

The Physiology of Mangrove Trees with Changing Climate

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Abstract Mangrove forests grow on saline, permanently or periodically flooded soils of the tropical and subtropical coasts. The tree species that compose the mangrove are halophytes that have suites of traits that confer differing levels of tolerance of salinity, aridity, inundation and extremes of temperature. Here we review how climate change and elevated levels of atmospheric CO₂ will influence mangrove forests. Tolerance of salinity and inundation in mangroves is associated with the efficient use of water for photosynthetic carbon gain which underpins anticipated gains in productivity with increasing levels of CO₂. We review evidence of increases in productivity with increasing CO₂, finding that enhancements in growth appear to be similar to trees in non-mangrove habitats and that gains in productivity with elevated CO₂ are likely due to changes in biomass allocation. High levels of trait plasticity are observed in some mangrove species, which

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potentially facilitates their responses to climate change. Trait plasticity is associated with broad tolerance of salinity, aridity, low temperatures and nutrient availability. Because low temperatures and aridity place strong limits on mangrove growth at the edge of their current distribution, increasing temperatures over time and changing rainfall patterns are likely to have an important influence on the distribution of mangroves. We provide a global analysis based on plant traits and IPCC scenarios of changing temperature and aridity that indicates substantial global potential for mangrove expansion.

Keywords Elevated CO₂ · Flooding · Plasticity · Salinity · Water uptake

Introduction

The trees of mangrove forests have fascinated physiologists for decades. The highly saline, tidally flooded environments of mangrove forests seem unlikely to support tree growth, yet mangroves are some of the most productive forests on the planet (Alongi 2009). Both the number of families and individual species of plants that have evolved the necessary traits to grow in mangrove habitats has been relatively small: 70 species in over 40 million years (Ricklefs et al. 2006), reflecting the complex suite of traits that are required for growth in intertidal environments. The position of these forests in the landscape, on the ecotone between terrestrial and marine habitats, also brings high levels of variation in soil conditions that range over a hierarchy of timescales: daily (e.g., tidal inundation), monthly (e.g., tidal cycles), annual (e.g. seasonal precipitation) and tens to hundreds of years (e.g., sea level rise). Such rhythmic and dynamic conditions require the trees that grow in these intertidal habitats to have high levels of plasticity.

In the present review, we focus on recent insights into the ecophysiological processes that enable mangrove forests to maintain productivity under both saline and anoxic soil conditions, how their physiology is limited by temperature and how these physiological attributes may affect responses of mangrove forests to the complex environmental changes anticipated under future conditions. Enhancements in our understanding of the underlying physiological bases of salinity tolerance in mangroves is important to the development of both salinity tolerant crops and predictive models for management of the wide range of ecosystem services provided by mangrove forests under changing environmental and climatic scenarios (Barbier et al. 2011). However, global climate and atmospheric change do not affect salinity in isolation. Other key environmental factors, namely atmospheric CO₂ concentration, temperature and sea level are also changing with far reaching consequences for the structure, function and distribution of mangrove systems.

Water Uptake in Saline Soils

Mangrove tree species tolerate a wide range of soil salinity (Lugo and Snedaker 1974; Odum et al. 1982; Hutchings and Saenger 1987) (Table 1) and are highly adapted to salt concentrations in soils that exceed concentrations tolerated by most other plants (Ball 1988a). However, both low and high salinity can limit mangrove growth and productivity (Clough and Sim 1989; Lin and Sternberg 1992; Ball 2002). Saline habitats present physiological challenges for plants because their survival depends on the extraction of almost freshwater from highly saline soils. The low osmotic potentials of saline soil water make water acquisition and transport more difficult than in wet, non-saline soils, leading to high carbon costs of water uptake and transport. These costs are reflected in the typically high water-use efficiency of mangroves which tends to increase with increases in both the salt tolerance of the species and the salinity in which the plants are grown (Ball 1988a). However, such water use characteristics come at the expense of other functions. Table 2 summarizes the traits associated with salinity tolerance in mangroves and indicates some of the putative costs associated with salinity tolerance, including reduced survival in the shade (Ball 2002; Lopez Hoffman et al. 2007), reduced growth rates (Ball 1988a) or loss of mechanical strength (Santini et al. 2012).

Growth in saline environments necessitates adaptations to maintain the low tissue water potentials needed to extract water from highly saline soils, and to limit the loss of extracted water from leaves. To this end, mangrove species can exclude, accumulate, and excrete salts; none of these are salt tolerance strategies per se, although each can be related to water uptake and the requirement for water conservation (Ball 1988a). Mangroves as a broad group are halophytes with a wide range of salinity tolerance among species (Krauss and Ball 2013; Reef and Lovelock 2014) (Table 1). All mangrove species exclude the majority of salt ions during water absorption by the roots (up to 80–95 %; Scholander et al. 1962; Scholander et al. 1968; Popp et al. 1993). Casparian bands and suberin lamellae provide barriers to apoplastic water flow through the root endodermis and are well developed close to the root tip (Lawton et al. 1980). Root traits vary among species. For example *Bruguiera* possesses a large root cap, high levels of phenolic deposits in cells and rapid development of vasculature to prevent salts from entering xylem vessels through this pathway (Lawton et al. 1981). In contrast *Avicennia marina* has a smaller root cap and vascular development is delayed, which may allow greater salt and water uptake (Fig. 1). Greater development of root apoplastic barriers among species reduces bypass flow, forcing water through the endodermis and enhancing efficient salt exclusion (Krishnamurthy et al. 2014). Indeed, concentration of salts within soils can pose a real dilemma for mangroves; recent stable isotope studies have shown that mangroves utilize less saline water sources when freshwater is available (Sternberg and Swart 1987; Ewe et al. 2007; Lambs et al. 2008; Wei et al. 2013). For example, in Florida *R. mangle* went from using 100 % shallow soil water in the wet season when that water was fresh to a mix of 55 % shallow soil water and 45 % deeper groundwater during the dry season when deeper

Table 1 Tolerance of some mangrove species to high salinity, high aridity, and low temperatures

Species	Relative tolerance		Occurrence in extreme climatic conditions				Monthly mean max temp (°C)		
	Salinity	Aridity	Low temperatures	High temperatures	Aridity index	Precipitation (mm/yr)		Extreme min temp (°C)	Monthly mean min temp (°C)
<i>Acrostichum aureum</i>	Mid	Mid	Mid	Low	Semi-arid	800–1200	0–5	8–12	34–37
<i>Aegialitis annulato</i>	High	High	Mid	Mid	Arid	<400	0–5	8–12	37–40
<i>Aegiceras comiculatum</i>	Mid	High	High	Mid	Arid	<400	-5 to 0	4–8	37–40
<i>Avicennia germinans</i>	High	High	High	Mid	Arid	<400	<-5	4–8	37–40
<i>Avicennia marina</i>	High	High	High	High	Arid	<400	<-5	4–8	>40
<i>Bruguiera gymnorhiza</i>	Mid	High	High	Mid	Arid	<400	-5 to 0	4–8	37–40
<i>Bruguiera sexangula</i>	Low	Mid	Low	Low	Semi-arid	>1200	0–5	12–16	34–37
<i>Ceriops australis</i>	High	High	Mid	Mid	Arid	<400	0–5	8–12	37–40
<i>Ceriops decandra</i>	Low	Low	Low	Mid	Dry sub-humid	800–1200	5–10	12–16	37–40
<i>Ceriops tagal</i>	Mid	High	Mid	Mid	Arid	<400	-5–0	8–12	37–40
<i>Excoecona agallocha</i>	Low	Mid	High	Mid	Semi-arid	400–800	-5 to 0	4–8	37–40
<i>Heritiera littoralis</i>	Mid	Mid	High	Mid	Semi-arid	400–800	-5 to 0	8–12	37–40

