangrove propagules. Columns indicate species investigated, whether significant effects among forest type/location were realized, duration of the investigation, geographical region, and source of data

Species	Cumulative predation, %±SE	Significant effect among treatments	Experiment duration (days)	Geographical region	Source
Aegialitis annulata	80.8±?	Yes	50	Northern Australia	Clarke and Kerrigan (2002)
Aegiceras corniculatum	–[a]	Yes	15	Northern Australia	Osborne and Smith (1990)
	100.0±0.0	Yes	50	Northern Australia	Clarke and Kerrigan (2002)
Avicennia alba	62.5±7.6	Yes	4	Malaysia	Smith et al. (1989)
Avicennia germinans	60.0±8.0	Yes	9	Belize	McKee (1995)
	72.0±8.8	Yes	4	Florida, USA	Smith et al. (1989)
	5.0±4.0	Yes	17	Saltmarsh, Louisiana, USA	Patterson et al. (1997)
	40.0±4.0	Yes	17	Mangrove, Louisiana, USA	Patterson et al. (1997)
	8.3±2.7[b]	Yes	28	Mid/Upper Intertidal, Panama	Sousa and Mitchell (1999)
	43.3±6.5[b]	Yes	28	Lower intertidal, Panama	Sousa and Mitchell (1999)
Avicennia marina	96.0±1.8	Yes	18	Northern Australia	Smith (1987a)
	57.7±6.9[c]	Yes	18	Northern Australia	Smith (1988)
	51.8±10.9	Yes	4	Northern Australia	Smith et al. (1989)
	~80.0±15.6	Yes	15	Northern Australia	Osborne and Smith (1990)
	100.0±?	No	20–22	Northern Australia	McGuinness (1997b)
	100.0±0.0[d]	No	47	Kenya, Africa	Dahdouh-Guebas et al. (1998)
	~80.0±<5.0	Yes	5	Intertidal mounds, New South Wales, Australia	Minchinton (2001)
	~20.0±<5.0	Yes	5	Intertidal flats, New South Wales	Minchinton (2001)
	97.1±?	Yes	50	Northern Australia	Clarke and Kerrigan (2002)
Avicennia officianalis	46.4±10.8	Yes	4	Malaysia	Smith et al. (1989)
	100.0±0.0[d]	Yes	14	Pambala, Sri Lanka, Asia	Dahdouh-Guebas (2001)
Bruguiera cylindrica	40.0±12.8	Yes	4	Malaysia	Smith et al. (1989)
Bruguiera exaristata	73.7±5.9	Yes	18	Northern Australia	Smith (1987a)
	63.0±?	Yes	20–22	Northern Australia	McGuinness (1997b)
	77.3±?	Yes	50	Northern Australia	Clarke and Kerrigan (2002)
Bruguiera gymnorrhiza	59.0±6.4	Yes	18	Northern Australia	Smith (1987a)
	57.7±6.9[c]	Yes	18	Northern Australia	Smith (1988)
	5.2±6.1	Yes	4	Northern Australia	Smith et al. (1989)
	100.0±0.0[d]	No	47	Kenya, Africa	Dahdouh-Guebas et al. (1998)
	93.3±6.7[d]	No	13	Galle, Sri Lanka, Asia	Dahdouh-Guebas (2001)
	50.0±25.2[d]	Yes	14	Pambala, Sri Lanka, Asia	Dahdouh-Guebas (2001)
	57.1±?	Yes	50	Northern Australia	Clarke and Kerrigan (2002)
	16.7±4.2	Yes	14	Kosrae, Micronesia	Krauss and Allen (in press)
Bruguiera parviflora	83.8±?	Yes	50	Northern Australia	Clarke and Kerrigan (2002)
Ceriops australis	70.6±?	Yes	50	Northern Australia	Clarke and Kerrigan (2002)
Ceriops decandra	57.1±?	Yes	50	Northern Australia	Clarke and Kerrigan (2002)
Ceriops tagal	71.7±4.3	Yes	18	Northern Australia	Smith (1987a)
	57.7±6.9[c]	Yes	18	Northern Australia	Smith (1988)
	83.0±?	No	90	Northern Australia	McGuinness (1997a)
	71.0±?	Yes	20–22	Northern Australia	McGuinness (1997b)
	93.3±6.7[d]	No	47	Kenya, Africa	Dahdouh-Guebas et al. (1998)

Table 6 (continued)

