

Resistance of red mangrove (*Rhizophora mangle* L.) seedlings to deflection and extraction

Sophie D. Boizard · Stephen J. Mitchell

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Abstract Red mangrove (*Rhizophora mangle* L.) is the dominant tree species in the intertidal zone of ecosystems on the Atlantic shores of the Caribbean and tropical western Atlantic. The propagules of this species are initially buoyant, becoming negatively buoyant before rooting in a variety of substrates. After establishment, these seedlings form aerial roots, leading to communities of plants with complex networks of stems and aerial roots. While established mangrove communities assist in stabilizing coastlines, seedlings are susceptible to wave, current and wind energy and this limits the habitats that they can successfully colonize. In this experiment, the mechanical resistance of seedlings growing at five locations with different substrate and canopy conditions was tested. The 78 seedlings tested ranged in height from 27 to 47 cm, had between one and ten pairs of leaves but had not yet formed aerial roots. Seedlings were pulled horizontally. The reaction force at 20° deflection in four cardinal directions and then force to failure in the landward direction was measured. Seventy-five percent of the seedlings failed in the root system. The remainder failed near the base of the stem. Larger seedlings were more likely to fail at the roots. Seedlings growing outside of mangrove overstory on coral rubble were 3.5 times more strongly anchored than those growing within the mangrove overstory on sand. In spite of directional loading by waves and on-shore breezes, the deflection resistance did not vary systematically with pulling direction. Seedling anchorage varies among locations with different overstory and

substrate conditions, likely due to differences in competition and acclimation to wind and wave energy along with differences in rooting among substrates.

Keywords Failure resistance · Mangrove · Mode of failure · Natural disturbance · *Rhizophora mangle* · Wave damage · Wind damage

Introduction

Mangroves are a specialized group of woody plants that form intertidal fringing communities along the coastlines of continents, islands and atolls throughout the tropics. Mangroves grow in one of the most mechanically challenging environments of all plants, being subject to a gradient of wind and wave energy from quiet lagoon environments to shorelines with full exposure to tropical storms (Doyle and Girod 1997; Tomlinson 1986). These communities provide a number of critical ecosystem services including shoreline protection from waves, storms and tsunamis, fisheries, carbon fixation and tourism. They are under considerable pressure from development, and the projected consequences of global warming, sea level rise and increased storm severity, will place these ecosystems under further stress (UNEP-WCMC 2006). The biomechanics and disturbance ecology of mangroves are complex. While established mangrove communities appear mechanically robust and dissipate routine wind and wave energy (e.g. Mazda et al. 2006), they are periodically damaged by extreme winds, wind driven waves, and storm surge during severe storms. For example, Hurricane Mitch in 1999 destroyed over 90% of the mangroves on islands in Honduras through defoliation, uprooting, burial, and erosion (Cahoon et al. 2003). Stoddart (1963) reported similar

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S. D. Boizard · S. J. Mitchell (✉)
Department of Forest Sciences, University of British Columbia,
3041-2424 Main Mall, Vancouver, BC V6T 1Z4, Canada
e-mail: stephen.mitchell@ubc.ca

levels of loss on Turneffe Atoll, Belize after Hurricane Hattie. Category 1 hurricanes with sustained winds in excess of 119 km/h and storm surge of 1 m have a return period of 25 years in this portion of the Caribbean (Johnson and Watson 1999). In between these storms, routine wind, wave and current energy affect recolonization patterns.

Red mangrove (*Rhizophora mangle* L.) grows in tropical and subtropical regions of the Atlantic and Pacific Oceans and is the dominant mangrove species in the Caribbean. It is a typical mangrove species, well adapted to growing in the intertidal zone with high salt tolerance, aerial roots, and viviparous reproduction (Tomlinson 1986). Red mangroves are also highly morphologically plastic, forming closed canopied stands of tall single stemmed individuals on fertile, sheltered sites, and open dwarf forests of open multi-stemmed individuals on low fertility peats (Piou et al. 2006). The largest trees are typically the most susceptible to damage during storms (Roth 1992). Recolonization of red mangrove seedlings requires the arrival of propagules from dispersal sites (Bowman 1917; Davis 1940). These seedlings must take root before being buoyed away by tidal or by wave action (Sousa et al. 2007), and must withstand substrate scouring (e.g. Tanaka et al. 2007). One might think that this would limit recruitment to zones with very low energy, but mangroves do establish across a gradient of substrates and wave energy (Lugo 1980, Chi personal communication). Once established, seedlings must develop firm anchorage to withstand periodic and seasonal peak forces imposed by wind, currents, and waves. During the early stages of colonization, seedlings are single stemmed and individually isolated. Sometime after establishment, seedlings begin forming aerial prop roots and secondary branching, and where seedling densities are high enough, this leads to communities of plants with complex, inter-crossing networks of branches and aerial roots.

This study is part of a larger program of research on red mangrove disturbance and regeneration dynamics. The main objective of this study was to characterize the range, nature and mode of seedling resistance to horizontal loads as a function of seedling size, substrate and overstory canopy condition. In addition, a conceptual framework is presented that links the physical properties of red mangrove seedlings at successive stages of development and seedling mechanical behaviour when exposed to moving water and air.