(continued)

Table 1 (continued)

Species	Relative tolerance			Occurrence in extreme climatic conditions					
	Salinity	Aridity	Low temperatures	High temperatures	Aridity index	Precipitation (mm/yr)	Extreme min temp (°C)	Monthly mean min temp (°C)	Monthly mean max temp (°C)
<i>Kandelia candel</i>	Mid	Low	Low	Low	Dry sub-humid	>1200	5-10	>16	34-37
<i>Kandelia obovata</i>	Low	Low	High	Low	Dry sub-humid	>1200	<-5	4-8	34-37
<i>Laguncularia racemosa</i>	Mid	High	Mid	Mid	Arid	<400	<-5	8-12	37-40
<i>Lumnitzera littorea</i>	High	Low	Low	Mid	Dry sub-humid	800-1200	0-5	12-16	37-40
<i>Nypa fruticans</i>	Low	Low	Low	Low	Dry sub-humid	>1200	0-5	12-16	34-37
<i>Osbornia > a octodonata</i>	Mid	Mid	Mid	Mid	Arid	<400	0-5	8-12	37-40
<i>Rhizophora apiculata</i>	Mid	Mid	Mid	Mid	Semi-arid	400-800	0-5	8-12	37-40
<i>Rhizophora mangle</i>	High	High	Mid	Mid	Arid	<400	<-5	8-12	37-40
<i>Rhizophora mucronata</i>	Low	High	Mid	High	Arid	<400	0-5	8-12	>40
<i>Rhizophora stylosa</i>	High	High	High	Mid	Arid	<400	-5 to 0	4-8	37-40

(continued)

Table 1 (continued)

Species	Relative tolerance		Occurrence in extreme climatic conditions				Monthly mean max temp (°C)		
	Salinity	Aridity	Low temperatures	High temperatures	Aridity index	Precipitation (mm/yr)		Extreme min temp (°C)	Monthly mean min temp (°C)
<i>Sonneratia alba</i>	Mid	Mid	Mid	Mid	Semi-arid	400–800	0–5	8–12	37–40
<i>Sonneratia larceolata</i>	Low	Low	Low	Low	Dry sub-humid	>1200	5–10	>16	34–37
<i>Xylocarpus granatum</i>	Low	Mid	Mid	Mid	Semi-arid	400–800	0–5	8–12	37–40
<i>Xylocarpus moluccensis</i>	Mid	Mid	Mid	Mid	Semi-arid	400–800	0–5	8–12	37–40

Species-specific relative tolerances categories were determined using information in Clough (1992) and Reef and Lovelock (2014) in combination with the climatic tolerance data presented here. The final four columns provide estimates of the extreme climatic conditions in which a species is present (highest aridity, lowest precipitation, lowest temperature). Species range data were obtained from Spalding et al. (2010). The aridity index data were obtained from Zomer et al. (2006). The precipitation and monthly mean, minimum and maximum temperature data were obtained from Hijmans et al. (2005). The extreme minimum temperature data were obtained from Maurer et al. (2009)

Table 2 Mangrove plant traits associated with salinity tolerance in mangrove tree species and the putative costs of the salt tolerance trait

Trait	Function	Putative costs	References
Suberized root cell walls, highly developed casparian strip	Ion exclusion	Reduced capacity for water uptake under fresh water conditions; salinization of soils	Lawton et al. (1981), Passioura et al. (1992)
High dependence on symplastic water uptake	Ion exclusion	Low rates of water uptake	Reef et al. (2012)
High salt concentrations in cell vacuoles	Maintenance of water potential in the vacuole	Metabolic/nutrient costs	Takemura et al. (2000)
High concentrations of osmotically compatible solutes	Maintenance of water potential and ion exclusion in the cytoplasm?	Metabolic/nutrient costs; reducing xylem water flow	Popp and Polanía (1989), Zimmermann et al. (1994), but see Becker et al. (1997)
Salt excretion	Ion balance; decreased VPD/reduced water loss	Metabolic	Reef and Lovelock (2014)
Low stomatal conductance	Reduced xylem tensions (reduced potential for cavitation)	Low rates of transpiration and photosynthetic carbon gain	Ball (1988a), Sobrado (2000), Clough and Sim (1989), Krauss and Allen (2003), Vandegehuchte et al. (2014)
Steep leaf angles	Thermal regulation, reduced water loss	Reduced light capture, reduced CO ₂ diffusion (less mass transfer—less air flow)	Ball (1988a), Lovelock and Clough (1992)
Reductions in leaf size	Thermal regulation, reducing water loss	Reduced light capture, increased structural construction costs	Ball et al. (1988b)
Abaxial stomata	Reduced water loss	Reduced capacity for CO ₂ fixation	Cheeseman (1994)
Leaf succulence	Thermal regulation and maintenance of ion balance	Increased resistance to CO ₂ diffusion, increased structural construction costs	Saenger (1982), Camilleri and Ribi (1983), Wang et al. (2007)
Thickened leaf cuticles	Reduced water loss	Reduced light capture, increased structural construction costs	Saenger (1982), Wang et al. (2007), Naidoo et al. (2011)

(continued)

Table 2 (continued)

Trait	Function	Putative costs	References
Leaf pubescence (hairs)	Uptake of atmospheric water vapour, reduced water loss, thermal regulation	Metabolic, reduced light capture	Reef and Lovelock (2014)
CO ₂ uptake of non-leaf tissues	Reduced whole plant water loss for carbon gain	Metabolic (nutrient demand imposed by chlorophyll and RUBISCO)	Reef and Lovelock (2014)
Small vessel size	Reduced potential for cavitation	Low rates of photosynthetic carbon gain	Ewers et al. (2004), Lovelock et al. (2006), Stuart et al. (2007)
Successive cambia (Xylem/Phloem/parenchyma bundles) in <i>Avicennia</i> and <i>Aegialitis</i>	Increased capacity to repair embolisms	Decreased mechanical strength; metabolic/nutrient costs	Carlquist (2007), Robert et al. (2011), Schmitz et al. (2008), Santini et al. (2012), Yáñez-Espinosa et al. (2004)
Root growth in patches of fresher water	Improved water balance	Biomass allocation below ground	Ewe et al. (2007), Wei et al. (2013), Sternberg and Swart (1987), Lambs et al. (2008)

groundwater had lower salinity than shallow soil water (Sternberg and Swart 1987; Ewe et al. 2007).

