Mangroves in arid regions: ecology, threats, and opportunities

MF Adame[1*], R Reef[2], NS Santini[3], E Najera[4], MP Turschwell[1], MA Hayes[1], P Masque[5,6,7], CE Lovelock[8]

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[1] Australian Rivers Institute, Griffith University, QLD, 4111, Australia

[2] School of Earth, Atmosphere and Environment, Monash University, VIC 3800, Australia

[3] Instituto de Ecología, Universidad Nacional Autónoma de México, Ciudad Universitaria, 04500, Mexico City

[4] World Wildlife Fund, La Paz, Baja California, 23000, Mexico

[5] School of Science, Centre for Marine Ecosystems Research, Edith Cowan University, Joondalup, WA, Australia.

[6] Institut de Ciència i Tecnologia Ambientals and Departament de Física, Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Barcelona, Spain.

[7] International Atomic Energy Agency, 4a Quai Antoine 1er, 98000 Principality of Monaco, Monaco

[8] School of Environmental Sciences, University of Queensland, QLD, Australia

*corresponding author: f.adame@griffith.edu.au

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Abstract

Mangroves are one of the few woody ecosystems that grow in hot-arid climates. They can survive extreme conditions of low precipitation, high solar radiation, wide temperature fluctuations and hypersalinity. These unique mangroves have distinct geomorphology, hydrology, forest structure, tree physiology, and soil biogeochemistry. In this review, supported by field data from Australia and Mexico, we explore the characteristics of mangroves in arid climates of the world. These mangroves are mostly tide-dominated with freshwater flows restricted to groundwater and sporadic tropical storms. They form dense forests with stunted growth dominated mainly by trees of the genus *Avicennia* that co-occur with salt marshes in the high intertidal. Their soils have low nutrient and carbon concentrations, and high soil δ15N and δ13C values compared to subhumid and humid mangroves. Mangroves in arid climates have relatively low human pressure due to sparse human settlements. Key threats to these mangroves, which often persist at the edge of their physiological tolerances, include extreme drought, reductions in groundwater inputs, altered hydrology, sea-level fluctuations and increases in nutrient loading. Restoration of mangroves in arid climates should focus on restoring their hydrology. Mangroves in arid zones are under-represented in global maps and assessment programs, as they may not be consistent with countries’ definition of “forests”. Improved global representation and understanding of the ecology of mangroves in arid climates could help sustain their valuable ecosystem services.

1.Introduction

Mangroves in arid climates (hot-arid BWh and hot semi-arid BSh, Köppen-Geiger climate classification, Geiger 1954) can be found within subtropical regions between latitudes 20° and 33° north and south. They can be classified according to their Aridity Index (AI), which is the ratio between mean annual precipitation and evapotranspiration, in semi-arid (0.2 < AI < 0.50), arid (0.05< AI < 0.2), and hyper-arid (AI <0.05, UNEP, 1992) environments. Mangroves in arid conditions can be found in the Gulf of California in Mexico, the Middle East, Western Australia, subtropical Africa, and Western South America. Mangroves in localised arid conditions due to topographic features affecting rainfall patterns can also be located in Southwest Mexico, Puerto Rico, Timor Leste, Galapagos, and Southern Madagascar (Fig. 1, Table 1).

Mangroves growing in arid climates experience low precipitation and high temperatures (annual mean usually > 18°C) with large daily fluctuations, high solar radiation, and high evaporation rates. As a result, mangroves in hot, arid climates experience low humidity and hypersalinity. Aridity causes physiological stress to mangrove trees as low freshwater availability, and low humidity reduce photosynthetic carbon gain (Ball 1988). As a result, these mangroves have relatively low productivity compared to mangroves in humid regions. However, mangroves in arid climates provide disproportionately high levels of regional ecosystem services, supporting fisheries (Aburto-Oropeza et al., 2008), biodiversity (Sievers et al., 2019), and carbon sequestration (Almahasheer et al., 2017; Adame et al., 2018b), as they are often the most productive woody ecosystem within these arid regions.

In this study, we provide a review of the available information on the characteristics of mangroves in arid regions of the world. Supported by field data from Australia and Mexico, we highlight how extreme climatic characteristics have shaped unique forests, with distinct geomorphology, hydrology, forest structure, physiology and soil biogeochemistry. Mangroves in arid coasts are threatened by multiple factors, and therefore, in this review, we also explore current opportunities for improved management, protection, and restoration.