Materials and methods

Study area

This study was conducted on Turneffe Atoll, 50 km east of mainland Belize, outside the Mesoamerican Barrier Reef. The atoll is *ca* 48 km long and 16 km wide and is

composed of low elevation islands or cayes. Our study sites were on reef-crest cayes along the eastern, storm-exposed side of the atoll. These low profile cayes are composed of sands and coral rubble and are fringed by red mangrove forests that are still expanding following the de-vegetation caused by Hurricane Hattie in 1961 (Stoddart 1963, Chi personal communication). Coral rubble consists of fragments of coral of irregular size (ranging from fine gravel to boulder) and shape, which are broken off and washed in from the reef crest during storms. The tides in this area are classified as mixed semidiurnal with an average range of less than 30 cm (Piou et al. 2006). The climate is tropical to subtropical, with distinct rainy and dry seasons. Annual rainfall ranges between 1,500 and 2,020 mm year⁻¹ (Piou et al. 2006). Winds are predominantly easterly, except during winter months, when the main climatic influences are cold fronts coming from North America, referred to as ‘Northers’ (Thom 1967). The likelihood of heavy rains and strong to catastrophic winds increases between July and November as a result of seasonal tropical storms and hurricanes typical of the Caribbean Region. The main coastal current flows from south-east to northward. However, the Gulf of Honduras is influenced by a anti-clockwise counter-current resulting in predominantly southerly water movements over the coastal shelf (Stoddart 1963).

Populations of red mangrove seedlings were sampled at five locations in close proximity to Calabash Caye (17°16′57.76″N, 87°48′41.96″W) on the east side of the atoll. The bathymetry and substrate particle size distribution within the study area indicates that energy due to tides and waves attenuates with distance from the reef (e.g. Hartstein and Dickinson 2006). The five sampling locations differed in the type of substrate (unconsolidated coral rubble, coral sand, and peat) and the degree of overstory red mangrove canopy under which they grew (canopy or open). Sand and rubble substrates are found both outside and within mangrove forests. However, since the peat is formed by leaf and fine root deposition, it is found only within or immediately adjacent to the areas of established mangrove canopy. Water depth at the locations with sandy substrates ranges from 0.15 to 0.40 m at high tide. On the rubble substrates, water depth at high tide ranged from 0 to 0.40 m. The rubble locations are closer to the reef crest than the sand locations. All locations were within 5 km of each other.

Soil characteristics

Each sampling location was approximately 30 × 40 m wide. Sample seedlings, substrate attributes, and canopy cover were obtained throughout each sampling location. Mangrove canopy cover was estimated with a convex spherical densiometer. Within each sampling location, six

sediment cores were taken with an aluminum cylinder coring device (7.5 cm diameter \times 40 cm depth). Particle size distribution analysis (PSDA) was performed using sieves. Cores extracted from plots within canopies were processed prior to sieving to separate the peat and root fraction from coral sediment. Large root material was separated by hand and root hairs and root fragments were separated by flotation. Roots were separated into two size categories (Coarse, >2 mm diameter; fine, <2 mm diameter), dried at 80°C and weighed. Coring the rubble locations was impractical. Instead, the surface particle size distribution (fine, 0.5–5 cm average diameter; medium, 5–20 cm average diameter, coarse, >20 cm average diameter) was visually estimated within a 20×20 cm quadrat. This method did not allow us to estimate the fraction of organic material or whether live roots or organic sediment were present within the substrate depth profile at coral rubble locations. The substrate resistance to penetration was measured with a soil penetrometer (precision 35 kPa, Dickey-John Corporation, Auburn, IL) every 5 cm to a depth of 40 cm. Two profiles were taken at each core location prior to coring and at each seedling location prior to pulling. Resistance to penetration was not sampled in rubble substrate because the cone penetrometer hit the point of refusal within the first few cm of substrate.

Morphometric measurement and pulling tests

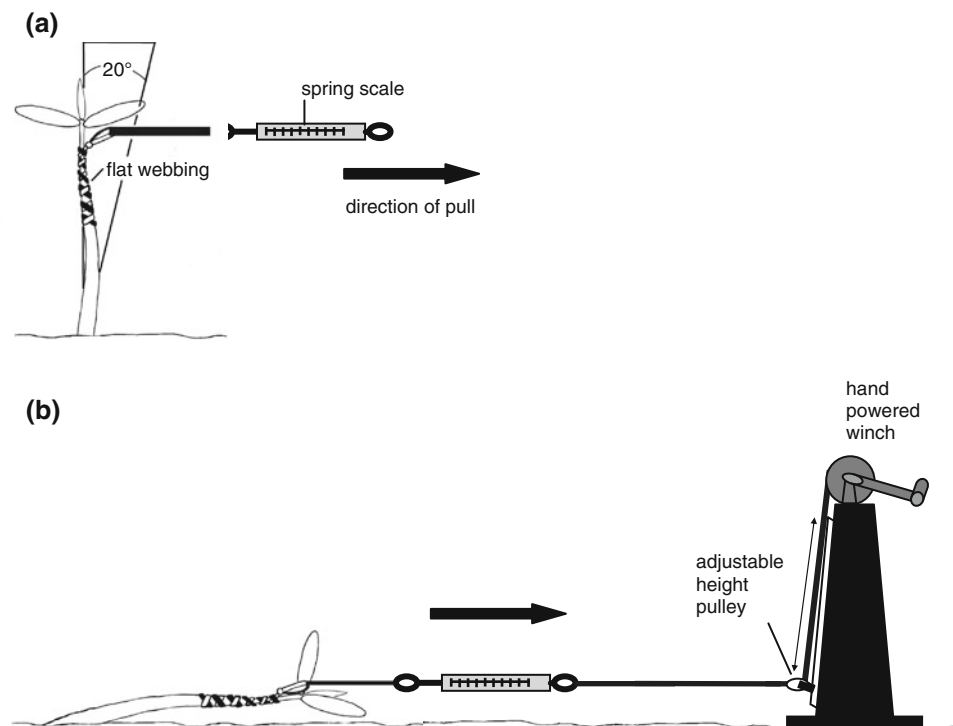
Seedlings growing in isolation from each other, and with no damage, branching or aerial prop roots were selected to represent a range of stem height classes. Prior to pulling, seedling height was measured from the substrate surface to the base of the terminal bud. Diameters were measured as follows: basal diameter just above the substrate surface, at the hypocotyl apex, midway along the first stem internode above the hypocotyl. The number of internodes and the number of leaves were also measured. Two measures of slenderness were calculated. The stem height divided by the basal stem diameter (slenderness 1) and the stem height divided by the first internode diameter (slenderness 2). Fresh mass was measured in the field immediately after pulling with a precision spring-scale. This mass included the stem and coarse basal roots. These coarse basal roots are similar in appearance and structure to the aerial prop roots that develop as seedlings grow in size. Coarse basal roots that broke during pulling were dug out to the best of our ability and added to the mass. Before pulling to failure, the horizontal force required to deflect each seedling laterally by 20° , defined further as the deflection resistance (F20) was recorded. This measure of deflection resistance was repeated for each of the four directions. These directions were (1) East, in the direction of the reef crest and incoming waves (E); (2) South (S); (3) West, in the direction of the backreef/