Reducing Water Loss Under Saline and Arid Conditions

Once water is transported to the leaves, mangroves are highly efficient in the use of water during photosynthesis (Farquhar et al. 1982; Sobrado 2000). Mangroves, which use a C₃ photosynthetic pathway, were as much as 35–56 % more efficient in water use than nearby tropical lowland tree species (Ball 1996) and can even surpass stand-level water use efficiency of co-occurring C₄ grasses in some settings (Krauss et al. 2014a). Photosynthetic water use efficiency (PWUE) is often reported as the ratio of leaf photosynthetic CO₂ assimilation rate to transpiration rate, while the intrinsic PWUE is calculated as the ratio of assimilation rate to stomatal conductance of water vapour. These values can be extremely high in mangroves, with intrinsic PWUE ranging up to 153–212 μmol CO₂/mol H₂O (Table 3) compared to 40–80 μmol CO₂/mol H₂O typical in tropical trees, and often increasing with

Bruguiera gymnorrhiza

Avicennia marina

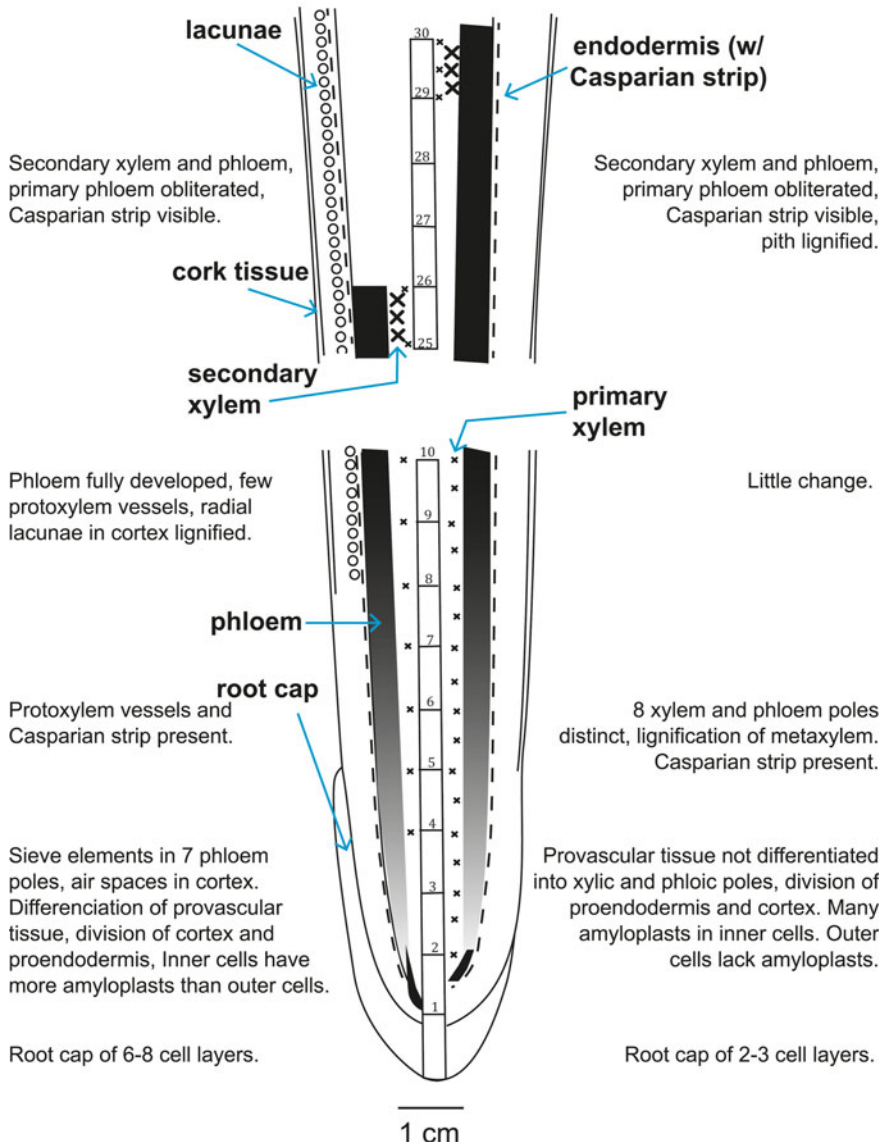


Fig. 1 Comparative longitudinal sections of representative *Bruguiera gymnorrhiza* roots (left) and *Avicennia marina* roots (right) showing endodermal layers, vascular tissue, and root cap characteristics (after Lawton et al. 1981). Numbers along the pericycle represent approximate distance (cm) from root tip

Table 3 Intrinsic photosynthetic water use efficiencies (PWUE) measured in seedlings, saplings, and trees in mangroves globally (updated from Barr et al. 2009)

Species ^a	Life stage	PWUE, <i>intrinsic</i> (mmol CO ₂ /mol H ₂ O)	Source
RHST	Tree	80–135	Andrews and Muller (1985)
AVGE, COER	Tree	10–100	Smith et al. (1989)
AVGE, LARA, RHMA	Seedling	35–90	Pezeshki et al. (1990)
BRPA, BRGY	Tree	40–100	Cheeseman et al. (1991)
RHMA	Tree	40–55	Lin and Sternberg (1992)
RHMA, LARA	Tree	10–30	Martin and Loeschen (1993)
AVGE	Seedling	100–130	Naidoo and von Willert (1995)
AEAN, AECO	Seedling	60–100	Naidoo and von Willert (1995)
AVGE, LARA, RHMA, COER	Tree	35–40	Snedaker and Araujo (1998)
BRGY, AVMA	Tree	50–90	Naidoo et al. (1998)
AECO	Tree	43–120	Youssef and Saenger (1998b)
AVMA	Tree	60–80	Sobrado and Ball (1999)
RHMU, CETA	Tree	50–100	Theuri et al. (1999)
AVGE, LARA, RHMA	Tree	40–65	Sobrado (2000)
AVGE, LARA, RHMA	Seedling	69–153	Krauss et al. (2006) ^b
AVGE, LARA, RHMA	Sapling	51–95	Krauss et al. (2006) ^b
SOAP, SOCA, KACA, AVMA, EXAG	Tree	75–212	Chen et al. (2008) ^b
LARA, RHMA	Seedling	33–110	Cardona-Olarte et al. (2013) ^b

^aRHST = *Rhizophora stylosa*, AVGE = *Avicennia germinans*, COER = *Conocarpus erectus*, LARA = *Laguncularia racemosa*, RHMA = *Rhizophora mangle*, BRPA = *Bruguiera parviflora*, BRGY = *Bruguiera gymnorhiza*, AEAN = *Aegialitis annulata*, AECO = *Aegiceras corniculatum*, AVMA = *Avicennia marina*, RHMU = *Rhizophora mucronata*, CETA = *Ceriops tagal*, SOAP = *Sonneratia apetala*, SOCA = *Sonneratia caseolaris*, KACA = *Kandelia candel*, EXAG = *Excoecaria agallocha*

^bActual values obtained from author

incremental addition of salinity (Ball 1988a; Clough and Sim 1989; Smith et al. 1989; Krauss et al. 2008). In a broad survey of 19 different mangrove species in Australia and Papua New Guinea, Clough and Sim (1989) discovered that intrinsic PWUE did not drop below 49 $\mu\text{mol CO}_2/\text{mol H}_2\text{O}$ for any species by site combination measured in the field, and ranged as high as 195 $\mu\text{mol CO}_2/\text{mol H}_2\text{O}$ for

Avicennia marina where sites were highly saline. Changes in PWUE are also manifest at the stand level; eddy-flux-derived CO₂ uptake from a mangrove forest in south Florida decreased 5 % for each 10 parts per thousand (ppt) increment in salinity (Barr et al. 2013). High levels of photosynthetic efficiencies in water use of mangroves are a consequence of structurally imposed limitations on the rates of water supply to the leaves (Sobrado 2000; Lovelock et al. 2006; Hoa et al. 2009; Vandegehuchte et al. 2014), as well as tight regulation of water loss at the leaf level (Ball and Farquhar 1984; Clough and Sim 1989).