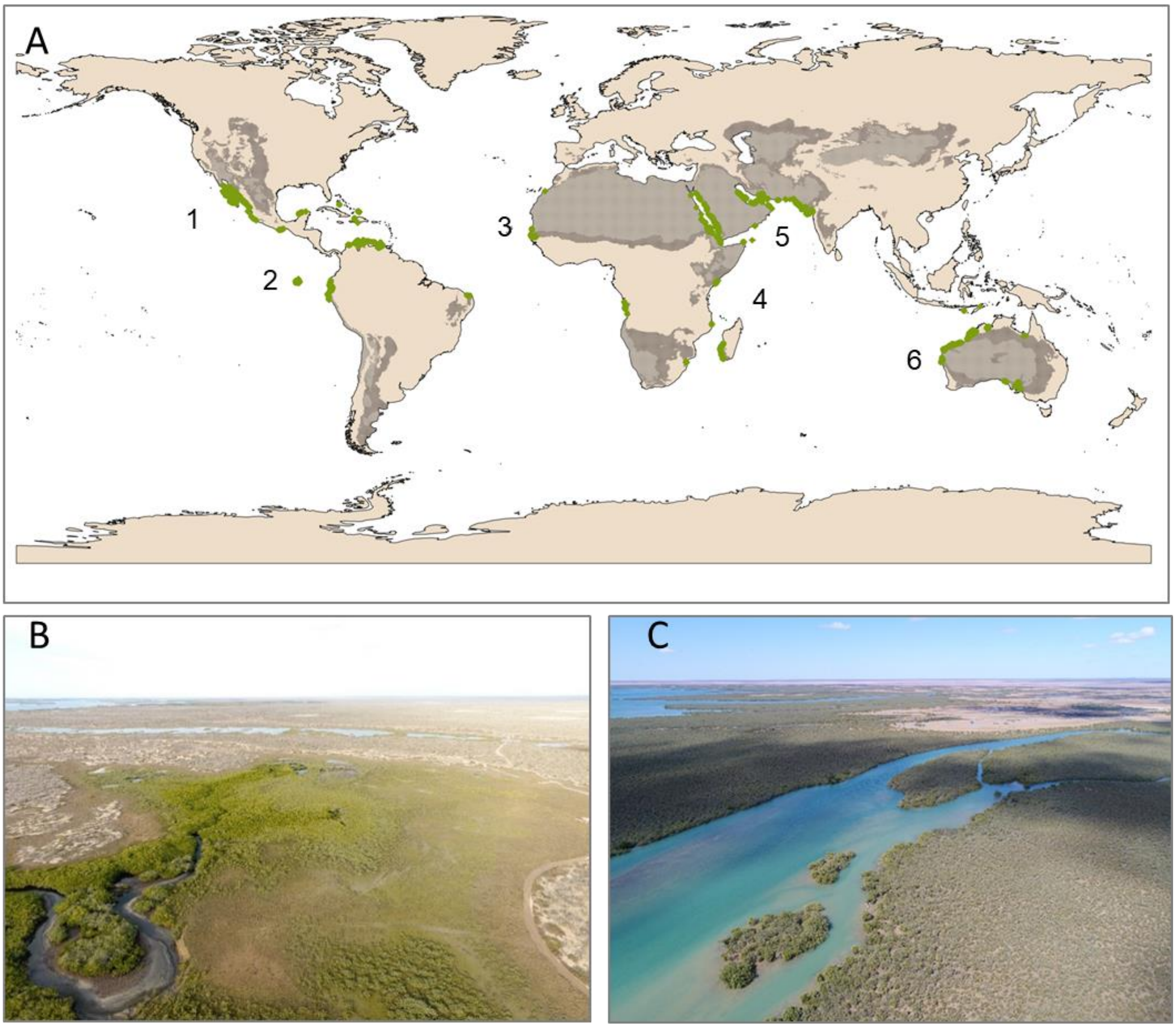

Figure 1. (A) Map of mangroves located in arid (grey) and semi-arid regions, (dark grey, BWh and BSh, Köppen-Grieger climate classification) corresponding to the following marine provinces of the world (Spalding et al., 2007): (1) Warm Temperate Northeast Pacific. (2) Tropical Eastern Pacific, (3) West African Transition, (4) Red Sea and Gulf of Aden, (5) Somali/Arabian, (6) Northwestern Australia; (B) mangroves in Bahia Magdalena, Baja California, Mexico and (C) Giralia Bay, Western Australia. Pictures from MF Adame and R Reef.

2. Geomorphology and Hydrology

Mangroves in arid climates are generally tide-dominated (Woodroffe, 1992), growing along tidal creeks with inverse salinity gradients, sometimes with hypersaline lagoons extending landward of the mangroves. River run-off is limited, and sediment deposition is often low, which compounded with low primary productivity, may result in reduced rates of vertical accretion. For instance, in the Gulf of Baja California, Mexico (Bahia Magdalena), two cores analysed for ^{210}Pb had negligible excess-^{210}Pb detected (Supplementary Information). These results suggest that in this region where precipitation is extremely low, erosion is a dominant process within these mangroves. Indeed, many mangroves in arid climates are found on ancient deltaic plains deposited before the Holocene, which are now eroding (Semeniuk, 1985).

Sediment deposition from land sources is restricted to sporadic events, such as during tropical storms, which deliver freshwater and large sediment loads for days or weeks at a time. For mangroves in arid climates, tropical storms can significantly alleviate hypersalinity, strong nutrient limitation, and temporarily boost their usually low productivity (Lovelock et al., 2011). Tropical storms can also cause erosion and re-deposition of large amounts of sediments (Semeniuk, 1996), changing the hydrology and modifying the configuration of the mangroves.

In arid regions, where marine inputs are dominant and terrestrial runoff is limited to sporadic and infrequent events, carbonates (limestone and dolomites) can be an important component of the mangrove soil. For instance, in the Arabian Gulf, carbonates accounted for 20-60% of the soil carbon (Saderne et al., 2018). In Giralia Bay, Western Australia, carbonate accounts for 35.1 ± 14.7 % of the soil mass in mangroves, 42.7 ± 6.1 % of saltmarsh, and 42.9 ± 9.6 % of sediments underlying the cyanobacterial mat habitats (Supplementary Data). The accumulation of carbonates could contribute substantially to their soil vertical accretion. For instance, in Saudi Arabia and Western Australia, accretion rates of 2-4 mm yr^{-1} have been estimated, with almost half of it due to the accumulation of marine carbonates (Cusack et al. 2018, Saderne et al. 2018, Lovelock unpublished data). The high proportion of carbonates over silicates or organic matter in these mangroves would also affect their carbon budgets and their role as carbon sinks (Cusack et al. 2018, Saderne et al., 2019).

3. Forest structure

Salt-tolerant species within the genus *Avicennia* often dominate mangroves in arid climates. In Western Australia, the dominant species is *Avicennia marina,* in the Middle East, *A. marina,* and *Avicennia macrostachyum*, and in the Gulf of California, *A. germinans Laguncularia racemosa,* and *Rhizophora mangle* (Santini et al., 2015; Schile et al., 2017; Adame et al., 2018a, Fig. 2). The low diversity of mangroves in arid regions has been attributed to low precipitation (Osland et al., 2017) with few species able to tolerate and maintain productivity under hypersaline soils and low humidity (Ball and Farquhar 1984). Mangrove distribution across the intertidal is usually limited to a narrow strip close to mean sea level that fringes tidal creeks, where sediments are inundated by tides at least once a day. Higher in the intertidal, salt flats (or sabkha) are dominated by cyanobacterial mats, microbial films, and tidal marshes comprised of succulent chenopods and other highly salt-tolerant species (Semeniuk, 1985; Lovelock et al., 2010, Fig. 2).