mangrove forest (W); (4) and North (N). Preliminary testing found that a 20° lateral displacement is within the elastic limit for these seedlings. A spring-scale (Pesola[®] 1 kg \pm 10 g, Yamato[®] 2 kg \pm 20 g) was attached to the seedling with a binder clip lined with rubber tubing to prevent damage to the seedling stem. This attachment point was at five-sixth of the stem height above the substrate, typically this was just below the first pair of leaves. The 20° deflection was measured from the base of the stem to the attachment point using a triangular template with a 20° angle (Fig. 1a). For pulling to failure, two pieces of flat webbing were woven around the stem for 10–20 cm (Fig. 1a). This webbing was tied into a loop at the top, at $5/6$ of the stem height, to which a spring scale (Yamato[®] 10 kg \pm 100 g, 50 kg \pm 500 g) was attached. This method, which mimicked a YaleGrip[™], allowed us to maintain a firm grip, avoiding slippage and damage to the stem, while enabling stem curvature at lower deflection angles. YaleGrips[™] are used as pulling and stopping grips in many oceanographical applications and consist of flat woven straps assembled in a four-leg configuration extending from a reinforcing, securing eye. The four straps are braided around a cylindrical object and this braid tightens around the object when it is pulled. Seedlings were manually pulled except for the largest seedlings, which were pulled using a small hand powered boat winch with a drum. This winch was secured to the top of a small wooden mount positioned a few meters away from the test seedling. The line from the winch ran down the side of the post and through a pulley from which it ran horizontally to the attachment point ($5/6$ of the stem height) on the seedling. The pulley position was moved down the post as the seedling deflected to maintain a horizontal pull (Fig. 1b). Seedlings were pulled horizontally at a constant rate of approximately 0.5–1 cm/s in the direction of the prevailing incoming waves and winds (i.e. pulled toward the west) until failure. The force at failure and failure mode (root failure or stem failure) were recorded.

Statistical analyses

Substrate resistance to penetration at successive depths was analyzed using repeated-measures ANOVA. The sphericity assumption was evaluated using Mauchly's test statistic and sphericity was corrected using the Greenhouse-Geisser correction (Field 2000). There was a scarcity of small seedlings at the Sand-Open location. As a result, seedlings were on average larger there than at any of the other locations. Statistical analyses were, therefore, carried out on data sample of 78 seedlings, which included only seedling size classes present at all five locations (stem height ranging from 27.5 to 47.5 cm). F20 values were compared graphically along the north–south and east–west bending axes and between the north–south and east–west axes. Differences in deflection resistance across axes of

Fig. 1 **a** Schematics of spring scale attachment to seedling for deflection test showing flat webbing woven around seedling stem and triangular template used to deflect seedlings of 20°, **b** schematics of winch, scale and webbing attachment for extraction test



bending and among locations were tested using repeated-measures ANOVA. A one-way ANOVA was used to test for differences in force at failure among locations. Normality and homoscedasticity assumptions were evaluated graphically (Normal Q–Q plots) and statistically (Levene's test). Data were log-transformed to meet assumptions when needed. Pearson's correlation coefficients were calculated to investigate relationships between failure resistance and morphological variables. Contingency tables with Chi-squared analyses were used to compare mode of failure among locations. All statistical analyses were performed using SPSS V.11 (SPSS Inc. Chicago, IL, USA). The level of significance for all statistical tests was evaluated using a value of $\alpha = 0.05$. All error values around the mean shown in the figures are ± 1 SE.

Results

The five sampling locations are referred to as rubble-open (e.g. rubble substrate, no mangrove canopy), sand-open, rubble-canopy, sand-canopy and peat-canopy. Substrate particle size fractions differed between the sampling locations (Fig. 2a). Organic material was dominant at the peat-canopy location but made up only a small proportion of the substrate at the sand-canopy location. Live roots were observed among the rubble at the rubble-canopy location, but in much lower quantities than at the peat-canopy

location. Particle sizes were smaller within mangrove canopy locations than in the open for both sand and rubble substrates.

Resistance to cone penetration at the substrate surface ranged from 0 (undetectable) to 430 kPa with an overall mean of 118 ± 9 kPa (mean \pm 1SE). At 38 cm below the substrate surface, soil resistance to cone penetration ranged from 34 to 1,207 kPa with an overall mean of 466 ± 24 kPa. Substrate resistance to cone penetration significantly differed among locations ($p = 0.011$) and with depth ($p < 0.001$), but differences among locations were not uniform across depth ($p < 0.001$; Fig. 2b). Close to the substratum surface, the two locations within mangrove forests, peat-canopy and sand-canopy were the most similar. As depth increased, however, substrate resistance to cone penetration increased greatly at the sand-canopy location becoming significantly greater than that at the peat-canopy location. It was observed that most seedling roots were located within the first 20 cm of substrate depth. At locations with coral rubble, the propagule was often partially buried.