Species	Cumulative predation, %±SE	Significant effect among treatments	Experiment duration (days)	Geographical region	Source
Laguncularia racemosa	28.0±9.0	n/a	9	Belize	McKee (1995)
	2.7±1.5[b]	Yes	28	Mid/upper intertidal, Panama	Sousa and Mitchell (1999)
	28.3±5.7[b]	Yes	28	Lower Intertidal, Panama	Sousa and Mitchell (1999)
Rhizophora apiculata	57.7±6.9[c]	Yes	18	Northern Australia	Smith (1988)
	6.3±2.0	Yes	4	Malaysia	Smith et al. (1989)
	19.8±6.3	Yes	4	Northern Australia	Smith et al. (1989)
	76.7±18.6[d]	Yes	13	Galle, Sri Lanka, Asia	Dahdouh-Guebas (2001)
	33.3±17.6[d]	Yes	14	Pambala, Sri Lanka, Asia	Dahdouh-Guebas (2001)
Rhizophora mangle	7.0±7.1	Yes	4	Lower intertidal, Florida/Panama	Smith et al. (1989)
	0.5±0.6	Yes	4	Upper intertidal, Florida/Panama	Smith et al. (1989)
	18.0±5.0	Yes	9	Belize	McKee (1995)
	3.3±1.6[b]	Yes	28	Mid/upper Intertidal, Panama	Sousa and Mitchell (1999)
	29.2±5.6[b]	Yes	28	Lower Intertidal, Panama	Sousa and Mitchell (1999)
	28.3±9.9[e]	n/a	14	Oahu, Hawaii, USA	Steele et al. (1999)
	58.0±10.0	n/a	14	American Samoa	Steele et al. (1999)
Rhizophora mucronata	86.7±6.7[d]	No	47	Kenya, Africa	Dahdouh-Guebas et al. (1998)
	40.0±6.7[d]	Yes	14	Pambala, Sri Lanka, Asia	Dahdouh-Guebas (2001)
Rhizophora stylosa	50.4±10.9	Yes	18	Northern Australia	Smith (1987a)
	57.7±6.9[c]	Yes	18	Northern Australia	Smith (1988)
	19.2±?	Yes	20–22	Northern Australia	McGuinness (1997b)
	22.5±?	Yes	50	Northern Australia	Clarke and Kerrigan (2002)
Sonneratia alba	100.0±0.0[d]	No	47	Kenya, Africa	Dahdouh-Guebas et al. (1998)
X granatum	100.0±0.0[d]	No	47	Kenya, Africa	Dahdouh-Guebas et al. (1998)
	22.4±8.6	No	34	Kosrae, Micronesia	Present study

[a] Not able to obtain actual rates from publication
[b] Actual predation rates were attained from personal communication with Wayne P. Sousa, University of California, Berkeley
[c] Predation averaged across all five species studied (*A. marina, B. gymnorrhiza, C. tagal, R. apiculata, R. stylosa*)
[d] Values represent maximum (not average) predation rates from an individual replicate plot; actual rates obtained from personal communication with Farid Dahdouh-Guebas, University of Brussels, Belgium
[e] Predation on propagules caused by rats (*Rattus* sp.) and/or Indian mongooses (*Herpestes auropunctatus*) and did not necessarily result in propagule mortality

pericarp were much less likely to survive and grow well than seeds with fewer boreholes. Only 3.3% of the seeds in our study had more than two boreholes and, overall, it appears that crabs were responsible for greater damage and more seed mortality than insects.

Tolerance of salinity, tidal flooding, and shade

Seedlings growing in the 23 ppt salinity treatments survived as well as seedlings in freshwater, and, though growth was reduced significantly in some cases, there were no indications that 23 ppt salinity is enough to cause severe physiological stress. Leaf Na:K ratios in the presence of 23 ppt salinity, for example, averaged 0.61 or less, which is below the 1.0 level often associated with severe stress in glycophytes (Wyn Jones et al. 1979) and well below the levels reported for some other mangrove species (Downton 1982; Ball and Farquhar 1984; Naidoo 1985; Popp et al. 1985). The increase in Na associated with 23 ppt salinity apparently does not interfere substantially with the uptake of either K or Ca, which is believed to occur with many other plant species (Marschner 1986; Grattan and Grieve 1999). Lowered K concentrations with high light, however, suggests that there may be a more substantial ion imbalance at high light levels. This might explain why Popp et al. (1985) reported that *X. granatum* leaves collected from mature trees (presumably exposed to light levels in excess of those in our greenhouse experiment) had Na:K ratios >1.0.