As a result of high salinity and low nutrients, mangroves in arid regions are growing at their physiological limits, resulting in low productivity and slow growth (Ball, 1988; Saenger and Snedaker, 1993; Lovelock et al., 2007). For example, *A. marina* trees growing under high saline conditions exhibit low growth rates (Santini et al., 2012, 2013), a pattern probably applicable to all mangroves in arid regions. For example, in Brazil, growth-assessed as radius increment per year- of *Rhizophora mangle* is 1- 2 mm yr^{-1} in saline forests where rainfall is low (< 50 mm) and inundation is infrequent, and 3.3 mm yr^{-1} where inundation is frequent, and salinity is lower (Menezes et al., 2003). For root growth, the patterns seem to be inverse, with relatively higher total root biomass and root:shoot in mangroves with high salinity compared to less saline forests (Adame et al., 2017). Mangroves in arid regions can grow at salinities of up to 90 (Practical Salinity Units, Semenuik, 1983). However, in some sites such as Puerto Rico and Western Australia, widespread mangrove mortality has been observed at 70, when salinities exceed long term averages (Cintron et al., 1978; Lovelock et al. 2017).

Typically, mangroves in arid climates tend to form dense forests of low stature (< 2m in height) in the high-intertidal. These are widely known as "scrub forests" (Lugo and Snedaker, 1974). Although scrub forms are not unique of mangroves in arid climates, they seem to be prevalent in regions where either salinity or nutrient limitation is high (Feller et al. 2010). Alternatively, low intertidal mangroves tend to be taller (2 – 3 m in height, Naidoo, 2006; Fig. 2). For example, in the Gulf of California, Mexico, we explored an area of over 700 km of mangroves. Within these forests, tree height ranges from two to three meters, and tree density exceeded 5,775 trees ha^{-1} at every site with some forests having over 25,000 trees ha^{-1} (Ochoa-Gómez et al., 2019 and Figure 1S). For comparison, mangroves in humid climates of Mexico have tree densities between 1,213 and 5,370 trees ha^{-1} (Adame et al., 2015b). High tree densities in the Gulf of California were associated with high interstitial salinity. Similar patterns were observed in Puerto Rico, where density increased linearly with salinity (Cintron et al., 1978). However, this pattern was not found in Western Australia (Lovelock, unpublished data), where mangrove trees become sparse high in the intertidal in the most saline conditions.

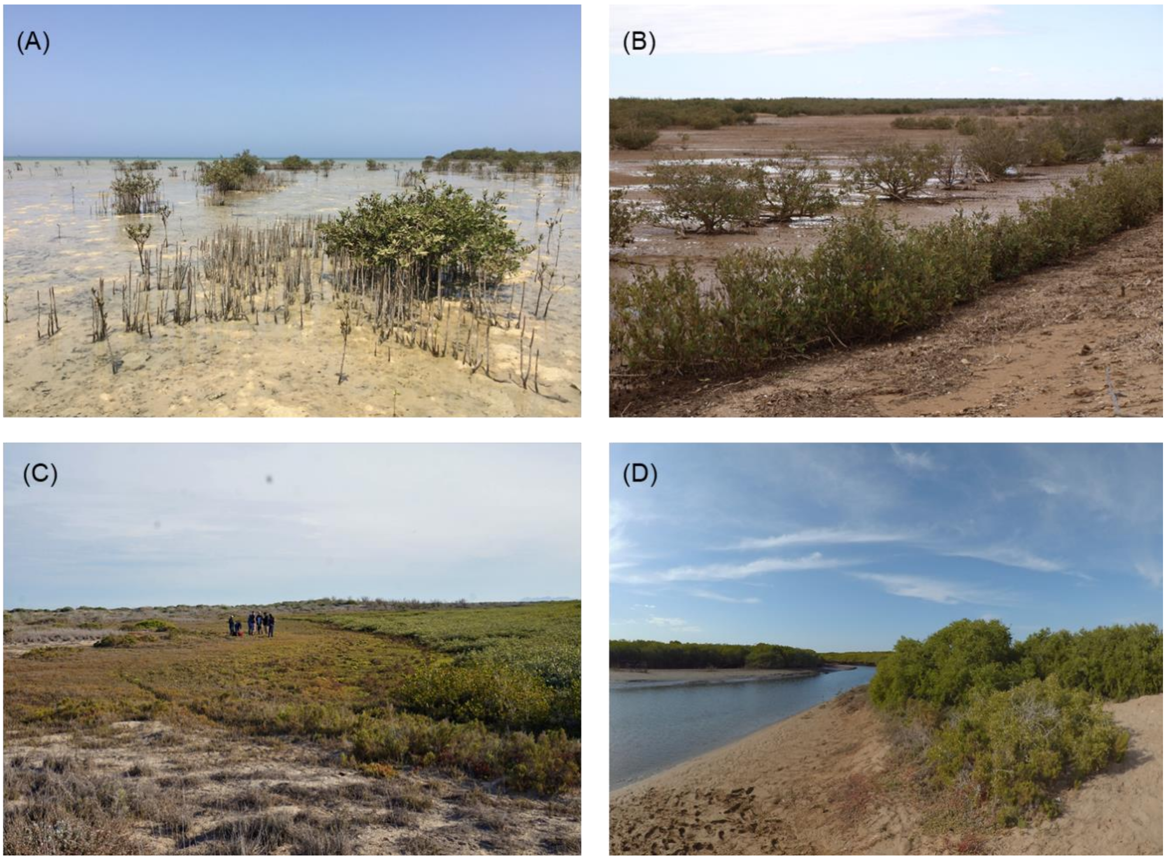

Figure 2. Mangrove in arid climates dominated by short trees (scrub forms) of a few species, (A) Red Sea, Saudi Arabia, mangroves dominated by *Avicennia macrostachyum*, (B) Giralia Bay, Western Australia, dominated by *A. marina* (C,D) and Bahia Magdalena, Baja California, Mexico, dominated by *A. germinans*, *Laguncularia racemosa* and *Rhizophora mangle.*

Mangrove species can form different forest structures depending on the climate; for example, *A.marina* grows in both, arid and subhumid regions of Australia. In arid areas of Australia, where porewater salinity exceeds 40, trees are between one to seven meters in height. In comparison, in subhumid regions where porewater salinity is below 36, the same species can reach 15 m in height (Vilas et al., 2019).