All of the study locations had establishing mangrove plants of various sizes ranging from newly stranded propagules to large plants with aerial prop roots extending from the main stem and from lateral branches. We restricted our study to seedlings with no secondary branching or aerial prop roots. Seedlings with this morphology ranged in height from 12.0 to 55.5 cm. However, since small

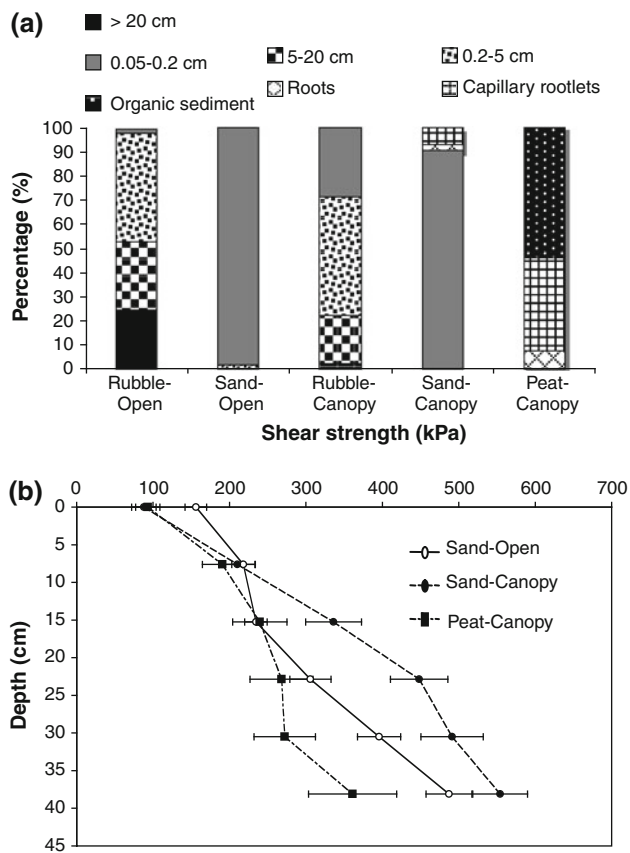


Fig. 2 Substrate characteristics. **a** Substrate particle size fractioning characterized from core samples taken at each of the five locations (coarse coral rubble >20 cm; medium coral rubble 5–20 cm; fine coral rubble 0.2–5 cm; sand 0.05–0.2 cm; coarse roots >2 mm; fine rootlets <2 mm; organic sediment); and **b** Substrate resistance to penetration (kPa) profile at the sand-open, sand-canopy and peat-canopy locations

seedlings were scarce at the Sand-Open location while large ones were scarce at other locations we further restricted the analysis to seedlings ranging in stem height from 27.5 to 47.5 cm, and averaging approximately 35 cm. Accordingly, differences in stem heights among locations were minimal, however, other morphometric parameters differed between locations (Fig. 3). We chose to restrict the sample based on seedling height, rather than other parameters because height is easy to measure in the field, and because in trees, height is less sensitive to competition effects than diameter (e.g. Oliver and Larson 1996).

There was no clear difference in deflection resistance (F20) between the northward (N) and southward (S) pulling directions or between the eastward (E) and westward (W) pulling directions (Fig. 4a, b). There was no difference between NS and EW axes (Fig. 4c), either. Repeated measures analysis of variance showed no difference in deflection resistance among pull direction (RM Anova within subjects, $F_{3,207} = 2.10$, $p = 0.10$). Deflection

resistance varied substantially among locations (RM Anova between subjects, $F_{4,69} = 75.65$, $p < 0.001$) (Fig. 5). At locations with coral rubble, seedling deflection was sometimes impeded by the presence of adjacent rubble pieces. There was no consistent relationship between mean deflection resistance and seedling size among the locations.

Seedlings were horizontal when failure occurred and failed in tensile pullout. There were two dominant modes of failure, stem break or root failure. Overall, 73% of the seedlings had root failure, the remainder failed near the base of the stem and these differed ($\chi^2 = 14.60$, $df = 1$, $p < 0.001$). Larger seedlings were more likely to have root failure (Fig. 6a). Failure mode also differed significantly among locations ($\chi^2 = 9.48$, $df = 4$, $p = 0.05$). Seedlings growing in open areas tended to have root failure, while those growing under a mangrove canopy were equally likely to have stem break or root failure (Fig. 6b). Peat-canopy seedlings showed a different mode of root failure, with roots detaching from the stem rather than pulling out of the substrate.

Force at failure ranged from 2 N to 481 N. On average, seedlings that broke near the base of the stem, failed at a substantially lower log-force than those that were uprooted ($F_{1,76} = 17.43$, $p < 0.001$; Fig. 7a). Larger seedlings required more force for root failure than smaller ones. The force required for root failure in seedlings was positively correlated with height, diameter (basal and of first internode) and mass (Table 1). The force for stem break was positively correlated with the diameter of the stem at the first internode and with mass. Log-force at failure differed among locations when seedlings with both failure modes were pooled ($F_{4,73} = 7.60$, $p < 0.001$; Fig. 7b).

Discussion

The five locations examined differed in canopy density and substrate properties, and presumably in the competition and mechanical stresses experienced by the seedlings. The analysis was restricted to seedlings of a comparable height range so that differences in allometry and resistance could be explored. The range and mean of seedling basal diameters were also similar, however, the seedlings growing under the canopy on sand and peat substrates had smaller diameters at the first internode (above the hypocotyl) and were in consequence more slender in the upper stem. Since resistance to bending is proportional to stem diameter raised to the fourth power (Niklas 1992), it is not surprising, therefore, that more slender seedlings required less forces for deflection by 20°. Slenderness is a widely used predictor of mechanical stability and Mitchell (2003) showed that overhead shade resulted in greater slenderness and reduced deflection resistance in Douglas-fir seedlings.