High levels of water use efficiency in mangrove tree species are associated with a range of traits, many of which lead to reductions in the leaf to air vapour pressure deficit (VPD). These traits include the presence of leaf pubescence (Reef and Lovelock 2014), the presence of salt on the leaf surface which occurs in salt secreting species and which may increase the humidity around the leaf (Reef and Lovelock 2014), and steep leaf orientations and small, thick leaves both of which affect the thermal balance of leaves (Ball 1988a). The characteristics that minimize VPD are likely to be particularly important in arid environments. Finally, photosynthetic CO₂ fixation in non-leaf tissues, which is acquired at lower water costs, could also be an important aspect of salinity tolerance. In *A. marina* re-fixation of respired CO₂ by corticular photosynthesis contributed up to 5 % of the CO₂ fixation by the plant (Schmitz et al. 2012). CO₂ uptake by roots, although not yet studied in mangroves, has been shown to be significant in other submerged and wetland plants (Raven et al. 1988; Brix 1990; Rich et al. 2008).

Implications of Physiological and Structural Adaptations for Function of the Whole Forest

Much ecophysiological research on mangroves has been directed to leaf-level processes in seedlings, saplings, and occasionally, trees. Saenger (2002) reviews this literature and concludes that with the combination of ecophysiological strategies (e.g., high leaf-level PWUE) and adaptations for living in saline settings (e.g., salt exclusion at the roots, low stomatal conductance), mangrove forests are likely to be very conservative in water use. Ironically, quantifying the absolute rates of water use in mangroves has not been the central theme of many research programs; however, the available data on sap flux indicate that mangrove trees use water at rates over 3 times less than other forest trees per unit size (Fig. 2a). Individual tree water use ranged from 0.4–64.1 L H₂O/day in mangroves (Hirano et al. 1996; Muller et al. 2009; Krauss et al. 2007, 2014a; Lambs and Saenger 2011) compared with 116 ± 16 (SE) L H₂O/day from trees in other forest types (Wullschlegel et al. 1998). Missing from this analysis are empirical data from large mangrove trees (>55 cm dbh).

Indeed, scaling ecophysiological processes from leaf to stand in mangroves provides insight into ecosystem CO₂ and H₂O fluxes. Lugo et al. (1975) found that two mangrove forests in Rookery Bay, Florida, USA took up 4.83 and 2.74 g

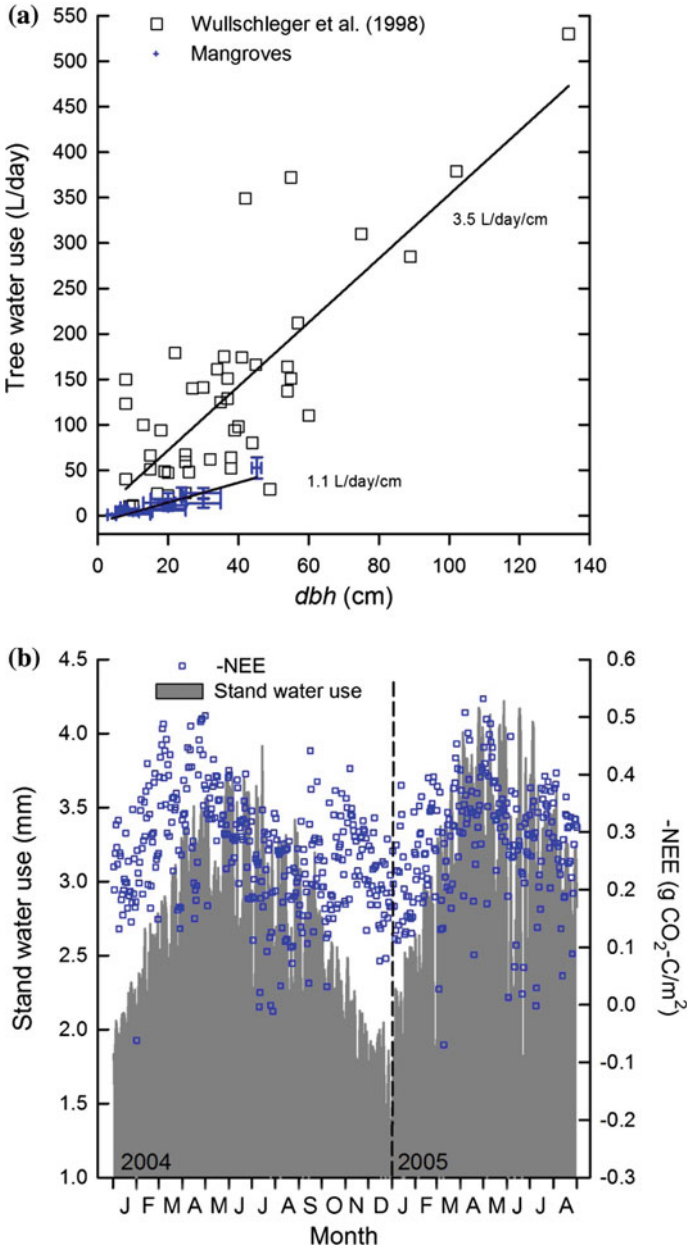


Fig. 2 **a** Water use (L/day) versus diameter at breast height (dbh) for individual trees from non-mangrove ecosystems (Wullschleger et al. 1998) versus data currently available from mangrove ecosystems. Bars presented for mangroves represent the absolute range of dbh versus water use values from specific studies (Krauss et al. 2007, 2014a, b; Muller et al. 2009; Lambs and Saenger 2011). **b** Stand water use (mm; Krauss et al. 2015) versus net ecosystem exchange (-NEE) of atmospheric CO_2 ($\text{g CO}_2\text{-C/m}^2$; Barr et al. 2010) from a mangrove forest along the Shark River, Everglades National Park, Florida, USA

C/m²/day through net ecosystem exchange (-NEE) while using 2.57 and 1.57 mm H₂O/day, respectively. Of that transpiration, 95–97 % was associated with the canopy. Estimation of -NEE of carbon using eddy covariance along the Shark River in Everglades National Park, Florida was remarkably similar to Lugo et al.'s estimates, ranging from 2–5 g C/m²/day (Barr et al. 2010). This was despite the fact that trees were nearly 8 m taller and forests had approximately 15 m²/ha greater basal area along the Shark River than in Rookery Bay. During the same period of time, estimated water use of the dominant canopy ranged to 4.22 mm H₂O/day for Shark River mangroves, averaging 2.5 mm H₂O/day (Krauss et al. 2015; Fig. 2b). Thus, considering that the mangroves along the Shark River registered among the highest rates of carbon uptake among 49 forest types in North America (Amiro et al. 2010), it is truly remarkable that canopy water use was efficient enough in mangroves to represent only 63 % of regional rainfall and 66 % of ET (Krauss et al. 2015). Inherent to this are month-to-month fluctuations in annual rates of canopy-level PWUE that require additional study (Fig. 2b).

Elevated CO₂ Effects on Water Use

High levels of water use efficiency in mangroves and the increased PWUE with increasing salinity leads to the expectation that there could be considerable gains in productivity of mangroves with increasing levels of CO₂ in the atmosphere as stomatal limitations to CO₂ uptake are ameliorated. The effects of elevated CO₂ on plant performance have not been studied in mangroves as extensively as in other forest habitats. Only a handful of experimental studies have been conducted on the response of mangrove seedlings to elevated CO₂. Due to the difficulties posed by the intertidal habitat, Free-Air Concentration Enrichment of CO₂ (FACE) experiments are yet to be conducted in mangroves and thus we have no experimental data for the effects of elevated CO₂ on mature trees. Despite the scarcity of data, it is becoming apparent that while elevated CO₂ has a significant effect on PWUE in mangroves, the expected alleviation of salinity stress and subsequent improvement in performance at high salinity does not occur to the extent initially anticipated. The increase in mangrove seedling growth rates observed in response to elevated CO₂ ranged from a 12 to a 47 % increase in growth relative to that under ambient CO₂ concentrations (Table 4), which is overlapping with the mean and range recorded for well watered tropical tree seedlings of different species experiencing similar elevated CO₂ conditions (Cernusak et al. 2011; Krauss et al. 2014b). Studies that have incorporated a salinity treatment in elevated CO₂ experiments in mangroves conclude that at supra-optimal salinity conditions, elevated CO₂ does not significantly improve seedling growth, despite a significant improvement to PWUE (Ball et al. 1997; Reef et al. 2014) and that a fertilization effect is only observed within the low to mid salinity range. This is likely due to the fact that salinity constrains tree growth in a manner other than water stress (e.g. ion toxicity).