4. Nutrients

Soil nitrogen (N) is the main nutrient that limits mangrove growth across arid, subhumid and humid regions (Reef et al., 2010). Soil N availability is a result of local productivity and external inputs. Natural sources of N are fixation, and external sources are marine and terrestrial productivity (e.g. litter and phytoplankton); common human-derived sources of N are sewage and fertilisers. For mangroves in arid regions, most of the N external inputs are transported via tidal inundation or groundwater (Adame et al., 2012). Overall, arid mangroves are low in N. In Giralia Bay, Western Australia, surface (0-20 cm) N (%) tends to decrease landwards (Supplementary Data). Mangroves fringing the sea have the highest N (0.30 ± 0.05%), followed by mangroves higher in the intertidal (0.17 ± 0.05 %), and lowest in scrub forests located at the landward edge of the mangroves (0.07 ± 0.02%). These values are lower than those from humid and sub-humid mangroves, such as Malaysia (0.47-0.72%), Southwest Mexico (0.32- 1.3 %), and the Caribbean (0.54- 1.32 %) (Adame et al., 2018c, 2015b, 2013). As a result, arid mangroves can be strongly limited by N availability (Naidoo, 2009; Lovelock et al., 2011; Almahasheer et al., 2016).

Phosphorus can also limit productivity in arid zones, although there are only a handful of studies to support this. For instance, microbial respiration in Giralia Bay, Western Australia, is limited by soil P, with concentrations < 0.001% (Lovelock et al., 2011; Davies et al., 2017). In the Red Sea, soil P was also relatively low, with values ranging between 0.03 and 0.08 % (Saderne et al., 2020). Due to the presence of carbonates in many arid coasts, P is likely to precipitate and become inaccessible for plant uptake and become an essential limitation for mangrove growth (Alongi, 2017). Even where nutrient enrichment may be intense, it may not be sufficient to stimulate growth in arid regions where high salinity limits mangrove productivity (Naidoo, 2009; Lovelock et al., 2011; Almahasheer et al., 2016). Additionally, mangroves can also be co-limited by other minerals that are scarce in arid zones, such as Fe in the Red Sea (Almahasheer et al., 2016), and Fe and Cu in northern Australia (Alongi, 2010, 2017).

Soil N content is closely associated with many processes in mangroves. Low N availability in mangroves has been associated with low denitrification rates (Adame et al., 2019), higher imports of N_2O (Maher et al., 2016), high N fixation, and high rates of NH_4 export (Adame et al., 2010). Isotopes of $\delta^{15}N$ can give insights into some soil biogeochemical processes in mangrove soils. For instance, N fixation results in $\delta^{15}N$ values close to zero, while denitrification, ammonia volatilization, and ammonia uptake increase $\delta^{15}N$ to values > 1 ‰ (Fry, 2006). Additionally, soil $\delta^{13}C$ can provide information on forest productivity, with higher values in organic matter where productivity is high (Fry, 2006; Adame et al., 2015a). The $\delta^{13}C$ values can also provide information on the origin of C accumulated in the soil, with values around -27 ‰ being typical of C_3 plants (e.g. trees), while values of around -22‰ common for marine phytoplankton (Fry, 2006).

We analysed surface (0-20 cm) soil samples from Giralia Bay, Western Australia (n = 18) and from the Gulf of California, Mexico (n = 39, See Supplementary Information) for $\delta^{15}N$ and $\delta^{13}C$ values. We compared our results with isotope values from soils of mangroves in the Red Sea (Almahasheer et al., 2017) and Iran, in the Arabian (Persian) Gulf (Etemadi et al., 2018). Mangroves in arid regions had consistently higher $\delta^{15}N$ and $\delta^{13}C$ values compared to some humid and subhumid mangroves, with highest values in the hyper-arid areas (Iran and Red Sea, Fig. 3). Higher $\delta^{15}N$ and $\delta^{13}C$ values possibly indicate differential acquisition of ammonia over nitrate (Yoneyama et al., 1991), or high marine contributions (Etemadi et al., 2018).