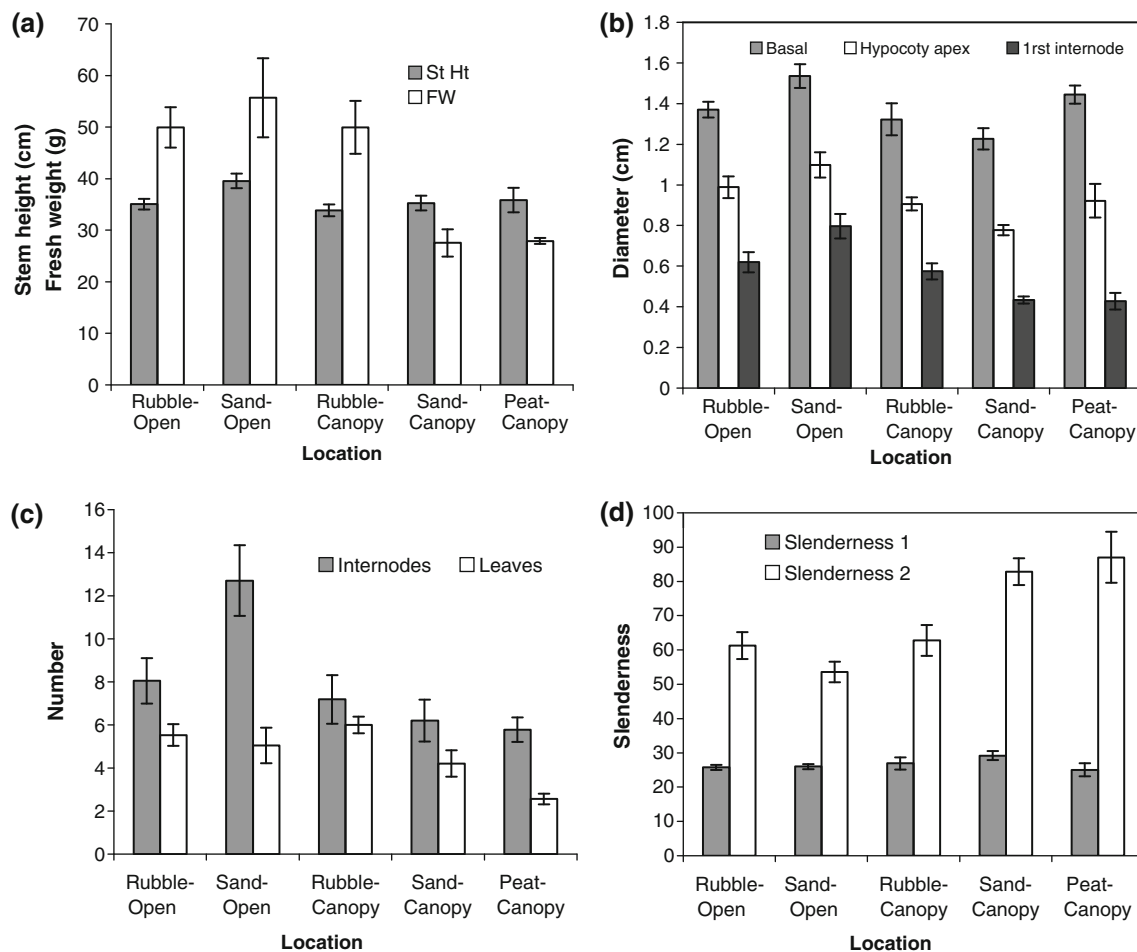


Fig. 3 *Rhizophora mangle* morphometrics. **a** Stem height and fresh weight; **b** stem diameters: basal diameter, diameter at hypocotyl apex and shoot diameter at first node; **c** total number of internodes and of leaves; and **d** slenderness (slenderness 1, height/basal diameter;

slenderness 2, height/1st internode diameter). See text for details. Sample sizes were 19 rubble-open, 20 sand-open, 16 rubble-canopy, 15 sand-canopy, 9 peat-canopy

In our study, the mangrove seedlings growing under canopy on the rubble substrate were similar in slenderness to the open grown seedlings, and were intermediate in deflection resistance between open grown and the other canopy locations. Presumably the presence of rubble within the canopy indicates periodic exposure to higher wind and wave energy, and the lower slenderness of seedlings in this location in spite of similar levels of canopy closure may reflect acclimation to the higher wave and wind loading of trees in this location.

The lack of directional patterns in resistance to deflection is surprising given the directionality of wave and wind loading, particularly for open grown seedlings. Root and stem asymmetry and directional strengthening of boles and roots occur in terrestrial trees growing in environments with strongly directional winds (Nicoll and Dunn 2000; Nicoll and Ray 1996; Stokes et al. 1995; Wade and Hewson 1979). However, it has been noted that acclimative growth is triggered by routine flexing (Telewski 1995) and

perhaps there is enough variability in direction of lower energy wind, wave and current loads in the study location for the plants to maintain symmetric growth. Certainly the seedlings under study did not have the visible asymmetries in foliage or stem form that were apparent in older plants. Furthermore, these seedlings remain highly flexible and likely shed loads via streamlining, and by reducing the frontal area exposed to wind and flowing water as the stem and foliage deflect in the direction of flow (e.g. Niklas 1992). It will be interesting to study progressively older plants to see how asymmetries develop as the seedlings increase in deflection resistance and frontal area with secondary branching and the development of aerial prop roots.

