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How mangrove forests adjust to rising sea level

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Contents

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Summary

Mangroves are among the most well described and widely studied wetland communities in the world. The greatest threats to mangrove persistence are deforestation and other anthropogenic disturbances that can compromise habitat stability and resilience to sea-level rise. To persist, mangrove ecosystems must adjust to rising sea level by building vertically or become submerged. Mangroves may directly or indirectly influence soil accretion processes through the production and accumulation of organic matter, as well as the trapping and retention of mineral sediment. In this review, we provide a general overview of research on mangrove elevation dynamics, emphasizing the role of the vegetation in maintaining soil surface elevations (i.e. position of the soil surface in the vertical plane). We summarize the primary ways in which mangroves may influence sediment accretion and vertical land development, for example, through root contributions to soil volume and upward expansion of the soil surface. We also examine how hydrological, geomorphological and climatic processes may interact with plant processes to influence mangrove capacity to keep pace with rising sea level. We draw on a variety of studies to describe the important, and often under-appreciated, role that plants play in shaping the trajectory of an ecosystem undergoing change.

I. Introduction

Mangroves are tidally influenced forested wetlands of the coastal saline margin of over 123 countries and territories, occupying an area of 137 760–152 308 km^2 globally (Spalding *et al.*, 2010; Giri *et al.*, 2011). Although the persistence of mangrove forests within the marine intertidal is influenced by regional sea-level rise and coastal geomorphology, vegetation also affects soil structure and surface *elevation change* – change in the location of the mangrove soil surface in the vertical plane. Thus, mangroves (and possibly

other vegetative communities) are not passive to changes affecting them; rather, they maintain a strong ability to modify their environment, promote habitat persistence naturally and serve as engineers for coastal adaptation (Cheong *et al.*, 2013). Certainly, over the Holocene (to 11 700 BP), mangrove forests have adjusted to sea-level rise by facilitating sediment deposition and building of peat (Fujimoto, 1997; McKee *et al.*, 2007; Ellison, 2008; Willard & Bernhardt, 2011). Such studies suggest that rainfall variability, increases in atmospheric CO_2 concentrations and mean sea-level change have the potential to influence habitat stability through feedbacks (reviewed by McKee *et al.*, 2012).

Elevation change in mangrove forests typically occurs at very slow rates (measured in millimeters per year), leading to directional changes over long time periods (decades to millennia), ultimately determining whether the ecosystem survives, is submerged or is supplanted by terrestrial vegetation. Over geological time periods, sea level has risen and fallen hundreds of meters and at varying rates of change (Chappell & Shackleton, 1986; Fairbanks, 1989). When the rate of sea-level rise exceeds the capacity of mangroves to keep pace, mangroves are lost (Woodroffe & Grindrod, 1991; Hashimoto *et al.*, 2006). By contrast, during periods of slower historical rise, for example, between 5000 and 7000 yr ago, mangrove soils were able to keep pace with sea-level rise by building vertically, and mangroves expanded in many locations (known as the 'Big Swamp Phase'; Woodroffe, 1988). For the past 18 000 yr since the last glaciation, sea level has been rising. However, records suggest greater sea-level stability during the late Holocene (but see Cronin, 2011), followed by a period of more rapid sea-level rise starting in the mid to late 19th century (Church *et al.*, 2008).

Based on satellite altimetry, which measures changes in ocean height (but not vertical soil surface movement), the current rate of global mean sea-level rise is 3.2 ± 0.4 mm yr^{-1} (mean ± SE) (updated from Nerem *et al.*, 2010). Local rates may be higher (e.g. 7.5 mm yr^{-1} for Indonesia) or lower (e.g. 1.9 mm yr^{-1} for the Caribbean) as a result of regional variation in ocean warming and other factors (Nerem *et al.*, 2010), and rates are predicted to accelerate (Nicholls & Cazenave, 2010). In addition, many mangrove forests (and other coastal wetlands) experience local soil surface movements, usually subsidence, which add to the rate of inundation (Syvitski *et al.*, 2009; Webb *et al.*, 2013). Together, increases in mean sea level plus local soil surface movement (i.e. *relative* sea-level rise) determine the rate of submergence. Elevation changes (positive or negative) in mangrove forests and other coastal wetlands are so finely balanced that minor changes over an annual cycle (e.g. 1 mm yr^{-1}) can alter the depth and duration of inundation sufficiently to affect mangrove survival.

In this review, we describe the capacity of mangrove ecosystems to influence elevation dynamics directly through the vegetation and indirectly through biophysical processes. Potential climatic and environmental feedbacks are also reviewed, particularly those associated with inter- and intra-annual variability in rainfall, increased atmospheric CO_2 concentrations and sea-level rise. In addition to establishing the importance of vegetation influences on elevation change in mangroves, we also briefly review geomorphological processes and describe the role played by the mangrove community in actively influencing its own survival.

II. Important characteristics of mangrove ecosystems

Approximately 70 species and/or hybrids of mangroves have been described globally (Duke *et al.*, 1998). Mangrove genera produce functionally distinctive, aerial root types that provide the primary interface between shallow, aboveground surface processes and soils (Tomlinson, 1986). Functional root types include prop roots (*Rhizophora* spp.), large and small pneumatophores (*Sonneratia*/*Avicennia* spp.), knee roots (*Bruguiera* spp.) and plank roots (*Xylocarpus*/*Heritiera* spp.; Fig. 1), which develop along various hydrological and geomorphological gradients in many forests. Important differences in root morphology among these root types can also extend below ground (McKee, 1996).

Landform characteristics of coasts control patterns in mangrove forest structure related to differences in hydrology and geomorphology (Odum *et al.*, 1982; Thom, 1982). For mangroves, distinctive hydrogeomorphic zones are often defined, and include overwash island, fringe, riverine, basin/interior, scrub and hammock mangroves (Lugo & Snedaker, 1974; Ewel *et al.*, 1998). Zones reflect the location of where mangroves occur in a regional landscape, as well as the interplay among hydrology, salinity and soil pedogenesis, which can influence elevation change. Mangrove soils mediate important biogeochemical processes that facilitate energy exchange with vegetation (Alongi *et al.*, 2005; Alongi, 2009), and drive elevation change through plant-mediated alterations in soil structure.

III. Patterns of elevation change in mangroves

Vertical changes in the position of the soil surface are driven by both physical and biological processes which lead to a net gain or loss in elevation over time. Physical processes that contribute to elevation gain include inorganic sedimentation, groundwater influx (causing soil swelling) and deep land movements (geological uplift or glacial isostatic rebound; Fig. 2). Also important, but often underappreciated, are biological processes, such as plant litter and woody debris deposition, root accumulation, sediment trapping by vegetative structures and algal mat development on the soil surface. Elevation losses can be caused by physical compaction or erosion of sediment, organic matter decomposition, dewatering and deep land movement (subsidence). Changes in surface elevation can be further influenced by disturbances, such as hurricanes and tsunamis, causing elevation losses (e.g. peat collapse following tree mortality) or gains (e.g. acute deposition of storm sediments). In addition, there are feedback relationships between plant processes and soil elevation (e.g. flooding effects on organic contributions to soil volume), which are poorly understood. The relative contributions of these various physical and biological processes determine the rates and patterns of elevation change in a particular mangrove ecosystem.

The Surface Elevation Table-Marker Horizon (SET-MH) system allows fine-resolution measurements of *elevation change* (total movement of the soil surface relative to a benchmark), *vertical accretion* (deposition on the soil surface) and *shallow subsidence/expansion* (movement of subsurface soil layers driven by

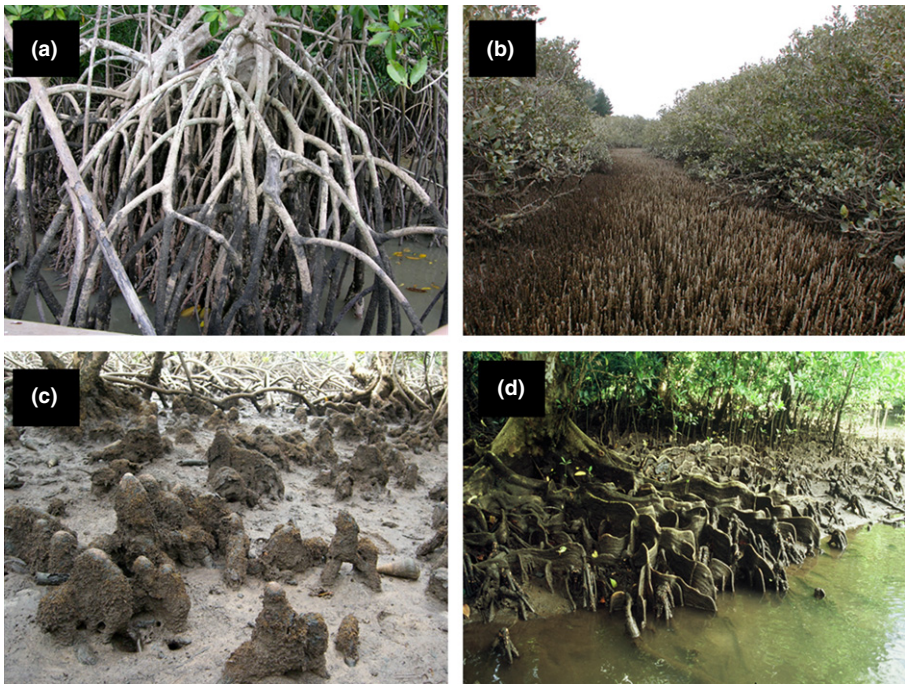

Fig. 1 Primary aerial root types formed by mangroves: (a) prop roots, *Rhizophora* spp.; (b) pneumatophores, *Avicennia* spp. (depicted) and *Sonneratia* spp.; (c) knee roots, *Bruguiera* spp.; and (d) plank roots, *Xylocarpus* spp. (depicted) and *Heritiera* spp. Image credits: (a–c) US Geological Survey, K. L. McKee (photographer). (d) USDA Forest Service, K. W. Krauss (photographer).