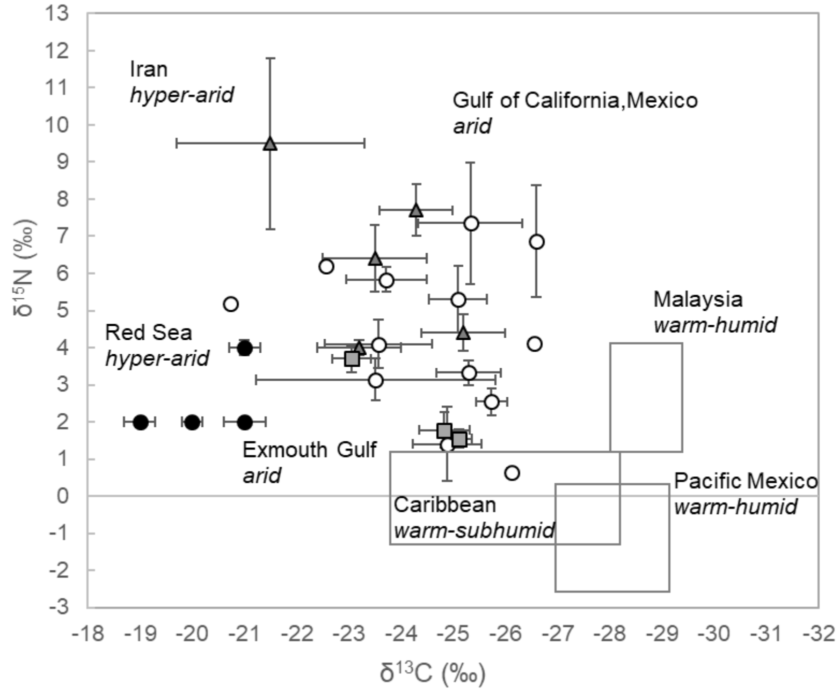

Figure 3. Soil $\delta^{15}N$ and $\delta^{13}C$ values (‰) of surface soil (0-20 cm) of mangroves in the Gulf of California, Mexico (open circles, n= 13 sites, three cores per site), Giralia Bay, Western Australia (grey squares, n= 3 sites, 6 cores per site), the Red Sea (black circles, from Almahasheer et al., 2017), and Iran in the Arabian (Persian) gulf (grey triangles, Etemadi et al., 2018) compared to ranges (depicted as squares) of tropical mangroves in the Caribbean (unpublished data, MF Adame), Tropical Pacific in Mexico (Adame and Fry, 2016) and Malaysia, Southeast Asia (Adame et al., 2018c).

5. Physiology

Arid regions have some of the highest seasonal and interannual variability in precipitation of the world (Nicholls and Wong, 1990). Rainfall variability can be more influential in the physiology of mangrove trees than low precipitation itself (Westbrooke and Florentine, 2005). In arid regions, mangroves have developed traits to survive hypersalinity and hypervariability of freshwater inputs.

Salt exclusion is an important mechanism for mangrove growth and survival in arid regions. Some specialised structures in mangroves roots, such as well-developed casparian bands and suberin lamellae, can filter up to 95% of the salt ions during water uptake (Scholander, 1968; Popp et al., 1993). Nevertheless, growing under hypersaline conditions comes at a metabolic cost, which is reflected as high water use efficiency (the ratio of carbon assimilation and transpiration) and reduced growth rates (Ball, 1988, 1996). Water use efficiency reported for mangroves is up to 56 % higher than that of adjacent tropical trees (Ball, 1996).

Arid zones are characterised by frequent periods of extremely low humidity, resulting in high leaf vapour pressure deficits. Mangroves can reduce stomatal conductance to minimise water loss during these events, resulting in low CO_2 uptake during photosynthesis (Ball, 1988, Mendez-Alonso et al., 2016). Mangroves can keep extremely low leaf water potentials (-5 MPa), maintaining safety in their hydraulic system. For example, vessel size is smaller, and more numerous under saline compare to brackish conditions (Verheyden et al., 2005; Robert et al., 2011) and have stomata mainly on the abaxial surface of the leaves to reduce water loss (Cheeseman, 1994). Genera such as *Avicennia* also have successive cambia, which could provide a mechanism to repair embolisms (Schmitz et al., 2007; Lovelock et al., 2016)

Mangroves can access sporadic freshwater by deploying deep and shallow roots (e.g. Ewe et al., 2007; Santini et al., 2015). *Avicennia* also exhibits features that facilitate water uptake from leaves, such as leaf hammer hairs and other structures that store and absorb water under arid conditions (Nguyen et al., 2017, Hayes et al. 2020). Overall, mangroves in arid climates have developed specialised structures, such as roots that filter salt and can efficiently absorb seasonally available freshwater, leaves that can uptake and minimise water loss, and stems that reduce the risk of embolisms. Altogether, these traits allow mangrove trees, especially from the genera *Avicennia*, to tolerate hypersalinity and take advantage of freshwater pulses when they are available.

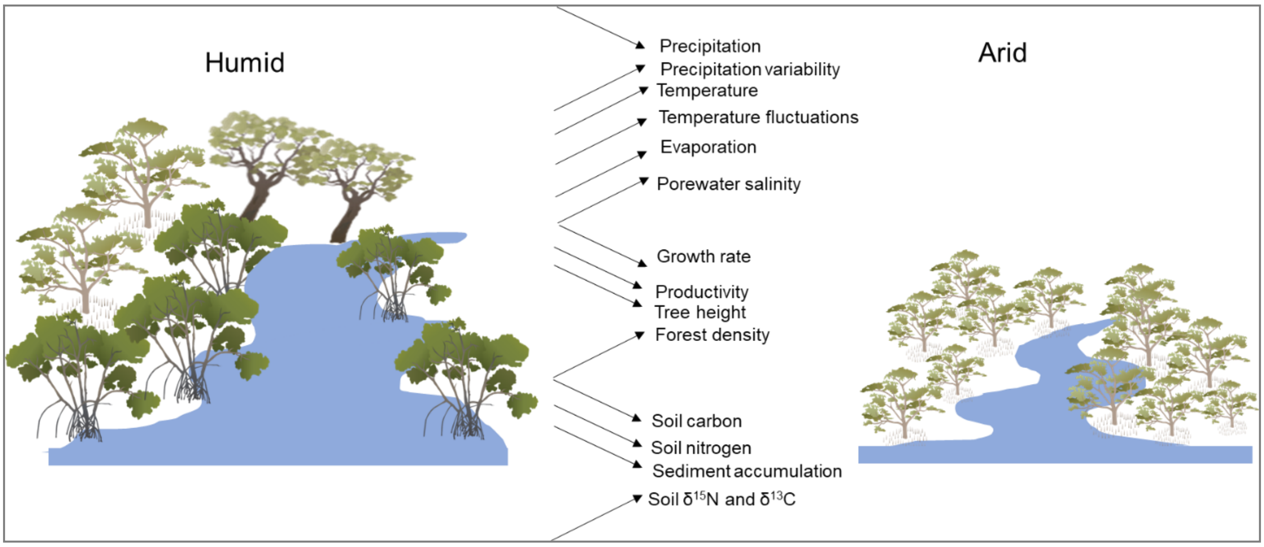

Figure 4. Schematic representation of the difference in environmental characteristics, physiological responses, and soil biogeochemistry of mangroves in humid vs arid climates.

