ARTICLE IN PRESS

SAJB-01511; No of Pages 13

South African Journal of Botany xxx (2016) xxx–xxx

Contents lists available at ScienceDirect

South African Journal of Botany

journal homepage: www.elsevier.com/locate/sajb

The mangroves of South Africa: An ecophysiological review

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ARTICLE INFO

Available online xxxx

Edited by JB Adams

Keywords:
Mangroves
Salinity
Waterlogging
Aerenchyma
Ecophysiology
Gas exchange
Nutrients
Avicennia
Bruguiera
Sea level rise

ABSTRACT

Mangroves are unique, highly productive forests that interface between marine and terrestrial environments in protected and sheltered habitats of tropical and temperate regions. In Africa, mangroves reach their southern distributional limit in the warm temperate zone at Nahoon Estuary (32°56′ S) in South Africa. Temperate mangroves are less diverse, slower growing and of smaller stature than those in the tropics. This review gives an overview of mangrove distribution in South Africa and factors that constrain their spread. This is followed by an ecophysiological overview of mangrove adaptations to survive in an intertidal environment characterized by heterogeneous salinity, waterlogging and low nutrients. These adaptations play critical roles in salt exclusion, maintenance of low tissue water potentials and conservative water and nutrient use. Adaptations range from macro to micro levels and include root, stem and leaf morphology. It also discusses characteristics of mangroves at higher latitudes that distinguish them from their tropical equivalents. The effects of anthropogenic pollution, climate change and sea level rise, as well as local threats in South Africa are also discussed. This review also includes a detailed list of research conducted on South African mangroves and makes suggestions for future work.

1. Introduction

Mangrove ecosystems occur in protected and sheltered environments in tropical and temperate regions and are important because of their global extent, high productivity and numerous ecosystem services. These forests are dominated by a small group of tree species that evolved special adaptations to survive in intertidal environments. Mangroves occur in coastal areas from mean sea level to the highest spring tides and are represented by 19 families, 28 genera and 70 species (Duke et al., 1998). The global coverage of mangroves is about 13,800 (Giri et al., 2011) to 15,300 ha (Spalding et al., 2010). Generally, mangroves are restricted to the tropics where mean air temperatures of the coldest months are >20 °C and where the seasonal range is <10 °C. The geographic limits of mangroves coincide with frost occurrence and are closely linked with the 20 °C winter isotherm for seawater (Duke et al., 1998). Mangroves that occur between latitudes 30°N and 30°S are considered tropical and account for about 98.6% of total coverage, while those that occur at latitudes greater than 30° are regarded as temperate and account for about 1.4% (Morrisey et al., 2010). Mangrove species richness and diversity decline with increasing latitude probably due to their cold tolerance, although differences in aridity, habitat and dispersal may play a role (Duke et al., 1998). In the southern hemisphere, temperate mangroves occur in South Africa, New Zealand, parts of Australia and eastern South America, and their distribution coincides with warm ocean currents. These mangroves may be relict populations which established during periods of warmer climate or their distribution may be limited by low temperate (Duke et al., 1998).

Along the east coast of South Africa, habitats suitable for mangroves are limited by the morphology and dynamics of river-dominated estuaries. Mangroves occur from Kosi Bay (27°S) in the north and reach their southern distributional limit in the warm temperate zone (32°56′S) at Nahoon Estuary. The mangroves at Nahoon were transplanted from Durban Bay in 1969 by Steinke and currently occupy extensive areas on intertidal mudflats in the estuary (Steinke, 1999). The total mangrove cover in South Africa is estimated at about 1900 ha (Ward and Steinke, 1982; Hoppe-Speer, 2013). Generally, mangroves occur in estuaries that have a permanent connection to the sea. In South Africa, as in other temperate mangroves, species richness and diversity decline with increasing latitude, with 6 species in Kosi Bay (*Avicennia marina*, *Bruguiera gymnorrhiza*, *Rhizophora mucronata*, *Ceriops tagal*, *Lumnitzera racemosa* and *Xylocarpus granatum*) and 3 in Nahoon (*Avicennia marina*, *Bruguiera gymnorrhiza* and *Rhizophora mucronata*,). The largest mangrove forests are found in the subtropical areas (28° to 29°S) at St. Lucia and Richards Bay (Table 1).