Unfortunately, limitations on available greenhouse space prevented us from testing seedlings over a wider range of salinity levels, such as an optimal level of around 8 ppt (Hutchings and Saenger 1987; Smith 1992), a full-strength seawater treatment, and a fluctuating salinity treatment. We believe, however, that the 25-week exposure to 23 ppt salinity effectively demonstrates that *X. granatum* seedlings are capable of surviving on sites representative of at the least mid intertidal zones, where mature *X. granatum* trees are generally absent or quite rare. Our design does not allow us to rule out the possible detrimental effects of occasional higher salinity pulses, but *X. granatum* reportedly grows on sites with maximum salinity levels of 34 ppt (Wells 1982; Smith 1992), a level rarely exceeded in mid intertidal habitats on Kosrae (Ewel et al. 1998a). Also, Bunt et al. (1982), in their study of mangrove species distribution along five rivers in northern Queensland, singled out *X. granatum* as a species whose distribution is poorly correlated with river water salinity, which suggests that it can grow over almost the complete salinity range from freshwater to seawater. Seed production and periodicity, on the other hand, may be influenced by salinity, potentially having a significant effect on the overall propensity for regeneration in *X. granatum*. Highly mobile seeds from ebbing/flowing tides and upland runoff likely decreases this effect on Kosrae.

Likewise, our tidal flooding treatment (albeit with shallower flooding and less reduced conditions than might occur in some mid to lower intertidal habitats) did not exceed the physiological tolerance of the species. Wells (1982) reported that *X. granatum* can withstand considerable periods of inundation by freshwater but occurs most frequently on brackish sites flooded infrequently by seawater. Our results, coupled with field observations, suggest *X. granatum* can also withstand regular flooding similar to that experienced in areas with semi- diurnal tidal regimes with water of two-thirds the salinity of full-strength seawater.

Shading clearly reduces *X. granatum* seedling growth and therefore might limit the capability of *X. granatum* to become established under forest canopies. Gaps, however, are not uncommon in any of the intertidal zones (Ewel et al. 1998b) and therefore shading alone should not be a factor limiting the intertidal distribution of the species. Shading interacted significantly with salinity or tidal flooding for only a few growth variables (Table 3), which might be further evidence that the salinity and flooding regimes examined were not near the limits of *X. granatum* physiological tolerance.

Implications for further research

Of the factors examined in this study, limitations imposed on seedling growth by salinity or tidal flooding appear to exert a slightly greater influence on the intertidal distribution of *X. granatum* than seed predation, but none of the factors tested clearly control the species distribution. Physiological effects of salinity or flooding on seed germination, the influence of tides and freshwater loading on dispersal, or leaf herbivory on seedlings might ultimately prove to be more important factors than those tested in this study and could be fruitful topics for future research.

One phenomenon we observed in the mid and lower intertidal habitats was that seeds that escaped predation still largely failed to become rooted in the substrate. In many such cases, the radicle had emerged from the seed, but the seed remained loose on the soil surface. We do not know whether this failure to establish is due to the frequent movement of the seed by tidal action (which might break fine roots beginning to enter the soil), a physiological limitation on root development, or some other cause.

It is possible that a variant of Rabinowitz's (1978) tidal sorting hypothesis might apply to *X. granatum*, even though the original form of the hypothesis has been largely rejected (Tomlinson 1986; Smith 1992). Seeds of *Xylocarpus* species float well (Hutchings and Saenger 1987), and although most are believed to be nonviable by then, they are frequently found on Pacific islands far from where they are naturally established (Degener and Degener 1974; Nakanishi 1981, 1983; Hacker 1990). Could it be that their ability to float so well, combined with their relatively slow germination and rooting, effectively sort most *X. granatum* seeds out of lower intertidal zones that flood essentially every day?

Another observation we have made in the field is that *X. granatum* seedlings are relatively common in some areas where mature trees are absent. No other mangrove species on Kosrae exhibits a similar pattern. In virtually every case, we have observed that *X. granatum* seedlings are heavily attacked by leaf herbivores (as of yet unidentified). Differential herbivory across the intertidal zone, or on sites dominated by mature *X. granatum* trees versus those that are not, therefore might be an important factor. This could prove to be a variation of the dominance-predation model originally proposed for mangroves by Smith (1987a), in which seed predation is expected to be relatively low under canopies dominated by conspecifics and relatively high under canopies dominated by other species. In the case of *X. granatum*, it might be better regarded as a dominance-herbivory model.

Smith (1987a) noted that no single factor is likely to account for the distribution patterns of all 45 woody species then known to occur in Australian mangroves. We agree and further believe that even for a single species, observed patterns of distribution will rarely be traced to only one factor. Instead, they will be explained much more effectively by the interactions of several biotic and abiotic factors.

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