compaction or root zone expansion) from wetland ecosystems (Cahoon *et al.*, 1995). The SET allows for precise (± 1.3 mm; Cahoon *et al.*, 2002), repetitive measurements of elevation change over both short and long temporal scales, depending on research objectives. The structure of the SET has evolved, but, when coupled with MHs that track the accretion of surface sediments separately, the SET can provide not only an account of elevation change, but also identify what component of the elevation change is attributable to vertical accretion, shallow subsidence or root zone expansion (see SET diagram, Fig. 2, and Supporting Information Fig. S1). When coupled with relative sea-level rise data from local tide gauges or a known increment of hydrological change, the SET-MH approach provides an accurate estimate of wetland vulnerability to submergence, together with a known driver of that change.

To date, at least 14 studies (cf. Webb *et al.*, 2013) have included rates of accretion and elevation change in mangrove ecosystems using the SET-MH approach, and eight studies have provided sufficient information to describe trends by hydrogeomorphic zone (Table 1). The duration of these elevation studies ranged from 1.0 to 6.6 yr. Among these, rates of elevation change ranged from −3.7 to 6.2 mm yr^{-1}, vertical accretion ranged from 0.7 to 20.8 mm yr^{-1}, shallow subsidence ranged from zero to 19.9 mm yr^{-1} (in Micronesia; Krauss *et al.*, 2010) and root zone expansion ranged from zero to 2.4–2.8 mm yr^{-1} (in Belize; McKee *et al.*, 2007; in Honduras; Cahoon *et al.*, 2003). The latter studies, conducted in sediment-poor settings, have particularly shown the importance of vegetative structures, especially mangrove roots, in contributing to elevation gain. Elevation changes vs vertical accretion among hydrogeomorphic zones from mangroves in Rookery Bay, Florida, USA depict the typical variation observed among SET-MH studies over small spatial scales related to different processes (Fig. 3).

IV. Biological influences on accretion and elevation change

Scientists have gained a better understanding of elevation dynamics in mangrove forests by not only documenting what differs among hydrogeomorphic zones and regions, but also through experimental studies to test specific hypotheses associated with biological processes of interest. Many of these same processes probably occur in other types of tidal wetland (see, especially, Morris *et al.*, 2002; Kirwan & Murray, 2007; Kirwan & Mudd, 2012). The following sections describe, in greater detail, the primary biological processes known to influence elevation gains or losses in mangrove forests, and some of the environmental factors that modify these effects.

1. Aerial roots and sedimentation

Up to 80% of the sediments delivered by the tides may be retained in mangrove forests (Furukawa *et al.*, 1997), but the actual mechanism of sediment retention is unclear. Aerial roots of mangroves can potentially slow water velocities and promote sedimentation (Furukawa & Wolanski, 1996). For example, vertical accretion was positively related to the density of artificial aerial root structures on accreting tidal flats in New Zealand (Young & Harvey, 1996) and Australia (Spenceley, 1977; Bird, 1986), which suggested that sedimentation rates might be influenced by aerial root density and/or type. A positive correlation between mangrove seedling densities and vertical accretion in Sri Lanka and Kenya supported this supposition (Huxham *et al.*, 2010; Kumara *et al.*, 2010). Studies on how pneumatophores of *Avicennia* and *Sonneratia* influence sedimentation patterns further suggested that their influence was less on sediment deposition and more through the binding and retention of sediments (Spenceley, 1977). Other work also found that filamentous algae, together with mangrove

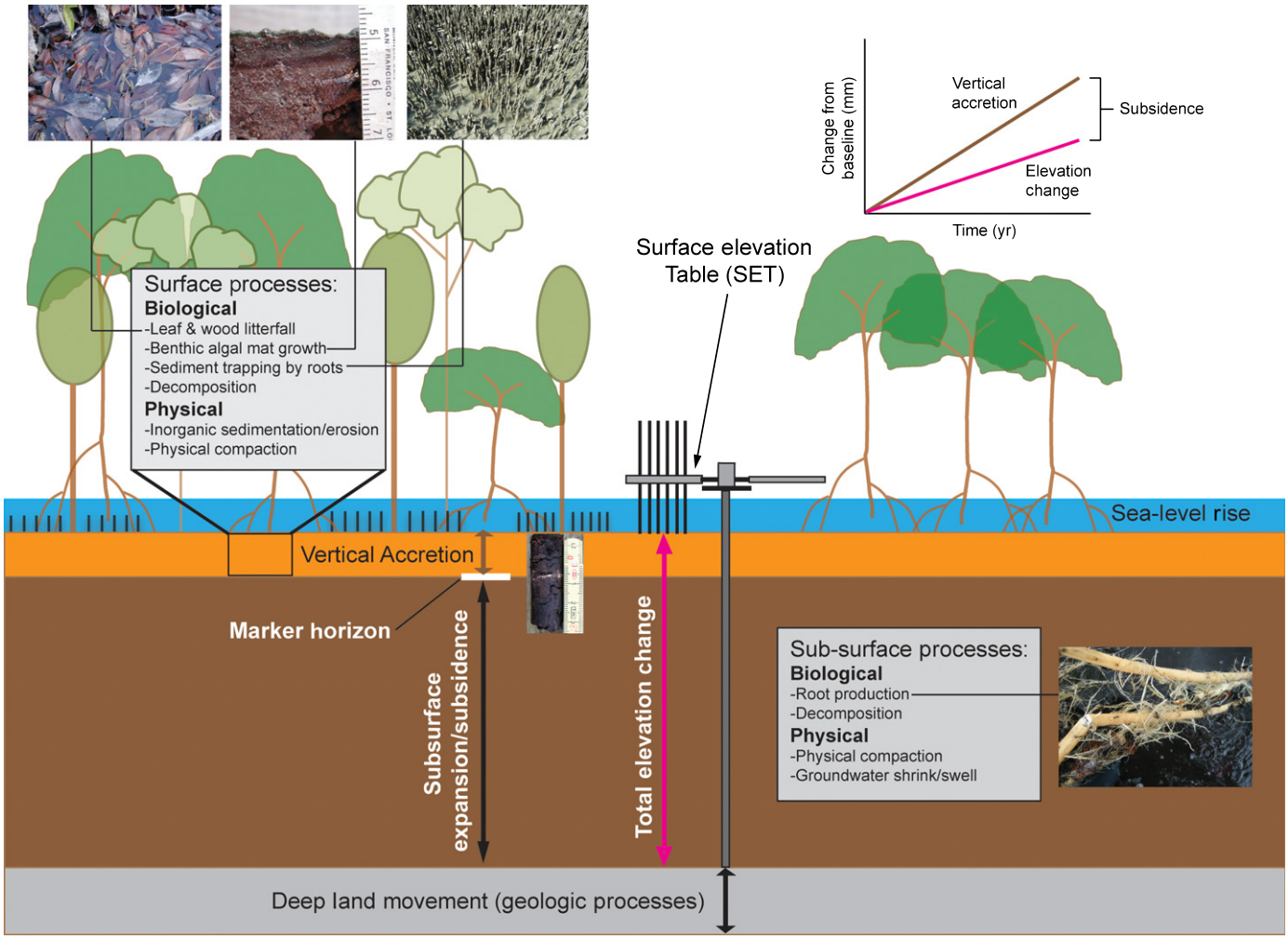

Fig. 2 Illustration (not drawn to scale) of how elevation change is measured, and the biological and physical processes that influence soil building in mangrove forests. Both surface and subsurface processes contribute to elevation change, which is measured with a Surface Elevation Table (SET). The inset graph shows a hypothetical time-course change in elevation (SET) and accretion on the soil surface (measured above a marker horizon, MH). The difference between rates of accretion and elevation change equals the subsurface movement. Subsidence results when accretion is greater than net elevation change. Root zone expansion occurs when net elevation change exceeds accretion. To avoid submergence, vertical soil development must equal relative sea-level rise, which is the combination of ocean height increase and local subsidence (both shallow and deep).

roots, aided in the trapping and retention of detrital particles and mineral sediment (McKee, 2011).

The influence of mangrove root type on accretion was explored in greater detail in Micronesia (Krauss *et al.*, 2003). There, three species with functionally different root types (Fig. 1; *Rhizophora apiculata*, *Sonneratia alba*, *Bruguiera gymnorrhiza*) develop as co-dominants among three hydrogeomorphic zones (fringe, riverine, basin/interior). Vertical accretion was generally higher in *Rhizophora* prop roots (11.0 mm yr^{-1}) than in either *S. alba* pneumatophores or bare soil controls (mean, 8.3 mm yr^{-1}), but losses to shallow subsidence tended to offset some accretionary gains created by prop roots (Krauss *et al.*, 2003).