Table 4 The effects of elevated CO₂ on mangrove seedling growth, photosynthetic water use efficiency (PWUE) and specific leaf area (SLA) presented as the % change relative to values measured at ambient CO₂ concentrations

Species	Ambient (CO ₂) ppm	Elevated (CO ₂) ppm	% increase in growth	% increase in WUE	% increase in SLA	Length of treatment (days)	Reference
<i>Rhizophora mangle</i>	350	700	47	1.72	NA	408	Farnsworth et al. (1996)
<i>Rhizophora apiculata</i>	340	700	31	15.2	-3	98	Ball et al. (1997)
<i>Rhizophora stylosa</i>	340	700	21	33.8	7.8	98	Ball (1997)
<i>Avicennia germinans</i>	365	720	17	NA	-10	540	McKee (2008)
<i>Avicennia germinans</i>	400	800	22	107	-1.1	132	Reef et al. (2014)
<i>Avicennia germinans</i>	280	800	12	218	-10	132	Reef et al. (2014)

In studies that included other factors (salinity, nutrient or humidity treatments) the CO₂ response was averaged over treatments

Mangroves respond to elevated CO₂ by reducing stomatal conductance and by producing leaves with lower stomatal densities (Farnsworth et al. 1996), but overall productivity of forests may increase. The observed reduction in transpiration rate on a leaf scale can have an effect on forest water use. However, elevated CO₂ can also lead to higher leaf area to total biomass ratios. In mangroves, increases in leaf area ratios with increasing [CO₂] were observed in most studies (Farnsworth et al. 1996; Ball et al. 1997; Reef et al. 2014). Furthermore, there appears to be a lowering of the light compensation point (LCP) of photosynthesis. In *A. germinans* grown under elevated CO₂ the LCP reduced from $52.3 \pm 1.36 \mu\text{mol m}^{-2} \text{s}^{-1}$ at (CO₂) of 280 ppm to $18.1 \pm 9.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ at [CO₂] of 800 ppm, $p = 0.03$; R. Reef unpublished data) suggesting that a positive carbon balance in leaves can be maintained under shaded conditions at elevated CO₂. Declines in specific leaf area (SLA) were also observed in response to elevated CO₂ (Table 4) and in a time series study of herbarium specimens, SLA declined as CO₂ has increased over time in *A. marina* (but not for *R. stylosa*, Reef and Lovelock 2014). These responses to elevated CO₂ could result in increases in leaf level productivity and leaf area index (LAI) at the stand level with rising CO₂ levels. Increases in LAI at the stand level could offset the reduction in water use by individual leaves and result in enhanced production, but no overall change to transpiration on larger scales.

An important parameter that can influence the response of mangroves to elevated CO₂ in the field is nutrient availability. Under low nutrient conditions, similar to those measured in many scrub mangrove forests, seedling biomass did not increase in response to elevated CO₂ (McKee and Rooth 2008). However, when given higher nutrient concentrations, at levels similar to those measured in soils along

creek banks, elevated CO₂ resulted in a significant 23 % increase in total biomass. Development of nutrient limitations to growth could also be the reason for a down-regulation of photosynthesis and reduced growth rates under elevated CO₂ conditions over time in *R. mangle* grown in pots (Farnsworth et al. 1996). Nutrient distributions are not uniform in mangrove forests due in part to their intertidal nature. Most nutrients are delivered by the tides, thus creating elevation driven gradients in nutrient availability. Furthermore, differences in nutrient inputs from rivers and other landward sources, soil salinity, inundation frequency and faunal activity affect the availability of nutrients (Reef et al. 2010, 2014). The response of mangroves to elevated CO₂ will thus likely be dependent on their position in the forest and local nutrient conditions.

Finally, in order to understand the effects of elevated CO₂ on forest structure and distribution, competitive interactions must be taken into account. Elevated CO₂ can improve mangrove salinity tolerance within the range of salinities already suitable for growth (Reef et al. 2014). This shift in the fundamental niche could translate into a range shift depending on competitive outcomes and could be a contributing factor in the observed mangrove encroachment into saltmarsh habitats observed at many locations (Saintilan et al. 2014). In the only experiment to investigate competitive interactions between mangroves and saltmarshes under elevated CO₂, McKee and Rooth (2008) found that elevated CO₂ does not improve competitive outcomes for the mangrove *Avicennia germinans* when grown in mixed culture with the saltmarsh species *Spartina alterniflora*. Although *S. alterniflora* is a very fast growing species and may not be representative of many saltmarsh species that have slower growth rates, this study highlights the difficulties in predicting the future of mangrove distributions in response to rising CO₂ concentrations.

Adaptations to Inundated Soils

Tolerance of periods of inundation by tidal water, flooding and storm surges are essential for mangrove tree species survival, and differences in species tolerances to flooding influences their distributions relative to changing hydroperiods with sea-level rise. Sea level has been relatively stable for the last five thousand years, but accelerating rates of sea level rise and associated geomorphological adjustments of the coast (Woodroffe 1990) are likely to result in vegetation transitions that are linked to inundation tolerance of species. A range of traits are linked to inundation tolerance (Table 5). Mangroves possess a number of elaborate, aerial root structures including prop roots (*Rhizophora*), pneumatophores (*Avicennia*, *Sonneratia*), knee roots (*Bruguiera*), and cable roots (*Xylocarpus*, *Heritiera*), prompting much early speculation into their role in aerating sub-soil roots and soils. Still, some mangrove species lack aerial roots (e.g., *Excoecaria*). Prominent on many of the aerial root structures and stems are lenticels, or gas exchange pores positioned above the soil surface. Air diffuses through these pores and via abundant aerenchyma tissues to belowground root structures facilitating aeration of roots embedded in oxygen-free

Table 5 Plant traits associated with tolerance of inundation in mangrove tree species and their putative costs

Trait	Function	Putative cost	Reference
Aerial roots with lenticels	Gas transport—air into below ground roots	Allocation of biomass to non-photosynthetic tissues; respiration	Scholander et al. (1955), Youssef and Saenger (1996), Skelton and Allaway (1996)
Rapid seedling root extension	Anchorage of seedlings	Reduced allocation to aboveground biomass	Delgado et al. (2001), Balke et al. (2011)
Aerenchyma	Gas transport and storage; oxidation of phytotoxic substances	Allocation of biomass to non-photosynthetic tissues; loss of mechanical strength	Scholander et al. (1955), Youssef and Saenger (1996, 1998a, b), Skelton and Allaway (1996), Purnobasuki and Suzuki (2004)
Suberized root cells	Limit oxygen leakage into soils; maintain availability of some essential elements close to the root surface	Enhance phytotoxic substances	Thibodeau and Nickerson (1986), Youssef and Saenger (1996), Reef et al. (2010)

soils (Scholander et al. 1955; Skelton and Allaway 1996; Allaway et al. 2001). The structure of mangrove roots facilitates gas exchange (McKee and Mendelssohn 1987; Youssef and Saenger 1996) which in addition to supporting respiration results in the oxidation of phytotoxic substances within roots (e.g., Fe^{2+} , H_2S) (Armstrong et al. 1992; Youssef and Saenger 1998a), although leakage of O_2 into the rhizosphere may affect the availability of some essential nutrients, particularly phosphorus which are more available under reduced conditions, and some microbial processes which are also favored under low oxygen concentrations (e.g. nitrogen fixation) (Reef et al. 2010) (Table 4). Early rapid root growth and investment in roots in seedlings are also important for the establishment of seedlings on exposed tidal flats and thus influences recruitment and forest expansion (Delgado et al. 2001; Balke et al. 2011).