6. Carbon sequestration potential

Due to their low productivity and low sediment accumulation, mangroves in arid regions tend to have relatively low soil organic carbon (SOC) stocks and low sequestration potential; however, globally, they store 12.3 million MgC. A global model of SOC, (Sanderman et al., 2018) predicted low soil stocks in arid regions, with most sites having values < 300 MgC ha^{-1} (Table 1). In the Gulf of California, Mexico, we collected soil cores from 18 sites within a latitudinal gradient encompassing 1,500 km from 22N° 41W' to 34N° 19W'. We sampled mangrove forests in the southern sites and marshes in the north. We also sampled a gradient from the low to high intertidal zones within mangroves of Giralia Bay, Western Australia (Supplementary Information and Data, and Adame et al., 2018b)

Our results show no apparent trend on SOC stocks with latitude and decreasing SOC stocks in the high intertidal (Fig. S2). Our data combined with the hyper-arid Red Sea and Arabian (Persian) Gulf (Almahasheer et al., 2017; Schile et al., 2017) and semi-arid Senegal (Kauffman and Bhomia, 2017) show low SOC stocks compared to other mangroves in humid and sub-humid regions, where mean values are 521 and 541 MgC ha^{-1}, respectively (Fig. 5, Adame et al., 2018a). The SOC stocks in arid mangroves although relatively low, were still 10 to 60 times larger compared to the adjacent terrestrial ecosystems (6.5 MgC ha^{-1} in Southern Baja California and 18.7 MgC ha^{-1} in Northern Baja California MgC ha^{-1}).

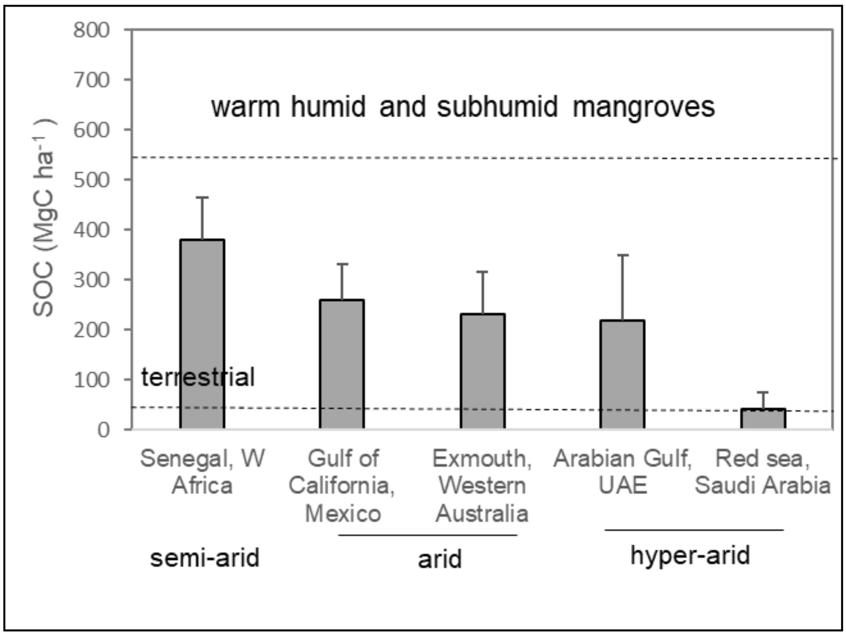

Figure 5. Comparison of soil organic carbon (SOC) stocks of mangroves in arid climates with mangroves in humid and subhumid climates. Data is from this study, Kauffman and Bhomia (2017) and Almahasheer et al. (2017), Schile et al. (2017) for the Red Sea and Arabian (Persian) Gulf. The hashed lines represent mean values for mangroves in warm-humid and sub-humid regions of Mexico (Adame et al., 2018a) and the adjacent terrestrial desert.

7. Global trends in mangrove area and condition

In general, mangroves in arid regions are located in areas with low population density (Table 1), especially, Northwest Australia (< 1 person km^{-2}), and parts of the Gulf of California (Magdalena Transition) and Western Arabian Sea (< 6 people km^{-2}). Higher populations are found in Guayaquil (Ecuador), West Africa, the Red Sea, and Arabian (Persian) Gulf, where population mean density ranges between 48- 86 people km^{-2}. Mangroves in arid regions are also less impacted by cumulative human pressures compared to those in non-arid regions. For example, the terrestrial human footprint (Venter et al., 2016) is relatively low for mangroves in arid zones, especially in the Somali/Arabian coast, Northwest Australia and Magdalena Transition (Gulf of California), with mean values < 5 (global ecoregion means range from 0-35; Table 1).

Deforestation rates in mangroves in arid climates from 2010-2012 were generally low, with many regions having losses that were not detectable from global datasets (Table 1). Key areas of mangrove loss were the Southern Red Sea (0.06%), Southern Gulf of California, Mexico (Cortezian and Magdalena Transition, annual 0.02% loss), Guayaquil, Ecuador (0.01% loss), and Exmouth, Western Australia (0.01%). There are various drivers of deforestation, but some factors have been locally identified. In the Americas (Northwest Mexico and Ecuador), shrimp pond construction has been an essential driver of deforestation (Valderrama-Landeros et al., 2017). While in Western Australia, tropical storms and fluctuating sea levels have been identified as significant causes of mangrove dieback (Lovelock et al., 2017; Sippo et al., 2018). In some arid regions, local increases in mangrove area have been observed. For example, there has been an expansion of 112 ha (or 33%) of mangroves in Iran between 1956 and 2012 (Etemadi et al., 2018) and mangrove expansion has been observed in some regions of the Gulf of California (López-Medellín et al., 2011). These localised mangrove gains may be attributed to the global trend in poleward migration of mangroves, sea level rise (Saintilan et al., 2014), and global efforts on mangrove restoration (Friess et al., 2020).