In addition, elevation gain was either greatest in pneumatophores (Krauss *et al.*, 2003) or where pneumatophore density was highest (Bird, 1986), which was in agreement with Spenceley's (1977) suggestion that pneumatophores may be better at retaining deposited sediments than other root types. Root growth was also greater in pneumatophore root zones than in either prop root or knee root zones (Gleason & Ewel, 2002). Disentangling intertidal elevation from aerial root type and density, which are both influenced by flooding, however, is challenging (Spenceley, 1982).

2. Litter and woody debris accumulation/decomposition

Accretion of organic matter on the soil surface through litterfall (i.e. leaf, reproductive and twig debris) can contribute to elevation gain in some mangrove forests (McKee, 2011). Litterfall contributions have been measured at 1.3–27.6 t ha^{-1} yr^{-1} for mangrove forests (Fig. 4), providing an important potential mechanism of accretion if this biomass is incorporated into the soil. In situations in which tidal flushing is limited, leaf-shredding crabs are absent and decomposition is slow (Middleton & McKee, 2001), leaf matter can accumulate and contribute to soil accretion (McKee, 2011). In Florida basin/interior forests, where tidal flushing is low, accretion rates of leaf litter in three basin/interior forests ranged from 1.1 to 3.4 mm yr^{-1} (McKee, 2011). However, few studies have

Table 1 Published ranges of soil surface elevation change, vertical accretion and subsurface change for different mangrove hydrogeomorphic zones as quantified using the Surface Elevation Table-Marker Horizon (SET-MH) technique

Hydrogeomorphic zone[1]	Soil surface elevation change (mm yr^{-1})	Vertical accretion (mm yr^{-1})	Subsurface change (mm yr^{-1})[2]	References
Fringe	−1.3 to (+5.9)	+1.6 to (+8.6)	−9.7 to (+2.4)	McKee *et al.* (2007) Lovelock *et al.* (2011a) Cahoon & Lynch (1997) Krauss *et al.* (2010) Cahoon *et al.* (2003) McKee (2011)
Riverine	+0.9 to (+6.2)	+6.5 to (+13.0)	−11.2 to (−0.2)	Lovelock *et al.* (2011a) Krauss *et al.* (2010) Whelan *et al.* (2005) Whelan *et al.* (2009)
Basin/interior	−3.7 to (+3.9)	+0.7 to (+20.8)	−19.9 to (+2.8)	McKee *et al.* (2007) Cahoon & Lynch (1997) Krauss *et al.* (2010) Cahoon *et al.* (2003) McKee (2011)
Scrub	−1.1	+2.0	−3.1	McKee (2011)
Overwash island	+0.6 to (+2.5)	+4.4 to (+6.3)	−3.8	Cahoon & Lynch (1997)

Studies ranged from 1.0 to 6.6 yr in duration.
[1]Data for 'hammock'-type mangroves could not be found.
[2]Negative values represent shallow subsidence, whereas positive values represent root zone expansion.

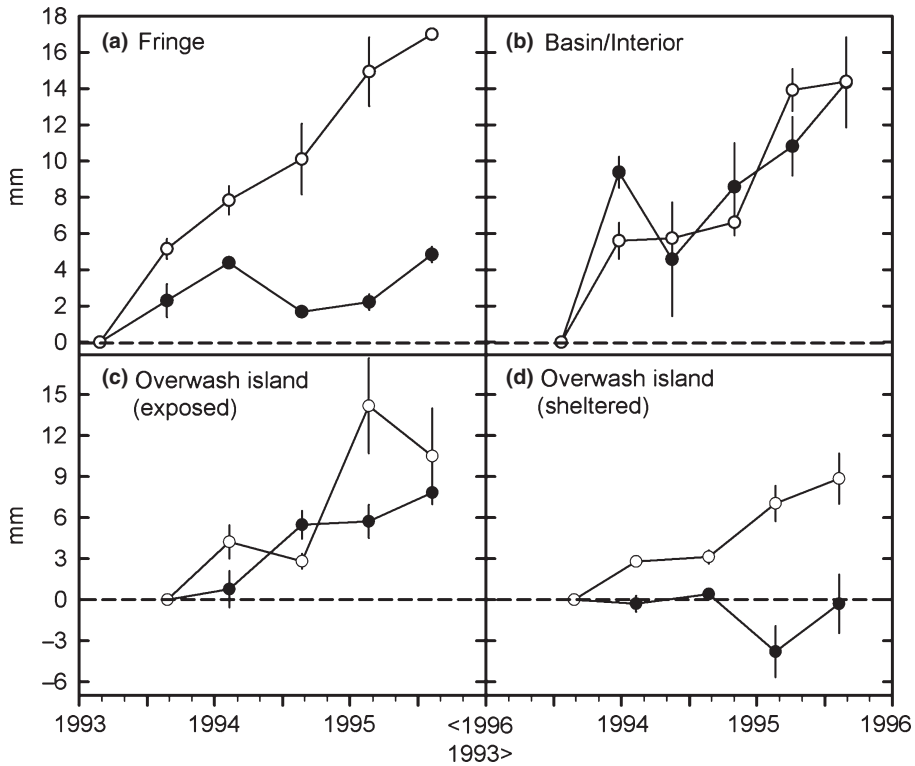

Fig. 3 Elevation change, vertical accretion and shallow subsidence for mangroves growing in (a) fringe, (b) basin/interior, (c) exposed overwash islands and (d) sheltered overwash islands in Rookery Bay, Naples, FL, USA. Open circles, vertical accretion; closed circles, soil surface elevation. Subsidence is the difference between elevation change and vertical accretion trends, and equals 5.8 mm yr^{-1} for fringe, not significant for basin/interior and 3.8 mm yr^{-1} for both overwash island mangrove types. The dashed line represents the original soil surface. Bars, ± 1SE of the mean. Reproduced from Cahoon & Lynch (1997) with kind permission from Springer Science and Business Media.

quantified actual rates of litter accumulation vs litterfall to the forest floor. Litter and twig accumulation in Bornean mangroves ranged from 44.4 to 66.2 t ha^{-1} yr^{-1}, which exceeded annual litterfall because of rapid burial by sedimentation, slow decomposition and a factor not often considered – tidal import of litter from other mangrove forests (Sukardjo *et al.*, 2013). The rate at which this litter decomposes is also important, because this process reduces the overall rate of litter accumulation. For example, decomposition of leaves ranged from 0.28 to 1.53% d^{-1} in a Belizean mangrove forest (Middleton & McKee, 2001).

Mangrove wood (downed trees, branches and twigs) volumes on the forest floor can range from 16 to 104 m^3 ha^{-1} (*c.* 9.5–23.8 t ha^{-1} yr^{-1}; Robertson & Daniel, 1989; Allen *et al.*, 2000; Krauss *et al.*, 2005). Because woody debris is more refractory

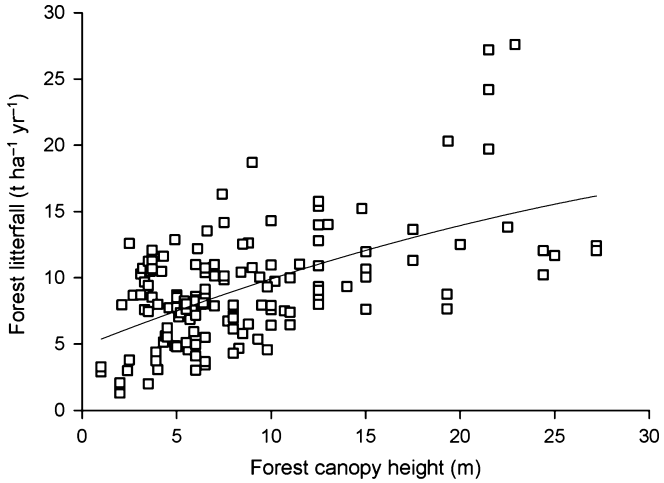

Fig. 4 Mangrove litterfall vs forest canopy height ($n = 148$, $r^2 = 0.33$, $y = 4.813 + 0.564x - 0.0054x^2$). Data were updated from Saenger & Snedaker (1993) and Conner *et al.* (2014), with additional data (Sukardjo *et al.*, 2013).

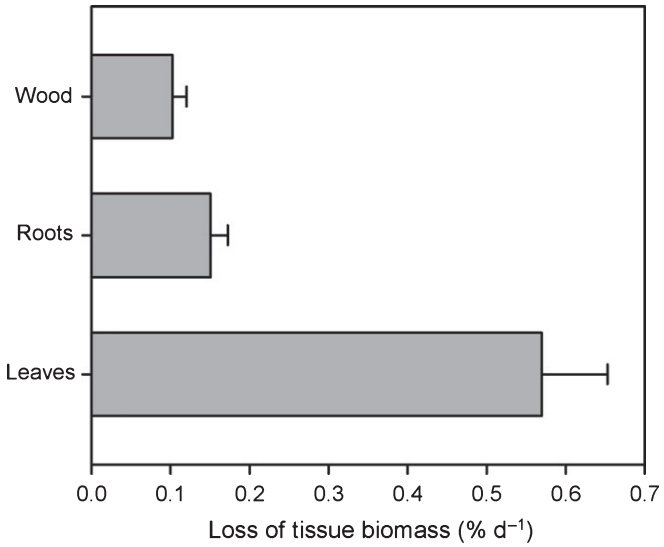

Fig. 5 Literature estimates of tissue biomass loss from mangrove wood ($n = 6$), roots ($n = 9$) and leaves ($n = 22$). Bars, +1SE of the mean. Data were reviewed in Middleton & McKee (2001), with additional data (Poret *et al.*, 2007).

than leaf litter (Middleton & McKee, 2001), and contains slowly decomposing components (Romero *et al.*, 2005; Fig. 5), it would be more likely to accumulate and contribute to soil volume. No studies to our knowledge, however, have examined wood volume contributions to vertical accretion or elevation change in mangrove forests. Long retention times for downed wood can influence site fertility, abate erosion, contribute to soil pedogenesis and trap propagules/seeds (Harmon *et al.*, 1986), all of which have the potential to influence elevation change on a variety of scales.