Avicennia marina has the greatest geographical range of all mangroves and is the most common species in temperate regions with a southernmost limit of 32°56′S in South Africa and 38°S in Australia

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http://dx.doi.org/10.1016/j.sajb.2016.04.014
0254-6299/

Table 1
Estimated mangrove coverage in South African estuaries (Ward and Steinke, 1982; Hoppe-Speer, 2013). Am = *Avicennia marina*; Bg = *Bruguiera gymnorrhiza*; Rm = *Rhizophora mucronata*; Ct = *Ceriops tagal*; Lr = *Lumnitzera racemose*; Xg = *Xylocarpus granatum*.

Province	Estuary	Area (ha)	Mangrove protection	Species present
KwaZulu-Natal	Kosi Bay	60.7	Yes	Am, Bg, Rm, Ct, Lr, Xg
	St Lucia	571	Yes	Am, Bg
	Mfolozi	26	No	Am, Bg
	Richards Bay	267	Yes	Am, Bg, Rm
	Mhlathuze	652.1	Yes	Am, Bg, Rm
	Mlalazi	60.7	Yes	Am, Bg, Rm
	Mgeni	20.3	Yes	Am, Bg, Rm
	Durban Bay	16	No	Am, Bg, Rm
	Sipingo	3.8	No	Am, Bg, Rm
	Mkomazi	2	No	Am, Bg, Rm
	Mtamvuna	0.25	Yes	Am, Bg, Rm
Eastern Cape	Mzamba	0.3	Yes	Bg
	Mnyameni	5	Yes	1982 Am, Bg 2013 none
	Mtentu	0.6	Yes	Bg
	Mzintlava	1.7	No	Bg
	Mntafufu	12	No	Am, Bg, Rm
	Mzimvubu	0.03	No	1982 Am,Bg 2013 none
	Mngazana	118	No	Am, Bg, Rm
	Mtakatye	10	No	Am, Bg, Rm
	Mdumbi	5	No	Am
	Mtata	31	No	Am, Bg, Rm
	Bulungula	0.014	No	1982 Am, Bg, Rm 2013 none
	Xora	25	No	Am, Bg
	Mbashe	9.2	Yes	Am, Bg
	Nqabara	11.8	No	Am
	Nxaxo-Ngqusi (Wavecrest)	9.5	No	Am, Bg
	Kobanqaba	6	No	Am
	Nahoon	1.62	Yes	Am, Bg, Rm
	Total	**1921**		

(Morrisey et al., 2010). Populations of *A. marina* from temperate regions are isolated, have higher levels of inbreeding, lower genetic diversity and lower gene transfer than do coretropical populations (Arnaud-Haond et al., 2006). Associated plant species in mangrove areas include *Acrostichum aureum* L. (a fern), *Barringtonia racemosa* (L.) Roxb. and *Hibiscus tiliaceus* L. At their southern distributional limit in South Africa, they are associated with salt marsh species such as *Spartina maritima* (Curtis) Fernald, *Juncus kraussii* Hochst., *Sarcocornia* sp. and *Triglochin* sp. (Hoppe-Speer, 2013). Taxonomically, mangrove species are unrelated but share a number of morphological, physiological and reproductive traits that allow them to survive in the intertidal zone. This work summarizes previous reviews (Macnae, 1963; Steinke, 1995, 1999) and then discusses recent advances in understanding the adaptations and responses of mangroves to environmental stressors. Threats to mangroves in South Africa such as anthropogenic pollution, climate change and sea level rise (SLR) are also discussed. This work includes a detailed list of research conducted on South African mangroves (Table 3) and makes suggestions for future research. Mangrove fauna has been reviewed elsewhere (Macnae, 1963; Steinke, 1995, 1999).