The extent of mangrove degradation has not been adequately measured throughout the world, but in some arid zones, degradation is higher than deforestation. For instance, in the Gulf of California, despite lowering deforestation rates in the past years, degradation has steadily increased since the 1990s, with over new 200 ha of mangroves showing signs of deterioration every year (Valderrama-Landeros et al., 2017). This phenomenon could be explained as mangrove in arid conditions s are at their limit of salinity tolerance, so changes in hydrology, climate or nutrient loads, even on a small scale, could cause extensive degradation (Lovelock et al. 2009).

Table 1. Mangrove area (Bunting et al., 2018) in arid and semi-arid ecoregions of the world (Spalding et al., 2007), mean soil organic carbon (SOC, Sanderman et al., 2018), aboveground C (Simard et al., 2019), deforestation rates (Hamilton and Casey, 2016), index of terrestrial footprint (Venter et al., 2016; mean ± SD) and adjusted population density (0-187, CIESIN, 2018).

Ecoregion	Area (ha)	SOC (MgC ha^{-1})	Aboveground (MgC ha^{-1})	Deforestation rate (%) 2010-2012	Human footprint index	Population density 2015 (people km^2)
1-Warm Temperate Northeast Pacific						
Southern California Bight	1,187	244.4	17.9	0	7.7 ± 6.0	159 ± 653
Cortezian	188,938	247.3	58.7	0.02	5.8 ± 5.6	30 ± 256
Magdalena Transition	32,045	296.1	43.0	0.02	4.4 ± 3.2	5 ± 68
2-Tropical Eastern Pacific						
Guayaquil	116,267	363.7	77.1	0.01	5.8 ± 6.1	61 ± 195
3-West African Transition						
Sahelian upwelling	179,941	318.4	69.2	0	5.4 ± 5.4	62 ± 609
4-Red Sea and the Gulf of Aden						
Northern and Central Red Sea	2,061	266.1	380.8	0	4.3 ± 6.8	86 ± 873
Southern Red Sea	9,442	272.6	208.5	0.06	6.6 ± 4.6	57 ± 232
Gulf of Aden	3,611	279.9	67.8	0	6.0 ± 3.6	48 ± 197
5-Somali/Arabian						

Arabian (Persian) Gulf	15,968	278.4	108.4	0	2.5 ± 3.5	53 ± 263
Gulf of Oman	1,929	266.2	232.1*	0	4.7 ± 4.5	21 ± 78
Western Arabian Sea	31.9	213.5	232.1*	0	2.5 ± 3.5	5 ± 27
6-Northwest Australia						
Exmouth to Broome	46,823	304.5	15.7	0.01	2.5 ± 3.1	0.3 ± 9
Ningaloo	27.1	327.4	3.2	0	4.6 ± 2.7	0.03 ± 1
Shark Bay	1,730	277.5	24.7	0	3.6 ± 2.2	0.1 ± 5

*Mean value of province

8. Threats to arid mangroves

Changes in land use in arid regions will result in changes in groundwater flows (Ferguson and Gleeson, 2012), which may strongly influence mangroves that are groundwater-dependent (Semenuik, 1983). For instance, increased terrestrial vegetation cover reduces groundwater levels, and drought reduces groundwater recharge rates (Scanlon et al., 2006). Land-use changes that increase groundwater use are likely to lead to periods of hypersalinity in arid and semi-arid regions (Jolly et al., 2008). These changes are likely to be pronounced in the hyper-arid Middle East, where high water extraction, in conjunction with reduced rainfall, will increase saline stress (Ward et al., 2016). Changes in groundwater supply will ultimately affect mangroves, as freshwater inputs could be essential for mangrove growth and productivity (Hayes et al., 2018), especially for mangroves of arid regions, which have high water stress (Santini et al., 2015; Vilas et al., 2019).

Excess nutrients are also a threat to arid mangroves as nutrients result in an excessive allocation of biomass to leaves, which under hypersaline conditions enhances their probability of mortality when arid conditions intensify (Lovelock et al. 2009). In the Gulf of

California, Mexico, urban developments, aquaculture and agriculture have not only resulted in direct losses of coastal wetlands (Berlanga-Robles et al., 2011) but also in increased nutrient inputs. For instance, every year, shrimp ponds discharge is over 9,000 t of N and over 2,000 t of phosphorus (Páez-Osuna et al., 2017). In the 1980s, the Gulf of California became the second-largest producer of shrimp from aquaculture ponds in the American continent (Berlanga-Robles et al., 2011). To date, the Gulf of California is one of the fastest-growing regions in Mexico (Lopez-Medellin et al., 2011), which has resulted in urbanisation and land clearing for agriculture and aquaculture (Berlanga-Robles et al., 2011).

Another threat for arid mangroves is the reduction of sediment supply, which, along with their relatively low productivity, can compromise their ability to keep pace with sea-level rise (Lovelock et al., 2015). In arid and hyper-arid regions, low rainfall is the leading cause for low sediment availability, while in semi-arid regions, dam construction, which reduces water and sediment delivery to the coast, is one of the highest threats (Ward et al., 2016). For example, in the Somone Estuary in Senegal, upstream dam constructions and extreme drought led to severe declines in mangrove area. Subsequently, the mangroves became dominated by more salt-tolerant taxa with increased coverage of hypersaline salt flats (Sakho et al., 2017).