3. Benthic mat formation

Benthic mats composed of microbial and/or algal material develop on the surface of soils in some mangrove forests and contribute to vertical accretion and elevation change (McKee, 2011). Intact mats, which bind sediments and resist erosion, were first described in the Bahamas (Neumann *et al.*, 1970), Sri Lanka (Gunatilaka, 1975) and Australia (Spenceley, 1982). Spenceley (1982) suggested that an act as simple as inserting a 30-cm-long metal peg through the mat might compromise this binding capacity and open up underlying soils to greater erosion potential. Benthic mats are quite common in mangrove forests, being more recently described in Florida and Belize (Cahoon & Lynch, 1997; McKee, 2011). Benthic mats associated with Caribbean mangroves have been further categorized according to their make-up: turf algal, leaf litter and microbial mats (McKee, 2011). Turf algal mats are composed mostly of filamentous algal species (Rhodophyta), and are common in fringe hydrogeomorphic zones in the Caribbean. Leaf litter mats are common in basin/interior hydrogeomorphic zones, where hydrological flushing is reduced. Microbial mats develop in scrub hydrogeomorphic zones with permanent or semi-permanent flooding.

The contribution of benthic mats to accretion has not been studied extensively, but data suggest that they may play an important role in settings such as the Caribbean where mineral sediment inputs are low. Turf algal and microbial mats exhibited similar rates of vertical accretion in Belize and Florida (2.1–2.7 mm yr^{-1}), whereas leaf litter mats accreted more slowly (1.9 mm yr^{-1}) and might be more ephemeral (see Saintilan *et al.*, 2013), especially where sediment burial is slow. The general role played by benthic mats in driving surface elevation dynamics *per se* is not very well known as the physical characteristics of mats are highly variable. Their main contribution to soil accretion is through organic matter accumulation, although they also appear to promote deposition or retention of inorganic material (McKee, 2011). These mats can also strengthen soils against shearing forces and thus minimize erosional losses (Spenceley, 1982). For example, turf algal mats have relatively higher shear strength in relation to mangrove surfaces lacking such mats (McKee, 2011; and on-line supplementary material in McKee, 2011).

4. Subsurface root accumulation

The most important biological contributor to soil volume and elevation change in some settings occurs below ground. Mangrove root accumulation has been shown to influence the direction and rate of change in surface elevation in Florida and the Caribbean (Cahoon *et al.*, 2003; McKee *et al.*, 2007; McKee, 2011).

Root production/decomposition Compared with leaves and wood, roots have a much greater potential to contribute to soil volume and elevation gain, because of their refractory nature as well as the anaerobic soil environment which slows decomposition (McKee & Faulkner, 2000a; Middleton & McKee, 2001; Saintilan *et al.*, 2013). Although root production rates may be lower than litterfall rates in some forests (McKee & Faulkner, 2000a; Cormier, 2003; Castañeda-Moya *et al.*, 2011), the lack of oxygen retards the decomposition of roots (McKee & Faulkner, 2000a; Middleton & McKee, 2001) and increases the relative proportion of root matter accumulating in the soil (Fig. 5). In sediment-deficient locations,

root accumulation is the primary organic component contributing to peat formation (McKee & Faulkner, 2000b; Middleton & McKee, 2001). In mangrove forests with minimal terrigenous sediment inputs (e.g. on offshore islands or atolls), vertical land development is often dependent on the accumulation of organic matter (i.e. peat formation; McKee & Faulkner, 2000b; McKee *et al.*, 2007; McKee, 2011). For example, some Caribbean mangroves have built peats to thicknesses of 10 m, allowing these forests to track sea-level rise over the Holocene (McKee *et al.*, 2007). In mangrove forests in Florida and Belize, roots accounted for 1.2–11.8 mm yr^{-1} of total vertical change in soil elevation (McKee, 2011). Where root production was high, elevation gains were found despite minimal surface accretion of inorganic sediment (McKee *et al.*, 2007). Rates of elevation change in Florida and Belize mangroves were positively correlated with both fine ($r = 0.75$) and coarse ($r = 0.69$) root accumulation (McKee, 2011).

Root structural traits The structural characteristics of mangrove roots may also be important in maintaining soil elevations, especially with respect to resisting compaction. The specific root length (SRL; root length per biomass) is a trait that describes the morphology of root systems. SRL has rarely been assessed in mangroves, but, for a similar growth rate, species with low SRL will contribute a greater volume to soils and thus to elevation gains. In solution culture (i.e. where roots form differently compared with fine sediments; Gill & Tomlinson, 1977), significant differences in SRL were found among mangrove species: 0.55 m g^{-1} for *Rhizophora mangle*, 1.05 m g^{-1} for *Avicennia germinans* and 1.70 m g^{-1} for *Laguncularia racemosa*. Although these measurements were made only on primary roots, which would probably have higher SRL, SRL values from mangroves were low relative to rainforest species which have SRLs that range from 5 to 40 m g^{-1} (mean of 10 m g^{-1}; Metcalfe *et al.*, 2008). Low values of SRL in mangroves reflect their thick roots compared with rainforest species. In rainforest species, the majority of root diameters are within the 0.2–0.5-mm size classes (Metcalfe *et al.*, 2008). By contrast, < 20% of roots were < 2 mm in diameter in a south Florida mangrove forest (Castañeda-Moya *et al.*, 2011). Thick roots are probably an adaptation to improve oxygen supply to root systems, as SRL was inversely related to the capacity to withstand root zone anoxia among mangrove species (McKee, 1996).

The accumulation of long-lived roots is also a mechanism by which soil volume can be maintained or increased over time. The longevity of mangrove roots in *R. mangle*-dominated forests (and mixed communities with *A. germinans* and *L. racemosa*) in Florida was estimated to be 1.7–4.4 yr for fine roots and up to 25 yr for coarse roots (Castañeda-Moya *et al.*, 2011), whereas longevity in Micronesian mangrove roots (dominated by *R. apiculata*, *S. alba* and *B. gymnorrhiza*) ranged from 5.2 to 25.6 yr (Cormier, 2003). These are extremely long lived in comparison with terrestrial trees, which have much shorter lifetimes (faster turnover rates). For example, in temperate trees, median root lifespan ranged between 95 and 336 d, and, for tropical trees, a mean of 135 d was found (Yavitt *et al.*, 2011; McCormack *et al.*, 2012). Currently, there are no assessments of differences in root lifetimes among mangrove species. However, in terrestrial species, root lifespan increases with root diameter, calcium content, tree wood density and carbon : nitrogen (C : N) ratios of tissues, whereas SRL and plant growth rate are negatively related to root lifespan (McCormack *et al.*, 2012). If mangroves follow similar trends to terrestrial species, we anticipate that species with thick roots and low SRL will have greater root contributions to soil volume than species with thinner roots and higher SRL.

The loss of root volume after the death of roots is also an important factor that will influence soil volume. After death, root structures collapse as a result of loss of cell contents and decomposition, and roots are compressed under the weight of soil and water. Many of these processes (collapse, decomposition, compression) may be influenced by differences in root structure among species. On death, larger roots of *R. mangle* can form channels that occupy 1–2% of the soil volume, which are often colonized by smaller roots, a response hypothesized to capture nutrients within these more oxygenated sites in the soil (McKee, 2001). Moreover, the collapse of root channels within the top meter of soil can cause subsidence of soil elevation, illustrating the importance of the maintenance of root structure to soil volume. For example, Cahoon *et al.* (2003) documented peat collapse of up to 11 mm yr^{-1} following acute mangrove forest mortality in Honduras.

The porosity of roots, which is a measure of the air spaces within the roots, may also be linked to the loss of volume during collapse, decomposition and compression of roots after death. One untested prediction is that low-porosity roots (with a low proportion of air spaces) will maintain soil volume better than high-porosity roots (with a high proportion of air spaces), unless the latter are fortified by secondary thickening (as in the case of major root branches) or possibly metal plaques. Root porosity varies significantly among mangrove species (McKee, 1996; Cheng *et al.*, 2012). For example, root porosity was lowest in *R. mangle* (*c.* 9%) and higher in *A. germinans* (*c.* 25%) and *L. racemosa* (*c.* 20%; McKee, 1996). Cheng *et al.* (2012) found that porosity in Indo-Pacific mangrove species ranged between 10% and 33%. The lowest root porosities were in *R. stylosa* (15%) and the genus *Heriteria* (10%), with higher porosities in the genera *Sonneratia*, *Aegiceras*, *Kandelia* and *Bruguiera* (*c.* 30%).