A strong association between failure resistance and plant mass has been observed in many studies with terrestrial trees (e.g. Nicoll et al. 2006). As expected, resistance to failure increased with increased plant size, particularly with plant mass, however, this relationship was not consistent among locations. Failure resistance was better

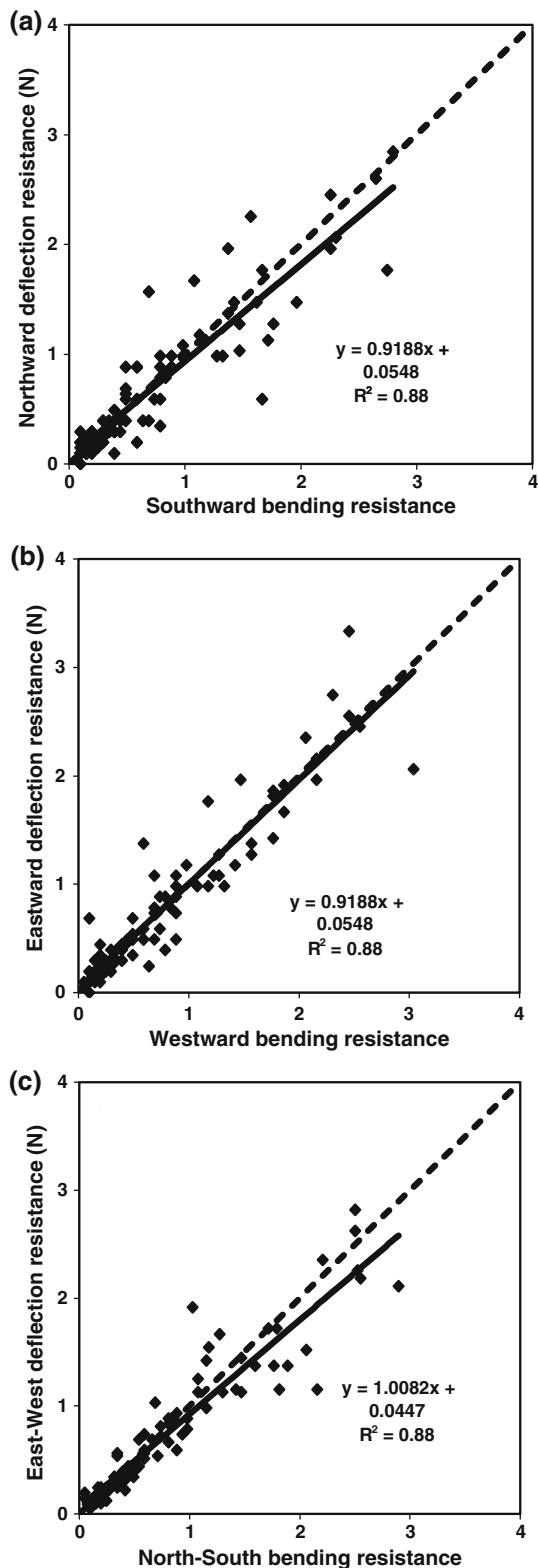


Fig. 4 Resistance (N) of the stem to a 20° deflection (F20). **a** Comparison between northward and southward directions; **b** eastward and westward directions; **c** comparison between the two axes of bending east–west and north–south. *Full line* represents the fitted line for the data. *Dashed line* represents the 1:1 ratio, i.e. H_0 : no difference in deflection resistance between directions or axes of deflection

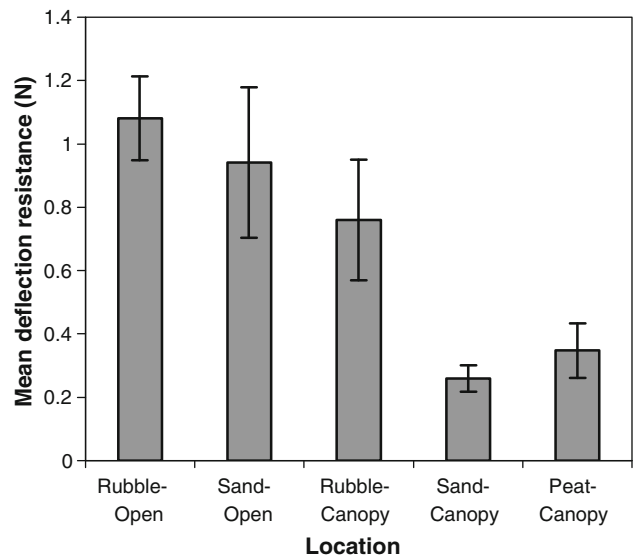


Fig. 5 Mean resistance (N) of the stem of *Rhizophora mangle* seedlings to a 20° deflection (F20) sampled at each of five locations

related to shoot diameter at the first internode (located above the hypocotyl) than to basal diameter. This is not surprising. Shoot extension is initiated only when the propagule has settled and anchored to the substrate. Shoot diameter is a better indicator of local growth conditions than hypocotyl basal diameter, which, in recently established seedlings, reflects the size of the propagule prior to its establishment. Secondary thickening of the hypocotyls is minimal at this stage. Much of the hypocotyl material consists of spongy cortical material rather than woody material. For its diameter, the lower portion of the stem within the hypocotyl is much less stiff than the upper shoot portion above the hypocotyl.

In addition, the degree to which the hypocotyl is buried in substrate varies between locations. More frequent and higher wave energy at coral rubble locations as well as closer proximity to the source of coarse material from the reef crest results in higher rate of rubble and sand deposition and thus of seedling burial. The hypocotyl of seedlings growing among coral rubble was generally buried deeper than that of seedlings growing in sand or peat. In a few cases, only a few centimeters of the hypocotyl was visible above the surface of the substrate. Excavations of root systems in rubble material indicated that seedling roots grow within the interstitial space among rubble fragments but also through the porous matrix of coral fragments. The fact that larger seedlings are more likely to fail in the roots than in the stem suggests that anchorage becomes an increasingly limiting factor as seedlings grow larger. Presumably, the subsequent development of aerial prop roots reverses this trend, but this will require further study to confirm.