There are differences among species in the capacity to withstand inundation. Experiments focused on gas exchange in root systems indicate that *A. germinans* and *Laguncularia racemosa* seedlings suffered a decrease in root oxygen concentrations when exposed to experimental hypoxia, while *Rhizophora mangle* did not (McKee 1996). McKee (1996) discovered that differences among species in response to anoxia were attributed to oxygenation of the roots through diffusive O_2 fluxes from the shoot, lower root respiration rates in *R. mangle* than *A. germinans* or *L. racemosa*, and less O_2 leakage from *R. mangle* roots to the surrounding soils. Oxygen tends to leak from *Avicennia* roots to a much greater degree than

Rhizophora roots (Thibodeau and Nickerson 1986). In a multi-species comparison, *Avicennia marina* and *Acanthus ilicifolius* had the highest concentrations of aerenchyma air space and the lowest diffusional resistance for O₂ to soil among eight mangrove species tested in Hong Kong (Pi et al. 2009) suggesting high levels of variation among Indo-Pacific species in their capacity to transport oxygen to and out of roots. Additionally, greater root porosity was found in pneumatophores than other root types of *Sonneratia alba* from Okinawa (Purnobasuki and Suzuki 2004) indicating variation in oxygen transport within root systems among wide-ranging species. Rates of oxygen leakage from roots not only vary among species but also with the strength of diffusion gradients between the root and soil (Sorrell and Armstrong 1994). O₂ leakage from the apical tips of *Kandelia candel* roots was higher than from the main root walls (Chiu and Chou 1993). Variation in oxygen leakage was attributed to the structure of the root surface, which is compacted and lignified in *Rhizophora* and *Aegiceras* and thinner with only 3–4 exodermal layers in *Avicennia* and *Bruguiera* (Youssef and Saenger 1996). The differences in mangrove species in the structure, growth and physiology of roots, including their ability to transport and retain O₂ within their roots, are likely to lead to differences in species responses to changing inundation regimes and associated hydrological change with sea level rise. Although many other factors are also likely to influence the distribution and composition of forests, including the space in the landscape for landward expansion, human and natural modifications of the coast (Doyle et al. 2010; Traill et al. 2011), underlying differences in species inundation tolerance are likely to be important.

Adaptations to Temperature Thresholds

Variations in temperature affect many processes in mangrove forests ranging from the fundamental metabolic processes of photosynthesis and respiration (e.g., Andrews and Muller 1985; Lovelock 2008) to carbon cycling (Alongi 2009) and reproductive success (Duke 1990). Temperature regimes greatly influence mangrove forest composition and structure with extreme temperature events playing an especially important role in some locations. Increasing global temperatures are likely to result in changes to growth and distribution patterns of mangrove forests on the edge of their ranges which are currently limited by low temperatures and in some locations aridity.

The effects of low temperature on mangrove physiology (Davis 1940; Stuart et al. 2007; Krauss et al. 2008; Ross et al. 2009) and distributions (e.g., West 1977; Sherrod and McMillan 1985; Woodroffe and Grindrod 1991; de Lange and de Lange 1994; Duke et al. 1998; Saenger 2002) have been widely studied, with recent studies focused on mangrove recruitment into warm-temperate salt marsh habitats (e.g., McKee et al. 2012; Osland et al. 2013; Cavanaugh et al. 2014; Saintilan et al. 2014). Mangrove species differ in sensitivity to low temperatures (Table 1), but none can survive the minimum temperatures that occur in cold-temperate climatic zones.

In general, mangrove forest biomass, structural development, and species richness are higher in wet tropical climatic zones. In colder climatic zones (e.g., subtropical or warm-temperate), low temperature stress typically produces mangrove trees that are short in stature with a shrub-like architecture (Woodroffe 1985; Osland et al. 2014a, b). Physiological stress due to low temperatures can be separated into chilling and freezing stress (Kozłowski and Pallardy 1997; Larcher 2003). Whereas chilling stress occurs at leaf temperatures above freezing (i.e., without ice formation), freezing stress occurs at leaf temperatures below freezing when intra- or extra-cellular ice formation occurs. The physiological effects and symptoms of freezing/chilling stress in mangrove trees include reduced metabolic rates, altered membrane structure and permeability (Markley et al. 1982), disrupted water and nutrient transport (Stuart et al. 2007), partial or complete loss of aboveground biomass (e.g., Osland et al. 2014a, b), reduced reproductive success (Duke 1990) and, in extreme cases, mortality (Ross et al. 2009).

Intra- and inter-specific differences in mangrove sensitivity to low temperature stress greatly influence the structure and composition of mangrove forests. There are many examples of differential species and life stage responses to low temperature stress (e.g., Lugo and Patterson-Zucca 1977; Lonard and Judd 1991; Olmsted et al. 1993; Ross et al. 2009; Chen et al. 2010; Pickens and Hester 2011). Climatic origin greatly influences intraspecific responses to chilling stress with mangrove individuals from colder climates typically being better adapted and more resistant to low temperatures (Markley et al. 1982; Sherrod and McMillan 1985). Species sensitivity to low temperature stress can be gauged using species distribution data in combination with multi-decadal climate data (e.g., Table 1; Quisthoudt et al. 2012; Osland et al. 2013). For example, whereas some mangrove species are highly sensitive to chilling stress and are only found in tropical climates (e.g., *Bruguiera sexangula*, *Sonneratia lanceolata*), other species have adaptations that enable them to be resistant to higher levels of chilling or freezing stress (e.g., *A. germinans*, *A. marina*, *Kandelia obovata*, *Aegiceras corniculatum*). Vulnerability to low-temperature induced xylem cavitation is especially high for mangrove trees due to the low xylem water potentials required for water transport in highly saline intertidal environments (Stuart et al. 2007). In a comparison of the most poleward mangrove species in Australia and the United States, Stuart et al. (2007) highlighted the effects of xylem embolism and show that species adapted to climates with colder mean annual minimum temperatures have smaller vessel diameters which enable them to better avoid embolism; however, narrow vessels also constrain water transport and productivity, possibly limiting mangrove forest structural development in these poleward locations. In addition to narrow vessels, variation in membrane properties also likely enables mangrove individuals and species from colder climates to maintain membrane fluidity during exposure to low temperatures (Markley et al. 1982).