Secondary thickening of smaller diameter (< 1 cm) mangrove roots is limited (Gill & Tomlinson, 1977), but mangrove roots often have a lignified epidermis that can persist and even form channels as described above (McKee, 2001). In addition, in terrestrial soils, chemical stabilization of root C with minerals is important for long-term C storage (Rasse *et al.*, 2005). Although mangroves do not tend to accumulate metals in roots (MacFarlane *et al.*, 2007), there is evidence of metal plaques in mangrove roots (Alongi *et al.*, 2004; Machado *et al.*, 2005; Pi *et al.*, 2011), which may contribute to the stabilization of soil C and the maintenance of soil volume. Larger diameter structural roots can account for up to half of root biomass where they occur (up to 50 kg m^{-3}), although their distribution is patchy (associated with stems; Komiyama *et al.*, 1987). Similar to woody debris from the canopy, these large roots may make an important, but as yet unquantified, contribution to soil volume.

V. Factors affecting root contributions to vertical soil development

A number of factors influence the extent to which roots may contribute to accretion and elevation change in mangrove forests. Here, we focus mainly on fine and coarse roots that grow on or below the soil surface, but also include information on aerial roots where relevant. The accumulation of root matter reflects the balance between the rate of production and decomposition. Production–decomposition processes are sensitive to nutrients, salinity, flooding, sediment characteristics (particle size) and disturbance. Environmental factors within the root zone may also influence root traits controlling the gain or loss of root volume. Below, we briefly review how some important factors may affect mangrove root accumulation (references are collated in Table S1).

1. Salinity

The response of root growth to salinity in mangroves is species dependent (Krauss & Allen, 2003), but glasshouse experiments generally show that allocation to roots remains unchanged or is only slightly reduced as salinity increases (Downton, 1982; Burchett *et al.*, 1984, 1989; Naidoo, 1987, 1990; Ball & Pidsley, 1995). By contrast, Ball (1988) observed an increase in the root : shoot (R : S) ratio with increasing salinity for *Avicennia marina* and *Aegiceras corniculatum* seedlings.

Studies of the effects of salinity on roots in field settings can be confounded by differences in inundation and nutrient availability which often co-vary with salinity. However, a multifactorial field study at a mangrove forest in the Dominican Republic dominated by *R. mangle* and *L. racemosa* showed that salinity was not an important factor influencing belowground biomass (Sherman *et al.*, 2003). Similarly, Saintilan (1997a,b) showed that most of the increase in the R : S ratio with increasing salinity in temperate and subtropical mangroves in southeast Australia was the result of decreasing aboveground biomass rather than a change in root biomass. However, although most plants, including most mangroves studied, show no decline or a weak decline in root biomass in response to shifts in salinity (Poorter *et al.*, 2012), exceptions have been described. For example, the root biomass of *Ceriops decandra* and *C. australis* declined at salinities above 25% and 50% seawater, respectively; at 100% seawater, root biomass was only 13% of the maximum biomass observed (Ball, 2002). The reduction in root biomass with salinity is not always associated with a reduction in R : S ratio allocation, but rather corresponds to the general decline in overall plant growth rates when salinity tolerance is exceeded (e.g. Naidoo, 1987; Ball & Pidsley, 1995; Krauss & Allen, 2003).

Salinity may have significant effects on root architecture of mangroves, but little information exists. In other halophytes, such as the herbaceous plant *Plantago maritima*, high salinity enhances the lengthening of primary roots, but strongly inhibits lateral root development (Rubinigg *et al.*, 2004). Such salinity-driven changes in root structure affect root decomposition rates (Graaff *et al.*, 2013). Thus, even though salinity differences may have little effect on mangrove root biomass production, indirect effects on elevation change through the alteration of root architecture and changing root turnover and decomposition rates should be considered.

2. Nutrients

Several studies have examined the effects of nutrients on mangrove growth and productivity (Reef *et al.*, 2010), but few have measured how nutrients affect root contributions to elevation change. Increased nutrient availability increases plant production, and this can be associated with a reduced allocation to the production of roots (Chapin *et al.*, 1990). In mangrove seedlings, the proportional allocation of biomass to roots was reduced under nutrient-replete conditions compared with low-nutrient conditions in both *A. germinans* and *L. racemosa* (but not *R. mangle*; McKee, 1995), but this was a result of an increased biomass allocation to the shoot rather than lower root biomass under nutrient-replete conditions. Higher nutrient availability (especially phosphorus, P) resulted in a decline in fine root biomass in mangroves across a natural nutrient availability gradient in Florida (Castañeda-Moya *et al.*, 2011).

Nutrient enrichment can reduce root accumulation and consequent contribution to soil volume in some settings by accelerating root decomposition. In other situations, root production is greatly stimulated by the added nutrient, but decomposition remains unchanged or is minimally increased because the decomposers may be limited by a different nutrient (Sundareshwar *et al.*, 2003). Changes to root architecture (e.g. root size distribution) may also affect soil volume through effects on root longevity and decomposition rates, which may vary with root type (e.g. fine vs coarse roots) or soil depth. In a manipulative experiment in a P-limited mangrove system, McKee *et al.* (2007) found that fine and coarse root production was stimulated by the addition of P (as PO_4), but not N (as urea), at some sites, which led to elevation gain by the promotion of root zone expansion (compared with controls, which lost elevation). However, root mortality was greater in N-fertilized plots, which experienced greater rates of subsidence (McKee *et al.*, 2007). Nutrient enrichment with some types of fertilizer can lead to elevation loss through increases in soil metabolism and rapid turnover of organic matter (Morris & Bradley, 1999; Deegan *et al.*, 2012). When comparing among studies, however, it is important to consider the form of fertilizer used. Although urea may stimulate the growth and activity of soil decomposers, NO_3-N additionally serves as an energetic redox couple in anaerobic soils (Reddy & DeLaune, 2008), potentially stimulating energy transformations. Elevated rates of root decomposition, combined with the potentially reduced storage of biomass below ground, suggest that nutrient enrichment has the potential to reduce root volume in some settings.

3. Flooding

Mangroves are adapted to flooded conditions. Despite this, increases in flooding depth and duration generally reduce root accumulation rates (McKee *et al.*, 2007), a response that probably reflects the effects of low-oxygen conditions on both root growth and decomposition. Laboratory studies, for example, have shown that root extension of mangroves slows when oxygen concentrations are low (McKee, 1996). Increases in flooding depth and

duration and lack of oxygen also inhibit mangrove root decomposition (Poret *et al.*, 2007) and can enhance the development of aerial root structures (Turner *et al.*, 1995). The biomass of fine roots decreased with increasing frequency of inundation in south Florida mangroves (Castañeda-Moya *et al.*, 2011). In a laboratory study, allocation to roots decreased when plants were permanently flooded compared with regular tidal flushing (Cardona-Olarte *et al.*, 2006). In the field, *Avicennia marina* saplings showed less annual biomass accumulation and lower R : S ratios at lower intertidal locations, also suggesting less proportional biomass allocation to roots with prolonged inundation associated with greater flooding (Lu *et al.*, 2013). Flooding, however, may promote greater biomass allocation to roots in some settings (McKee, 1993; Krauss, 2004).

The effect of flooding on root production can be hard to predict. Flood-tolerant trees that may show fastest aboveground growth at intermediate flooding levels, because of greater availability of nutrients and oxygen in the soil, may respond differently with root growth (Day & Megonigal, 1993). At the same time, rates of organic matter decomposition also vary with flooding and oxygen availability. To promote root accumulation and soil volume expansion, there must be an optimal balance between root production and decomposition. Few studies, however, have shown experimentally that root accumulation contributes directly to elevation change (McKee *et al.*, 2007; McKee, 2011). In Belizean mangroves, where root accumulation was low along an elevation/flooding gradient (in permanently flooded sites), there was a net loss in elevation; elevation gains occurred along shorelines with less frequent flooding and higher root accumulation rates (McKee *et al.*, 2007). This gradient in root contributions to elevation gain was not only caused by flooding, but also by low availability of nutrients, particularly P (McKee *et al.*, 2002). Fertilization of subsiding *R. mangle* plots with P (as PO_4) for 3 yr led to increased root accumulation and a dramatic change in elevation trajectory, ultimately raising soil surfaces an average of 7 cm above control plots (McKee *et al.*, 2007). Mangrove species, however, may respond differently to variation in hydroperiod and oxygen deficiency (McKee, 1996; Pezeshki *et al.*, 1997), and thus may have differing capacities to influence soil elevations. In addition, insight gained from studies on seedlings might not accurately reflect the response of mature plants, which have more fully developed aeration pathways and oxidized rhizospheres (Thibodeau & Nickerson, 1986).

4. Soil texture

Soil texture influences tree root growth (Kozlowski, 1999 and references therein). In general, high soil bulk density (dry mass of soil per unit volume) decreases root growth, especially in environments with high proportions of silt or clay (Jones, 1983). Early experiments by Gill & Tomlinson (1977) found that belowground roots of mangroves were sensitive to variation in soil texture. They provided descriptive evidence of differences in root branching. In hydroponic culture, roots were smooth and relatively unbranched, compared with those in sandy and muddy substrates, which were highly branched. In New Zealand, growth rates of plants were enhanced in muddy relative to sandy habitats (Lovelock *et al.*, 2007), indicating that soil texture is important to the growth of mangroves and may influence root production. A study of 12 different wetland plant species showed that soil type was a significant factor in determining growth rate and biomass allocation to roots (Lenssen *et al.*, 1999). Although the interpretation of these findings was confounded by variations in organic matter and nutrient availability among the different soil types, all species allocated more growth below ground in the mineral sediment, which had the highest bulk density of the sediment types tested (Lenssen *et al.*, 1999). The sensitivity of roots to soil structure is also demonstrated by roots of *R. mangle* which proliferate in old root channels compared with the bulk soil (McKee, 2001). There is evidence that soil texture influences SRL and productivity, but the influence of soil texture on rates of change in soil volume has not yet been explored in mangrove habitats.