2. Importance of mangroves

The protection, conservation and sustainable use of mangroves are important as they make valuable contributions to ecosystem functioning, providing a wide variety of goods and services. Mangroves protect coastal areas from storms and tsunami, provide nursery grounds for faunal species and support coastal fisheries. Mangroves provide wood for firewood and construction and for fixing and storing significant amounts of carbon (Krauss et al., 2008). In South Africa, mangroves are used for charcoal, firewood, building material for housing, fences and fish traps. Mangroves have also been considered efficient systems for the removal of nutrients and other pollutants (Lewis et al., 2013). Globally, anthropogenic activities that have been detrimental to mangroves include coastal development, pollution, tree felling, the large-scale conversion of forests to ponds for shrimp aquaculture and changes in inland freshwater management (Krauss et al., 2008).

3. Distribution of mangroves

Mangroves occur along the east coast of South Africa in 37 estuaries, lagoons and tidal basins (Table 1). Many of these estuaries are subject to inlet closure by sand bars during periods of low freshwater discharge but are reestablished by high river flows during the wet summer. The largest mangrove forests occur in large, shallow, sandy estuaries of northern KwaZulu-Natal province because of the presence of extensive intertidal flats. The Kosi, St. Lucia, Mfolozi and Mhlathuze Estuaries account for about 75% of mangroves while the Mngazana Estuary has the third largest area. There has been little change in mangrove coverage since 1982 (Table 1) probably due to increased sedimentation of estuaries, harvesting and lack of conservation protection in many areas (Adams et al., 2004). Currently there is a need to re-evaluate the distribution of mangroves in South Africa more accurately.

4. Morphological and anatomical adaptations

Some morphological and physiological characteristics of five of the six mangrove species in South Africa are indicated in Table 2. Mangroves grow in soft substrates so that they have a bottom-heavy tree form and accumulate large amounts of belowground biomass. The rooting system is shallow with spreading cable roots and smaller vertically descending anchor roots. Several species produce aerial roots (Table 1) that possess lenticels and extensive aerenchyma that may account for up to 70% of the root volume. The root system is efficiently ventilated by the diffusion of oxygen down partial pressure gradients from the atmosphere to the roots. In several species leakage of oxygen from the roots causes the rhizosphere to be oxidized (McKee et al., 2007). *Rhizophora mucronata* produces an extensive aerial prop root system which enables the species to flourish in waterlogged sites. The pneumatophores of *Avicennia* are slender, pencil-shaped and arise vertically from cable roots. Some mangroves e.g. *A. marina* possess salt glands on both leaf surfaces (Fig. 1) and exhibit a lignified root epidermis, exodermis and endodermis which decrease apoplastic water uptake (Nguyen et al., 2015). In the endodermis, the Casparian strips develop earlier and closer to the root apex under saline conditions so that water must enter the stele symplastically through membranes that are highly permeable to water (Nguyen et al., 2015). These anatomical strategies reduce the intake of salt, and as a consequence, of water and nutrients, and require greater allocation of resources to root growth. Whether other mangrove species possess such suberized and lignified root cells and highly developed Casparian strips like *Avicennia* need to be investigated.

Many species reduce leaf size as salinity increases. Smaller leaves have higher stomatal conductance and lower leaf temperature which reduce evaporative cooling while maintaining high photosynthesis (Ball, 1988). Several mangroves (e.g. *Ceriops*, *Lumnitzera*, *Rhizophora* spp.) develop leaf succulence which lowers internal ion concentrations, increases leaf heat capacity, reduces evaporative cooling and thereby increases salt tolerance. Mangroves exhibit several water-conserving features such as thick cutinized epidermis, short tracheids that terminate vein endings, leaf pubescence (Table 1), compact palisade mesophyll with small intercellular spaces and numerous sclerenchymatous cells (Werner and Stelzer, 1990). Peltate trichomes on the abaxial surface in *Avicennia* (Fig. 1) reduce water loss by creating a thick boundary layer (Naidoo and Chirkoot, 2004).

Please cite this article as: Naidoo, G., The mangroves of South Africa: An ecophysiological review, South African Journal of Botany (2016), http://dx.doi.org/10.1016/j.sajb.2016.04.014