Arid regions in the subtropics are particularly exposed to extreme climatic events, including severe drought, cyclones and hurricanes, which can cause substantial mangrove mortality (Sippo et al., 2018; Krauss and Osland, 2020). Large mortality events (> 5,000 ha) have been observed in arid and semi-arid regions of Australia (Duke et al., 2017), some of which have been associated with intense El Nino events, which resulted in hypersalinity of the soil (Lovelock et al., 2017). However, some mangrove trees in arid regions demonstrate remarkable resilience to these conditions and can live for over 160 years (Santini et al., 2013).

Future changes in sea level rise and macroclimatic factors, such as temperature and precipitation, will affect mangroves globally (Osland et al., 2016). Decreased precipitation in arid regions could result in reduced canopy height, biomass and lower productivity and thus, decreased carbon sequestration ability (Feher et al., 2017). Simultaneously, an increase in the frequency of tropical storms in some arid regions could temporarily boost productivity and provide sediments that could help mangroves keep pace with sea-level rise (Lovelock et al., 2011). The confounding effects of temperature, rainfall and extreme climatic events will be variable across different locations. However, the extreme conditions in which mangroves survive in arid climates, means that any small increase in aridity could result in drastic and irreversible changes (Berdugo et al., 2020). Additionally, because mangroves in arid climates depend on a single or a few foundation species, they are likely to be more vulnerable to environmental changes than multi-species forests (Ellison et al., 2005).

9. Restoration projects

There are some restoration projects of mangroves in arid and semi-arid regions of the world. For example, a large-scale restoration project (700 ha) has taken place in Senegal, where dam construction, changes in hydrology, and low rainfall, caused the degradation and loss of mangroves (Diop et al., 1997). The loss of the mangroves, from which many local communities depended, resulted in social upheaval (Conchedda et al., 2011) and prompted this restoration project. The objective of the restoration program was to recover ecosystem services, using carbon credits (VERRA). Although this restoration project is mostly perceived as successful (see: www.livelihoods.eu/projects/oceanium-senegal), social conflicts associated with restricted use of the mangroves by communities under the conditions which carbon offsets were sold have also been reported (Cormier-Salem and Panfili, 2016).

Other examples of restoration projects are the reestablishment of tidal flows in a site previously exploited for salt production in South Australia (Dittman et al., 2019), and in the Gulf of California, where mangroves were replanted in a previously cleared forest (Toledo et al., 2001). The planted trees had a 77% survival rate after two years and showed some signs of functional recovery -measured as N_2-fixation- 12 years after reforestation (Toledo et al., 2001). In other arid regions, such as in the United Arab Emirates, afforestation programs have increased the area of mangroves by almost 4,000 ha (Almahasheer, 2018). In Eritrea, mangrove afforestation has been conducted to support the livelihoods of local communities (Sato et al. 2005).

However, to date, many restoration projects are still focused on plantations species, which are often not the dominant ones, sometimes in sites not previously occupied by mangroves, such as in seagrass meadows. This approach has largely failed to restore the function of mangroves globally (Lee et al., 2019). Restoration should be focused on restoring the natural hydrology and encouraging the regeneration of native and dominant species (Lee et al., 2019). While this is important for all mangrove forests, it is particularly crucial for arid mangroves, where a small increase in salinity, can exceed the physiological tolerance of mangroves, even for species highly adapted to hypersalinity, such as *Avicennia*.

The lessons from the restoration projects in arid regions to date are: 1) these mangroves are highly vulnerable to changing hydrology and rainfall, 2) loss of mangroves has negative social consequences both because of losses and through complexities associated with restoration projects, and 3) restoration should be focused on reinstalling hydrological connectivity reintroducing native species adapted to arid conditions. Improved practices that consider the biophysical, as well as the social environment, are crucial for these restoration projects to be successful (Scales and Friess, 2019).

10. Improved management

Because of the short stature and open canopies of many arid mangroves, they often do not meet the country's definitions of forests. For instance, Mexico has defined 'forests' under their commitments to the United Nations Framework Convention on Climate Change (UNFCCC) as having trees that are at least 4 m in height with 30% canopy cover (Sasaki and Putz, 2009). As a result, most mangroves of arid regions are excluded within their forest conservation and management programs (e.g. REDD+). Global maps of mangrove cover have often used a base map of "forest" cover, which excludes vegetation less than 2 m in height (Hamilton and Casey, 2016), hence most of the mangroves from arid regions. Additionally, global mangrove height maps (Simard et al., 2019) cannot detect short stature mangroves. Consequently, arid mangroves are in general, underrepresented in mapping, legislation, management, and restoration programs. Fortunately, a new mangrove area map (Global Mangrove Watch, Bunting et al., 2018) has included small-statured mangroves, providing improved estimates of the global and regional area of mangroves in arid climates.

Improved management and restoration of mangroves is especially attractive for countries where mangroves are often the most productive forest in the landscape and one of the few options for participating in land-based carbon trading schemes. For example, Abu Dhabi included mangroves in their greenhouse gas accounts because mangrove losses form a significant component of their national emissions associated with land-use change (LULUCF).

Conclusions and Recommendations

Mangroves in arid climates are unique ecosystems characterised by extreme conditions of temperature, radiation, precipitation, and salinity. They occur in mostly tide-dominated geomorphic settings with freshwater flows restricted to groundwater or during sporadic tropical storms, which makes them vulnerable to changes in hydrology and reduced freshwater inputs. Mangroves in arid conditions form stunted forests of salt-tolerant species, especially of the genus *Avicennia*. Despite their low productivity and low C and N content, there is potential for stimulating their restoration through carbon offsetting mechanisms. However, improved approaches to the protection and restoration of these mangroves are still needed. Restoration should be focused on restoring hydrology, supporting species adapted to arid conditions. Due to their short stature, mangroves in arid regions are generally underrepresented in global programs because they usually do not comply with the definition of “forests”. Mangroves in arid climates would benefit from the enhanced representation of their area, threats and values in global mangrove assessments and programs.

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