5. Disturbance

Biotic factors Organisms that influence the branching patterns of roots, those that feed on root and wood detritus in soils and those that burrow in soils could have a strong, but as yet unknown, influence on the maintenance of soil volume and elevation change in mangrove soils. Isopods that damage tips of aboveground roots of *Rhizophora* alter root productivity and branching (Simberloff *et al.*, 1978; Brooks & Bell, 2002). Detrital feeding species, particularly shipworms (Teredinidae) which consume wood in the marine environment (Robertson & Daniel, 1989), may also have a negative influence on soil volume through the consumption of woody roots and downed branches, but also a potentially positive influence through the contribution of calcified tubes that they form. Mangrove soils are habitat to a wide range of burrowing invertebrates, dominated by crabs. Their roles in the aeration of soils and in processing organic matter have been widely recognized (Kristensen, 2008; Lindquist *et al.*, 2009), as has their contribution to soil surface topography (Warren & Underwood, 1986).

Acute deposition of sediments Large deposits of sediments can cause mangrove mortality (Ellison, 1998), presumably by blocking aeration pathways through aerial roots; as roots collapse and no new roots are produced, soil compression and shallow subsidence lead to elevation losses (Cahoon *et al.*, 2003; Cahoon, 2006). By contrast, rapid deposition of sediments from acute storm surges can provide important sources of elevation capital to specific wetlands, especially those that are undergoing rapid subsidence (Cahoon, 2006; Smoak *et al.*, 2013). Smith *et al.* (2009) described up to 8 cm of sediment deposition within mangrove forests during a hurricane (Wilma) in south Florida, where sediment deposition decreased by *c.* 3.0 mm for every linear kilometer inland from the edge of the Gulf, attenuating almost completely by 15 km inland. Mangrove vegetation facilitates the deposition of sediments as currents are slowed by root structures, stems and the gradually sloping landscape (Furukawa & Wolanski, 1996; Furukawa *et al.*, 1997).

Only with recent hurricanes have we begun to understand the fate of these acute storm deposits and the influences of vegetation in facilitating and retaining deposition. For instance, vertical

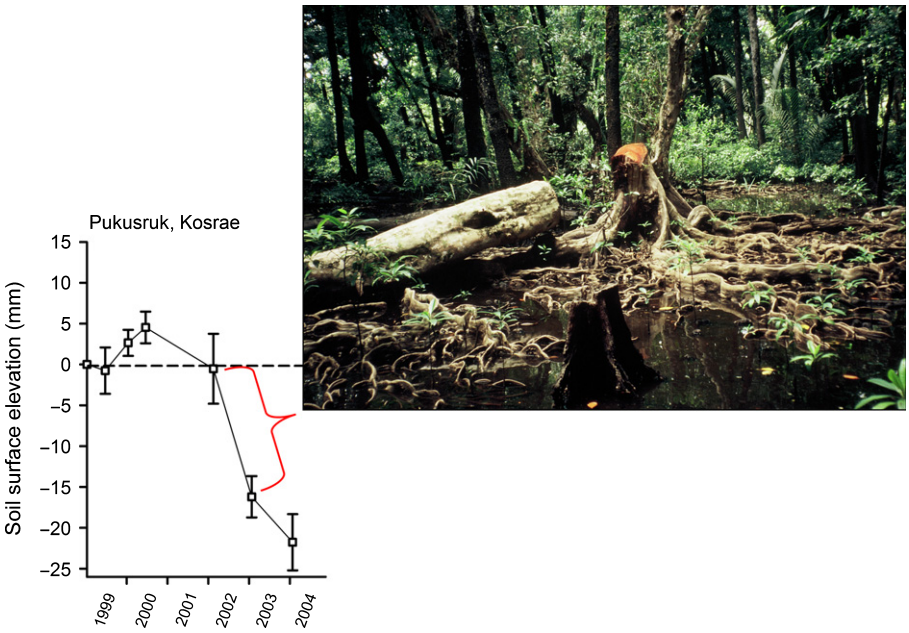

Fig. 6 (a) Harvested *Xylocarpus granatum* mangrove tree in Micronesia, and (b) impact of harvesting a few nearby mangrove trees on elevation change. Reproduced from Krauss *et al.* (2010) with kind permission from Springer Science and Business Media.

accretion had previously been reported to be 6.6 mm yr^{-1} on south Florida mangrove sites (Whelan *et al.*, 2005). Hurricane Wilma deposited 37.0 ± 3.0 mm of sediment on top of previously established marker horizons, but the realized elevation gain was 42.8 mm from this single event (Whelan *et al.*, 2009). The differential was attributed to root zone expansion immediately after the storm. Over the next 6 months, erosion and settling accounted for 10.5 mm of loss from these acute deposits of sediment. Thus, the previous rate of vertical accretion was adjusted to 11.5 mm yr^{-1}, 43% of which was attributed to a single storm event (Whelan *et al.*, 2009). The colonization of storm deposits by rootlets was relatively rapid, and appeared to stabilize residual storm deposits after the initial 6-month settling period to become part of the longer term soil profile (Whelan *et al.*, 2009). Organic C burial rates were 1.3–2 times higher in recent storm sediment deposits than in older sediments in south Florida mangroves (Smoak *et al.*, 2013). By contrast, episodic, storm-related deposits of sediment in a temperate Australian mangrove forest were quickly lost, possibly because sedimentation occurred during the winter when rates of algal and root colonization were at their lowest (Rogers *et al.*, 2013).

Storm damage and lightning Mortality of mangrove trees by any mechanism has the potential to compromise elevation by killing roots. Cahoon *et al.* (2003) measured elevation change and vertical accretion 18–33 months after Hurricane Mitch made landfall in the mangroves of Honduras. Where trees were killed by excessive flooding, defoliation and stem breakage from the storm, soils lost the most elevation after the storm, probably as a result of compression of the live roots on death. Soils were subsiding at rates of up to 11 mm yr^{-1} as a result of widespread root zone collapse (Cahoon *et al.*, 2003). The storm killed mangroves in several other locations as well, where, despite having initial positive gains in elevation after the storm, they also began to exhibit root zone collapse 2.5 yr later (Cahoon *et al.*, 2003). The delay in soil collapse was attributed to greater soil strength in more prolific root zones before the storm.

Lightning strikes also cause elevation loss around trees. Lightning can affect single trees, or kill groups of trees as energy is dissipated through multiple stems simultaneously. For example, canopy gaps in south Florida, Australia and Caribbean mangroves are often associated with the mortality of multiple stems affecting fairly large areas (range, 27–1600 m^2; Sherman *et al.*, 2000; Whelan, 2005; Amir, 2011). Whelan (2005) studied the effects of lightning strikes on elevation change in south Florida mangrove canopy gaps created by new lightning strikes (1–3 months old) and old lightning strikes (7–10 yr old), in comparison with reference forests. Newly formed lightning gaps showed higher concentrations of dead roots, which promoted elevation loss in some, but not all, gaps. Elevation losses were also reported in lightning gaps in the Dominican Republic, which may have been sufficiently severe to increase hydroperiods and possibly reduce the growth of regenerating seedlings of some species (Sherman *et al.*, 2000).

Harvesting Many mangrove forests are also periodically harvested. In 1999, elevation studies were installed in a backswamp (basin/interior) setting on the island of Kosrae, Micronesia (Pukusruk; Krauss *et al.*, 2010). Elevations remained relatively stable through the early part of 2002, but elevation decreased by 21.3 mm over the ensuing 2 yr (Fig. 6). As plots were not trampled, the most probable cause of this elevation loss was small-scale, individual tree harvesting immediately adjacent to study plots, which prevented new root production from offsetting turnover (Krauss *et al.*, 2010), indicating that elevation change might be rather sensitive to seemingly innocuous human or natural impacts.

Large-scale impacts of forest mortality (e.g. Lugo, 1997) on elevation change have also been described. Elevation studies deployed in a regenerating mangrove forest in Homebush Bay, Australia documented a reduced rate of elevation change (2.9 mm yr^{-1}) relative to a nearby reference forest (7.2 mm yr^{-1};

Rogers *et al.*, 2005). This disparity documents a transitional stage of mangrove forest recovery after local engineering modifications forced chronic dieback (and then regeneration) of mangrove vegetation between 1978 and 2000. In fact, elevation change exceeded vertical accretion in these regenerating forests, suggesting strong root zone recovery and control over elevation change, even after a major disturbance event (Rogers *et al.*, 2005). Accordingly, areas cleared of mangroves lost elevation at 9–38 mm yr^{-1} vs gains of up to 14 mm yr^{-1} within intact mangroves in New Zealand (Stokes *et al.*, 2009).