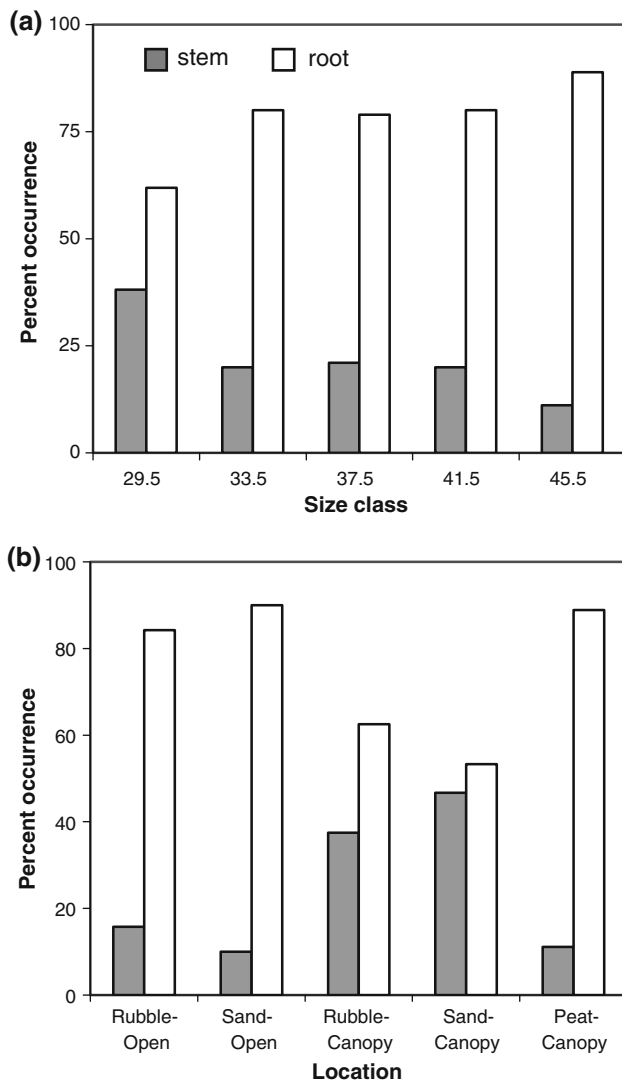


Fig. 6 Percent occurrence of stem break and uprooting **a** among stem height classes; and **b** at each of the five locations

Extraction resistance varied between substrates, but was not directly related to penetration resistance of these substrates. Extraction resistance was higher for rubble than for sand and peat. We were unable to measure penetration resistance of the rubble. It was generally unconsolidated but the irregularity and roughness of the particle surfaces promotes interlocking. Where rubble had accumulated around the seedling and the lower portion of the stem was buried, the buried portion of the stem behaved like a tap root, contributing to higher resistance to failure. The strength of anchorage on peat was higher than sand. As has been found in other studies (e.g. Gopinath 2009), peat had lower resistance to penetration than sand, at least through the lower portion of the rooting zone. The lower resistance to penetration of sand in the upper rooting zone may reflect a lack of substrate consolidation in this zone. Sandy areas colonized by mangrove seedlings were located well behind

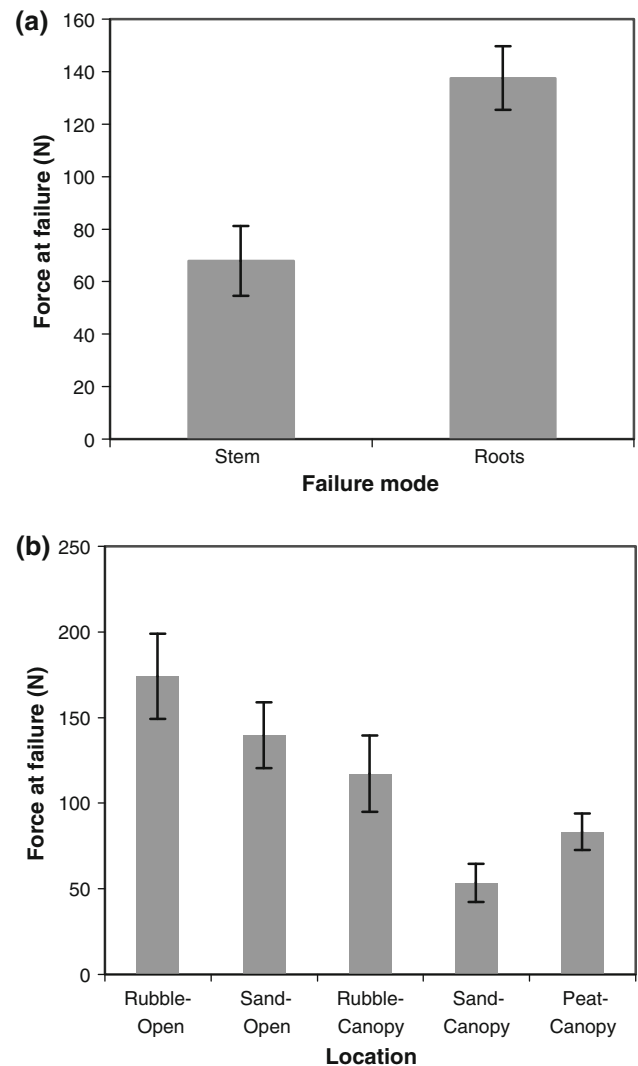


Fig. 7 Mean force at failure (N). **a** For stem ($n = 18$) and root system failure ($n = 60$); and **b** of *Rhizophora mangle* seedlings at each of five locations

Table 1 Pearson correlation coefficients (r) between the force at failure and morphological variables for significant relationships

Force at failure	Morphological variables	r
Stem failure ($n = 18$)	Height	ns
	Basal diameter	ns
	First internode diameter	0.50
	Fresh weight	0.50
Root failure ($n = 60$)	Height	0.29
	Basal diameter	0.44
	First internode diameter	0.56
	Fresh weight	0.66

the reef crest and were either associated with seagrass beds (open areas) or clusters of mature mangrove aerial prop roots (canopy areas), which further dampen water motion.