On some continents, the frequency and intensity of extreme winter events greatly affect mangroves. For example, near the poleward mangrove limit in China and the southeastern United States, mean winter temperatures are not as cold as mean winter temperatures found near the poleward limit of mangroves in Australia or New Zealand. However, extreme minimum temperature events are more intense in

China and the southeastern United States which can result in sudden leaf loss, xylem embolism, branch and stem reductions, and, in the most extreme cases, tree mortality (Davis 1940; Lugo and Patterson-Zucca 1977; West 1977; Lonard and Judd 1991; Everitt et al. 1996). In these areas, the spatial extent of mangrove forests expands and contracts in response to the frequency and intensity of extreme winter events (West 1977; Sherrod and McMillan 1985; Stevens et al. 2006; Giri et al. 2011). In North America, *Avicennia germinans* is a species that is especially adapted to and resistant to extreme winter events. In parts of northern coastal Florida, Louisiana, and the northern coast of Texas, *A. germinans* individuals often lose a large portion of their aboveground biomass due to freeze events; however, *A. germinans* is capable of vigorous resprouting from the base of stems after freeze-damage due to the presence of epicormic buds (Lugo and Patterson-Zucca 1977; Tomlinson 1986; Osland et al. 2014a, b). Using data in Table 1 we graphically show the breadth of tolerance of mangrove species in the biogeographic provinces of the Atlantic and Eastern Pacific Ocean region (Fig. 3a) and the Indian and Western Pacific Ocean region (Fig. 3b) to temperature extremes and to aridity and salinity. Those species that are currently documented as expanding in their range (e.g., *A. germinans* and *A. marina*) have the broadest tolerance to low temperatures and to other environmental factors, while species that have restricted distributions (e.g., the palm *Nypa fruticans*) are less tolerant of low and high temperatures, high salinity and aridity.

In contrast, the effects of high temperatures on mangrove trees have not been as extensively considered. Early research indicates that photosynthesis in tropical species of Rhizophoraceae is depressed as leaf temperatures exceed 34 °C (e.g., Andrews and Muller 1985; Cheeseman et al. 1991). Most of this effect is associated with the strong stomatal closure required to minimize rates of water loss that can increase dramatically if leaf temperatures become higher than air temperatures or if high air temperatures are accompanied by low humidity (i.e. increasing leaf-to-air VPD). However, more research is required to understand how mangroves, particularly those in warm tropical climates that may already be close to their thermal limits, will respond to the projected increases in global temperature of at least 2 °C in the coming century. Clark (2004) suggested that productivity of tropical

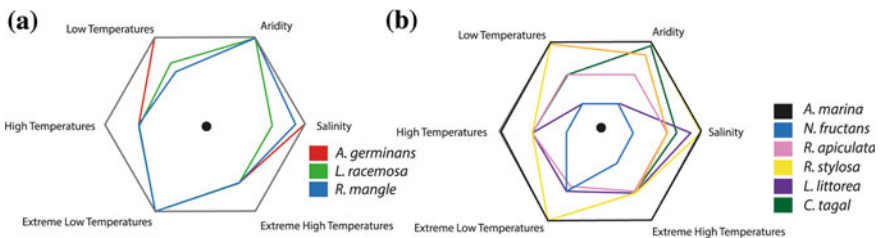


Fig. 3 Spider plots of the overlapping tolerances of mangrove species to high and low temperature and high and low temperature extremes, salinity and aridity (based on data from Table 1). **a** Common species from the Atlantic-East Pacific biogeographic region; **b** common species from the Indo-West Pacific region

rainforests could decline with increasing temperature due to increases in respiration and declining photosynthetic rates (Slot and Winter this volume). As yet there has been no assessment of this hypothesis in mangrove forests.

Plasticity of Traits Gives Rise to Different Capacity to Adjust to Climate Change

Plasticity of traits is a key feature of plants that allows them to acclimate to changing conditions, including climate (Jump and Penuelas 2005). Some mangrove species occur over broad ranges of environmental conditions and often assume different forms in different habitats, e.g., scrub and tall fringing forms of *R. mangle* in the Caribbean (Feller 1995; Medina et al. 2010) or for *A. marina* in New Zealand and southern Australia (Lovelock 2008; Martin et al. 2010) (Fig. 4), displaying high levels of both physiological and morphological plasticity (Lovelock et al. 2006). In fact, plasticity in PWUE among and within mangrove species is a primary reason why water use characteristics in mangroves have not been fully assessed; water use can depend strongly on site or experimental conditions limiting blanket assessments



Fig. 4 Examples of high levels of morphological plasticity within mangrove tree species. The upper left and right photos are of tall (15 m), forests fringing water ways and short (<2 m), scrub forests of *Rhizophora mangle*, respectively, from Belize. The lower left and right photos are of tall (5 m), fringing forests and short (<1 m), scrub forests, respectively, in New Zealand

Table 6 Variation in plasticity in growth (height, stem extension, biomass or relative growth rate, RGR) for mangrove species grown in comparative experiments

Species	Parameter	Treatment	Coefficient of variation	Reference
<i>Ceriops australis</i>	Stem height	Salinity and competition	0.21 ± 0.01 (14)a	Smith (1988)
<i>Ceriops tagal</i>			0.16 ± 0.02 (10)b	
<i>Avicennia marina</i>	Biomass	Salinity	0.20 (5)	Clough (1984)
<i>Rhizophora stylosa</i>			0.17 (5)	
<i>Sonneratia alba</i>	Stem height	Salinity	0.14 ± 0.03 (6)a	Ball and Pidsley (1995)
<i>S. lanceolate</i>			0.10 ± 0.02 (4)a	
<i>R. stylosa</i>	RGR	Salinity and humidity	0.14 ± 0.04 (6)b	Ball et al. (1998)
<i>R. apiculate</i>			0.13 ± 0.02 (8)b	
<i>A. germinans</i>	RGR	Salinity and nutrient availability	0.12 ± 0.02 (14)a	Ewe S., Lovelock C.E. unpublished data
<i>Laguncularia racemosa</i>			0.07 ± 0.01 (13)b	
<i>R. mangle</i>			0.24 ± 0.04 (15)c	
<i>Aegiceras corniculatum</i>	Stem height	Inundation	0.042 ± 0.002 (8)a	He et al. (2007)
<i>A. marina</i>			0.083 ± 0.007 (8)c	
<i>Bruguiera gymnorhiza</i>			0.078 ± 0.005 (8) bc	
<i>R. stylosa</i>			0.067 ± 0.006 (8)b	
<i>A. germinans</i>	RGR	Oxygen around roots	0.11 (2)	McKee (1996)
<i>L. racemose</i>			0.19 (2)	
<i>R. mangle</i>			0.24 (2)	
<i>A. germinans</i>	Stem extension	Nutrient availability	0.35 ± 0.07 (3)a	Lovelock and Feller (2003)
<i>L. racemose</i>			0.36 ± 0.04 (3)a	
<i>A. marina</i>	Stem extension	Nutrient availability	0.22 ± 0.05 (3)a	Lovelock CE, Feller IC unpublished
<i>C. australis</i>			0.48 ± 0.10 (3)a	
<i>R. stylosa</i>	Stem extension	Nutrient availability	0.21 ± 0.03 (3)a	Lovelock CE unpublished
<i>C. australis</i>			0.50 ± 0.06 (3)b	

(continued)

Table 6 (continued)

Species	Parameter	Treatment	Coefficient of variation	Reference
<i>Lumnitzera racemosa</i>			0.19 ± 0.03 (3)a	
<i>R. stylosa</i>	Stem extension	Nutrient availability	0.15 ± 0.06 (3)a	Lovelock CE unpublished
<i>C. australis</i>			0.49 ± 0.13 (3)b	