VI. Some potential climatic and environmental feedbacks

Climate variability and change also influence elevation change, both by direct effects and by affecting vegetation. Many of the processes described in the previous sections can be influenced by changing climate (increased CO_2 concentrations, sea-level rise), as well as inter- and intra-annual variation in rainfall.

1. Rainfall variability

Rogers & Saintilan (2008) measured mangrove elevation change and groundwater levels fortnightly over a 4-month period following a heavy rainfall event, during which time elevation increased in concert with groundwater, and then declined. Over broader spatial and temporal scales, drought and flood phases are likely to exert a strong influence on elevation, as wetlands de-water and peats compact during drought (Drexler & Ewel, 2001; Whelan *et al.*, 2005). The direct role of vegetation in this may be significant. Rogers & Saintilan (2008) demonstrated a correlation between the Southern Oscillation Index, an indicator of the intensity of the El Niño Southern Oscillation, and mangrove elevation change over a 2–3-yr period across a network of sites spanning 2000 km of coastline. Elevation declined up to 25 mm during intense drought conditions, reflecting a combination of groundwater influences (up to 80% of change) and root zone contraction. Root growth may also be suppressed during periods of low rainfall as tree growth and overall site productivity are slowed (Krauss *et al.*, 2007; Lovelock *et al.*, 2011b).

Fluctuations in rainfall over decadal scales alter vegetation composition and structure, potentially affecting biological contributions to elevation change. The encroachment of mangroves into coastal salt marshes is one such trend, observed in many places in the world over the past half century (Saintilan & Williams, 1999; Krauss *et al.*, 2011; Saintilan *et al.*, in press). In subtropical Queensland, the proportion of mangrove over salt marsh vegetation in estuarine intertidal zones is strongly associated with rainfall (Bucher & Saenger, 1991; Eslami-Andargoli *et al.*, 2009). However, mangrove encroachment is also associated with higher relative sea levels (Rogers *et al.*, 2006). Elevation gain in mangroves can exceed that in salt marshes where these communities co-exist (Rogers *et al.*, 2006; Lovelock *et al.*, 2011a); salt marshes encroached by mangrove were generally those that previously had lost elevation because of subsidence and sea-level rise.

2. Response to elevated atmospheric CO_2

CO_2 can facilitate the growth of mangrove vegetation directly, thereby affecting elevation change dynamics. Most assessments of growth enhancements with elevated CO_2 come from studies on aboveground components. Poorter & Navas (2003) found that, among a number of studies conducted on elevated CO_2 in terrestrial plants, leaf and photosynthetic traits were affected for five out of eight variables: for example, smaller leaf area per unit plant mass, greater whole-plant photosynthesis per unit leaf area and greater whole-plant C concentrations with elevated CO_2. Relative growth rate (RGR: increase in plant biomass per unit biomass) was not affected significantly in the meta-analysis (Poorter & Navas, 2003); however, RGR and biomass were consistently enhanced under elevated CO_2 in the few available mangrove studies (Fig. 7; Farnsworth *et al.*, 1996; Ball *et al.*, 1997; McKee & Rooth, 2008). It is uncertain whether the response to long-term exposure to CO_2 can be predicted on the basis of short-term experiments, and will probably depend on modeling efforts using data from both controlled experiments and field studies (see review by McKee *et al.*, 2012).

Elevated CO_2 had little influence on RGR of two mangrove species at high salinity, but enhanced RGR in both species at low salinity (Ball *et al.*, 1997). Greater RGRs were observed for the less salt-tolerant species, *R. apiculata*, which grew much more vigorously than the more salt-tolerant *R. stylosa*. Changes in root mass per unit leaf area for both mangrove species under elevated vs ambient CO_2 were inconsistent among the combinations of humidity and salinity simulated (Ball *et al.*, 1997), indicating that biomass partitioning to roots can be fairly sensitive to correlative factors. For example, N stimulated root growth in the mangrove *A. germinans* under both elevated and ambient CO_2, but both aboveground and belowground production were stimulated more under elevated vs ambient CO_2 when N availability was high (McKee & Rooth, 2008).

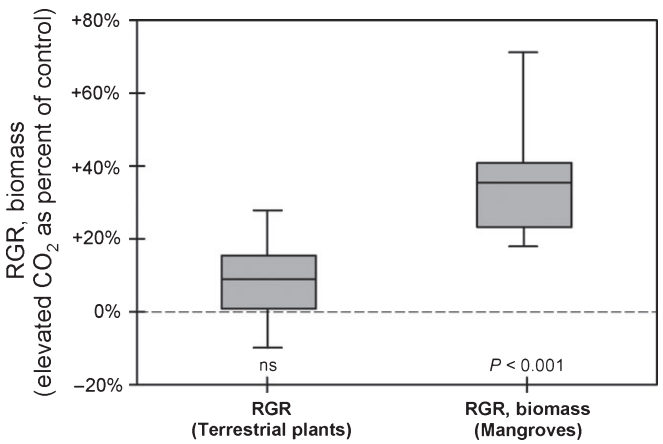

Fig. 7 Relative growth rate (RGR) of terrestrial plants (approximated from Poorter & Navas, 2003) vs RGR or biomass for mangroves growing under elevated CO_2 (Farnsworth *et al.*, 1996; Ball *et al.*, 1997; McKee & Rooth, 2008). Statistical significance indicates whether means differed from zero for terrestrial plants ($n = 130$, Poorter & Navas, 2003) and mangroves ($n = 8$, $t = 6.09$, $P = 0.0005$). Boxplots indicate the 5th, 25th, 50th, 75th and 95th percentiles of the distribution. ns, not significant.

Studies of coastal marsh communities have suggested that the basal expansion of shoots or the stimulation of root growth under elevated CO_2 can promote elevation change by small, but significant, positive increments relative to hydrology, salinity and/or nutrient gradients (Cherry *et al.*, 2009; Langley *et al.*, 2009). The relationship between aboveground production and elevation change was dependent on whether marsh plants had C_3 ($r = 0.87$) or C_4 ($r = -0.65$) photosynthetic pathways, with C_3 plants having a greater ability to benefit growth, as elevated CO_2 partially ameliorated the effects of increased salinity (Cherry *et al.*, 2009). Additional study is needed for mangroves, which are also C_3 plants.

Secondarily, increases in CO_2 may concentrate non-structural carbohydrates in leaf tissues (Poorter *et al.*, 1997), which could slow the decomposition of litter incorporated within the soil to promote greater soil building. This effect would probably be greater in mangroves accumulating surface leaves (e.g. basin/interior mangroves), but concomitant shifts in root tissue chemistry with elevated CO_2 might also occur. Although elevated CO_2 increased leaf tissue lignin concentrations by 6.5% and reduced N concentration by 7.1% across a range of woody and herbaceous plant species, no consistent effect of decomposition (or respiration) was found (Norby *et al.*, 2001). This observation suggests that, although shifts in leaf chemistry can occur with exposure to elevated CO_2 (but see McKee & Rooth, 2008), the influences of other factors controlling leaf decomposition and affecting elevation change may be larger.

3. Feedback effects related to sea-level rise

Sea-level rise can influence the position and persistence of mangrove ecosystems in the intertidal zone (McKee *et al.*, 2007; Gilman *et al.*, 2008; Rogers & Saintilan, 2008); however, the degree to which long-term changes in sea level *per se* control elevation change directly by influencing root growth (or other factors) is not well known. Belowground biomass represents 30–60% of the total biomass in many mangrove forests (Golley *et al.*, 1962; Briggs, 1977; Tamooh *et al.*, 2008), and the relative balance of productivity between aboveground and belowground components within individual trees can be fairly sensitive to hydrology (Castañeda-Moya *et al.*, 2013).

Some research suggests that root contributions, driving upward soil expansion, are essential for some mangrove ecosystems to keep pace with rising sea level, especially where the accretion of mineral sediment is insufficient (McKee *et al.*, 2007; Gilman *et al.*, 2008; McKee, 2011). As reviewed previously, excessive flooding commonly, but not always, inhibits root growth and can enhance stem elongation of some mangrove species (Pezeshki *et al.*, 1997; Ye *et al.*, 2003, 2004, 2010; Lu *et al.*, 2013), resulting in lower, not higher, R : S ratios. Rapid leaf production and decreased root biomass relative to aboveground growth would decrease the oxygen requirement for long-term external rhizosphere oxidation, and shorten the oxygen diffusion path to the growing root tips (Ye *et al.*, 2010).

By contrast, *R. mangle* seedlings grown experimentally for 2.5 yr using simulated high (+16 cm, sea-level rise), normal and low (−16 cm, sea-level drop) tides did not respond with different R : S ratios among these treatments (Ellison & Farnsworth, 1997). Over the first year, normal tides and high tides (simulating sea-level rise) produced seedlings with faster growth, but the growth rate for seedlings subjected to high tides slowed into the second year. R : S ratios for all treatments increased over time, but not differentially by treatment (Ellison & Farnsworth, 1997). Overall growth rates were eventually reduced with longer inundation, suggesting that any growth benefit related to other global change factors (e.g. increased atmospheric CO_2; Fig. 7) may be countered by reduced growth with greater duration of inundation as sea levels rise (Ellison & Farnsworth, 1997) if mangrove soil surfaces do not adjust vertically with the rise in sea level. Eustatic sea-level rise is 3.2 mm yr^{-1} (Nerem *et al.*, 2010), which would influence hydrology at a much slower pace (cf. Ellison, 2008) than that used in experimental studies. Nevertheless, accounts of peat deposition from mangrove root growth tracking sea-level rise over the Holocene (Fujimoto, 1997; Hashimoto *et al.*, 2006; McKee *et al.*, 2007) suggest a capacity for root zone influence on elevation change associated with water level changes over geological time frames.