The top layer of substrate was usually a mixture of unconsolidated fine sand and silt. There is a high level of activity by tube worms (class Polychaeta) and other burrowing invertebrates in the upper levels of the sandy substrates and this substrate turn-over presumably reduces consolidation and resistance to penetration, and may disrupt fine rooting. In contrast, the peat has a large component of mangrove roots and root interlocking may increase seedling anchorage, in spite of the lower penetration resistance of the peat substrate.

The presence of the canopy appears to be more important than substrate type in failure resistance. Open grown seedlings had thicker stems, greater resistance to bending and to failure than canopy seedlings of similar height. This may reflect better growing conditions or greater mechanical acclimation (e.g. Mitchell 2003). It is also possible that any seedlings that were less resistant to failure have been removed by routine wave activity in these more exposed locations. Similar logic might explain why seedlings on rubble were more resistant to failure than seedlings growing on sand since rubble is deposited in areas of higher wave energy in proximity to the reef crest (Gourlay 1988; Oak 1984; Stoddart 1963). Seedlings growing under a canopy were more likely to break at the stem than ones growing in open areas. The greater occurrence of stem break in canopy seedlings is likely the result of root–root interactions. Fine root production is prolific under the canopy, leading to the establishment of a thick matrix of tightly interwoven capillary rootlets within which seedlings anchor. Peat-canopy seedlings broke at the roots unlike the

other canopy seedlings. However, they broke where the roots joined the stem base. While root interactions likely strengthen seedling anchorage on peat, light competition and preferential allocation of growth resources to height and foliage production may reduce overall root system development (Waring and Schlesinger 1985).

The red mangrove is well adapted to grow in intertidal environment, where it is often found at the leading edge of the mangal. Mangrove seedlings face a unique set of physical and mechanical constraints during their dispersal and establishment phases and it is interesting to consider the phases of mangrove establishment and the interaction of plant design and mechanical environment at each phase. The following conceptual framework should assist in the design of further biomechanical investigations, and is summarized in Table 2. Dispersal is facilitated through a free-floating phase during which positively buoyant rod-like propagules are dispersed by tidal currents and waves to new environments. After a period of several weeks (Banus and Kolehmainen 1975), the propagule distal end becomes negatively buoyant, making contact with the substrate. The long, fluted shape of *R. mangle* and upright position of the floating propagule facilitate stranding among coral rubble, within the rhizomes of seagrass (mainly *Thalassia testudinum* and *Halodule wrightii*) or among the aerial prop roots or pneumatophores of mature mangroves. Once propagules have come to rest, root development starts (Gill and Tomlinson 1969). This is followed by an up-righting stage achieved through the production of tension wood (Tomlinson and Cox 2000). Once initial anchorage is

Table 2 A conceptual framework of the stages of seedling establishment that links seedling physical properties to behaviour in moving water and air

Stage in seedling establishment	Seedling properties	Reaction of plant to moving water and air
Free-floating dispersal	Positively buoyant propagule	Dispersal by tidal currents and waves
Settling	Distal end of propagule becomes negatively buoyant, before the propagule loses its buoyancy completely	Uprighting the propagule in the water column; stranding at low tide or due to the presence of obstacles (e.g. crevices among coral rubbles, depressions in sand or among the rhizome of seagrass, prop roots or pneumatophores of mature mangroves)
Anchoring	Root development; substrate accretion, production of tension wood	Anchors seedling; increase seedling holds, facilitating anchorage; upright seedlings
Establishment (load shedding morphology)	Shoot extension; development of small, smooth leaves; shoot remains thin and flexible promoting bending when loaded; leaves are relatively small and smooth promoting reconfiguration and load shedding; further root development	Shoot extends quickly through water column to reach water surface; shoot remains flexible, bending with incoming wave; small leaves result in low drag
Secondary growth (load resisting morphology)	Secondary thickening of the primary shoot; emergence of lateral branches and prop roots from primary shoots	As morphology becomes more complex and size increases, secondary thickening of the shoot and development of prop roots oppose bending and buckling under load
Vegetative expansion	Expansion via lateral branch and aerial root development	Lateral expansion leads to branch and root interlocking further stabilizing trees

achieved, the first pair of leaves is produced and shoot extension begins. These leaf pairs are similar in shape to adult foliage but are held horizontally, are much smaller and, therefore, offer less resistance when exposed to current or waves. Water density being much greater than that of air, seedlings at this stage are exposed to much greater force than if they were exposed to winds of similar velocities (Denny and Gaylord 2002). The long, narrow, flexible shoot above the hypocotyl promotes load shedding through stem bending and drag reduction, while the relatively stiff arrangement of leaf pairs maintains the exposure of leaves to light when the seedling is not flexed. Once the seedling has grown tall enough to stay above the water at high tide, secondary thickening of the shoot, followed eventually by lateral branching and the development of aerial prop roots occur. Stem flexibility decreases and resistance to bending increases as secondary thickening proceeds (Niklas 1992). But reduced flexibility also increases the potential for large loads to develop. The advent of aerial prop roots further stabilizes the stem, reduces the length of the moment arm and, therefore, minimizes bending in the lower portion of the main stem. The architecture of adult trees becomes increasingly complex as lateral branches extend and send down aerial roots along their length. In closed canopied stands, there is substantially interlocking of lateral branches and aerial roots, adding further mechanical stability at the community scale. This sequential development of plant architecture enables mangroves to progressively colonize newly exposed substrates, or recolonize following disturbance, and is a vivid illustration of the versatility of plant design.

Conclusion

In red mangrove seedlings, resistance to horizontal loads is size dependent and varies with substrate and canopy cover. It seems probable that for seedlings that have not yet developed aerial prop roots or lateral branches, successful colonization depends on quickly developing good anchorage coupled with the ability to deflect under extreme loads. For these small seedlings, burial, substrate scour and abrasion by moving debris are likely more important sources of mechanically induced mortality than failure under direct loading of waves and winds during storms.

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Conflict of interest The authors declare that they have no conflict of interest.

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