Plasticity is represented by the coefficient of variation (based on a mean of means over treatments). The number of mean values used (N) is in parentheses. The most salt tolerant species is underlined. Where sufficient data were available differences among species were tested and significant differences at $P < 0.05$ are indicated with different letters after the mean

of water conservation in mangroves (see e.g., Becker et al. 1997 vs. Zimmermann et al. 1994; Krauss et al. 2015). In a comparison of the levels of plasticity in different traits over variation in fertility in *R. mangle*, whole plant architectural traits (e.g. leaf area index, shoot extension and hydraulic properties of stems) had much higher levels of plasticity than leaf level traits (e.g. photosynthesis, specific leaf area) (Lovelock et al. 2006). As the most plastic traits are often the ones that determine overall plant fitness (Agrawal 2001, Poorter and Lambers 1986; Callaway et al. 2003) this suggests that plasticity in growth rates, canopy development and hydraulic function are potentially the most important traits for successful dominance of mangrove habitats. A high level of plasticity in belowground growth is also likely, but as yet remains relatively unexplored (e.g., McKee 1996; Casteneda Moya et al. 2011; Lang'at et al. 2013). In Table 6 we contrast plasticity in growth (stem extension, relative growth rate or biomass expressed as a mean coefficient of variation) for a range of species where contrasts have been made over variation in treatments. Plasticity in growth varies significantly among mangrove species and tends to be greater in response to variation in nutrient availability than to other treatments. Species with the highest plasticity tend to be the most salt tolerant and widely distributed and may be favored with global climate change. The fitness cost of high levels of plasticity is difficult to determine, but could be associated with being inferior competitors; although with few competing species in mangrove forests (compared to tropical rainforests) there may be few disadvantages to high levels of plasticity, particularly in the biogeographic province of the Atlantic and East Pacific Ocean region where species diversity is particularly low.

Conclusions: Change in Distribution and Productivity of Mangrove Forests

As a group, mangrove species possess many physiological adaptations and life history characteristics that could enable them to adapt positively to future climate change. However, the complex interactions between climatic drivers are only just

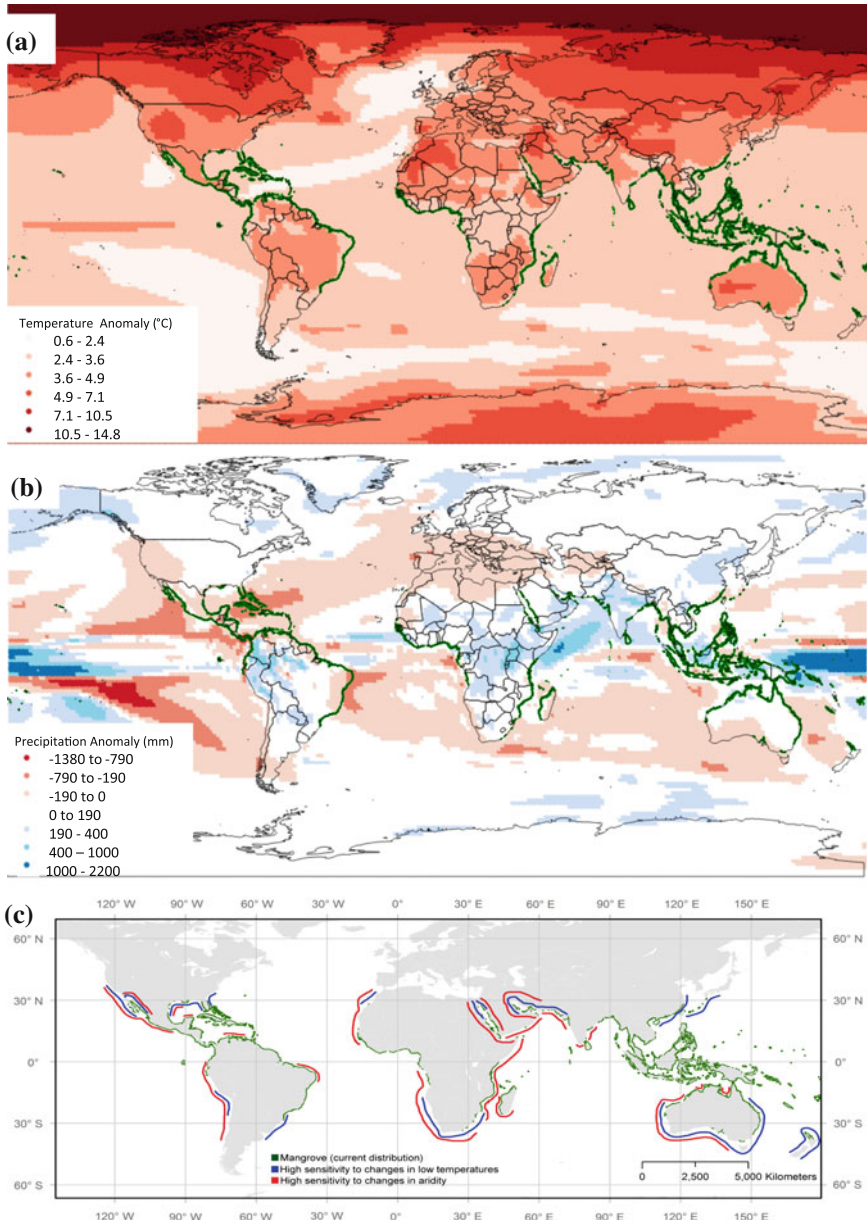


Fig. 5 The global mangrove distribution (*green*) overlain on: **a** predicted change in mean temperature (IPCC 2007, A1FI scenario); **b** predicted changes in annual precipitation (IPCC 2007, A1FI scenario); and **c** regions where mangrove distribution is sensitive to changes in aridity (*red*) or low temperatures (*blue*)

starting to become clear, and mangrove ecosystem responses to climate change will be highly context dependent (e.g., Saintilan et al. 2009; McKee et al. 2012). In the past, the global distribution and spatial extent of mangrove forests has expanded and contracted in response to changes in sea level, temperature and freshwater availability (Sherrod and McMillan 1985; Woodroffe and Grindrod 1991; Saintilan et al. 2014). In the future, climate change is expected to greatly alter the distribution, composition and ecological properties of mangroves forests and their adjacent ecosystems (i.e., salt marsh, salt flat, seagrass ecosystems) (Fig. 5). On some continents (e.g., North America, Northwest Asia, Australia), warmer winter temperatures will likely lead to poleward mangrove forest range expansion and development at the expense of salt marsh habitat (Osland et al. 2013; Cavanaugh et al. 2014; Saintilan et al. 2014). The southeastern United States is an area where the ecological effects of mangrove migration are expected to be especially large due to the large amount of salt marsh that could be replaced by mangrove forests (Osland et al. 2013). Moreover, increases in sea level, freshwater availability, elevated CO₂ and human influences including nutrient enrichment will also affect the productivity, composition and distribution of mangrove forests. In response to sea level rise, mangrove forests are expected to migrate landward where migration corridors exist (Doyle et al. 2010; Traill et al. 2011), although landward coastal wetland migration will be obstructed in some areas by natural and anthropogenic barriers (e.g., sea walls, hydrologic barriers). Species differences in inundation tolerance are likely to influence the composition of forests as sea level rise accelerates. In arid and semi-arid climatic zones, the abundance and composition of mangrove forests and other coastal wetland ecosystems will be greatly influenced by changes in freshwater availability (Smith and Duke 1987; Bucher and Saenger 1994; Saintilan et al. 2009; Semeniuk 2013; Osland et al. 2014a, b). Whereas increased aridity and/or reductions in freshwater input will likely result in reduced mangrove coverage and diversity, the converse is also true; in some areas, increased freshwater inputs, increases in humidity and increases in CO₂ could result in changes in communities, higher mangrove coverage, structural development and productivity (Reef and Lovelock 2014; Osland et al. 2014a, b).

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