VII. Perspectives

Mangrove ecosystems serve as a focal point for the study of processes controlling elevation change in intertidal settings. Many of these processes are directly or indirectly influenced by mangroves: root growth and morphology; accumulation of woody debris and leaf litter; benthic mat development; and aerial root structure and density. Sea-level rise is a special concern for coastal land managers, especially as many mangrove ecosystems are unable to migrate inland because of artificial barriers, such as sea walls and dikes. From these studies, we have reviewed what is known about plant-mediated elevation processes in mangrove ecosystems, and have identified a suite of biological relationships mediated by mangrove vegetation that might be applicable to other coastal wetland types throughout the world. The relationship between elevation change and habitat stability is particularly vital, as this determines whether mangrove forests can keep pace with rising sea level. Vegetation can influence habitat stability through direct and indirect contributions to vertical accretion and soil expansion, processes that are mediated by feedback effects of soil elevation and tidal action on plant growth and organic matter accumulation.

We need to learn much more about the specific mechanisms controlling plant influences on mangrove elevation dynamics through both glasshouse and field studies of interacting environmental (e.g. flooding, salinity) and plant (e.g. root accumulation) variables. In addition, the study of mangrove areas undergoing natural or anthropogenic disturbance (or regeneration) can be used to assess how the presence or absence of the vegetation may modify the capacity of the land surface to keep pace with sea-level rise. Efforts to monitor accretion and elevation change in multiple sites globally (Webb *et al.*, 2013) will be particularly necessary to develop a broader understanding of mangrove habitat stability in different sedimentary settings and disturbance regimes. Empirical and observational data can be used in combination with modeling

approaches to predict long-term impacts of external drivers, such as changes in atmospheric CO_2, rainfall, temperature and sea level, which are difficult or expensive to simulate under field conditions. Through such combined approaches, more specific management plans can be designed to better protect and conserve the world's mangrove forests.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Photographs depicting measurements using the Surface Elevation Table-Marker Horizon (SET-MH) system in mangrove forests.

Table S1 Summary of studies on plant traits that may influence elevation change in mangrove forests

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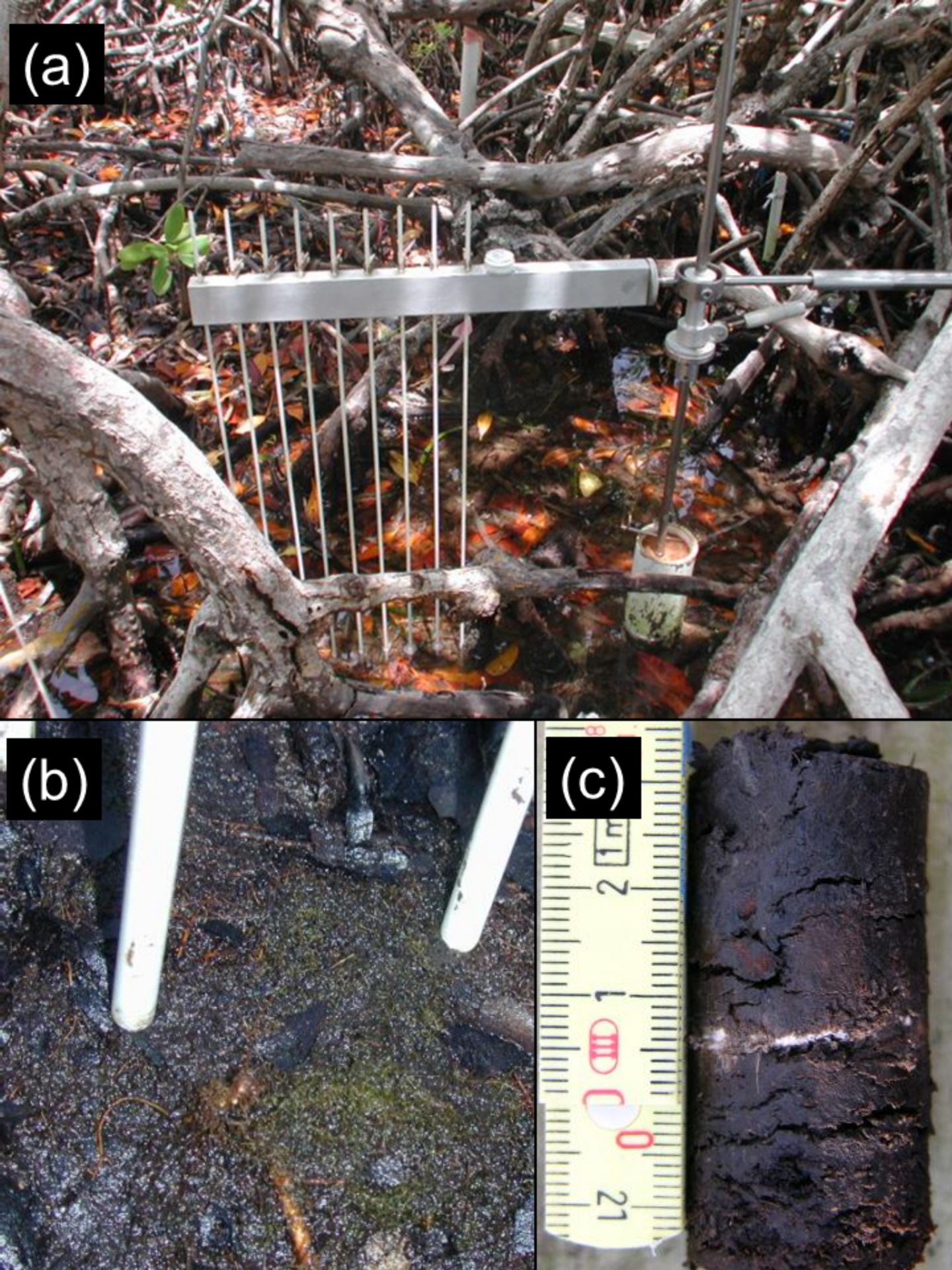
(a)
(b)
(c)

Supporting Information Table S1 Summary of studies that assess the effects of a range of plant traits that may influence elevation change in mangrove forests.

	Plant traits influencing root volume		Plant traits influencing loss of root volume (collapse, decomposition, compression)			
Root zone factor	Root growth and/or allocation to roots	Specific root length (SRL)	Root growth and/or longevity	Porosity	Secondary thickening/ plaques	Diameter
Species	Clough, 1984; Pezeshki *et al.* , 1990; McKee, 1996; Pi *et al.* , 2009	McKee, 1996	Middleton & McKee, 2001	McKee, 1996; Cheng *et al.* , 2012; Youssef & Saenger, 1996	Gill & Tomlinson, 1977; Alongi *et al.* , 2004	McKee, 1996
Salinity	Burchett *et al.* , 1984; Clough, 1984; Pezeshki *et al.* , 1990; Ball & Pidsley, 1995; Smith & Snedaker, 1995; Saintilan, 1997a, b; Sherman *et al.* , 2003; Ye *et al.* , 2010; Poorter *et al.* , 2012		Ball, 1988; Ball, 2002; Cormier, 2003; Castañeda-Moya *et al.* , 2011			
Nutrient availability	McKee, 1995; McKee, 1996; Ellison & Farnsworth, 1997; Naidoo, 1990; McKee *et al.* , 2007	Giraldo Sanchez, 2005	Cormier, 2003; Feller *et al.* , 2003; McKee *et al.* , 2007; Poret *et al.* , 2007; Castañeda-Moya *et al.* , 2011		Pi *et al.* , 2011	
Hydroperiod	McKee, 1993; Pezeshki *et al.* , 1990; Ellison & Farnsworth, 1997; Pezeshki *et al.* , 1997; Ye *et al.* , 2003; Ye *et al.* , 2004; Cardona-Olarte et al., 2006; Ye *et al.* , 2010; Lu *et al.* , 2013	McKee, 1996 Giraldo Sanchez, 2005	Poret *et al.* , 2007	Ellison & Farnsworth, 1997		
Soil texture	Gill & Tomlinson, 1977; McKee, 2001; Lovelock *et al.* , 2007	Gill & Tomlinson, 1977				Gill & Tomlinson, 1977
Biotic factors	Simberloff *et al.* , 1978; Brooks & Bell, 2002		Robertson & Daniel, 1989			

Supporting Information Legends to Fig. S1, Table S1 and References to Table S1

Fig. S1 The surface elevation table-marker horizon (SET-MH) system is used to measure elevation change and accretion in mangrove forests. (a) SET in a mangrove forest in Belize. The measuring arm is attached to a benchmark rod and leveled; pins are lowered to the soil surface and the distance above the arm is recorded on each measurement date. (b) Close-up of pins resting on the soil surface. (c) A core showing accretion of sediment and organic material above a marker horizon of feldspar clay. Image credit: US Geological Survey, K. L. McKee, photographer.

Table S1 Summary of studies that assess the effects of a range of plant traits that may influence elevation change in mangrove forests. Most studies have focused on species effects on plant traits, root growth, and allocation to roots, with far fewer studies on plant traits that influence the loss of root volume.

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