Journal of the Royal Society of Western Australia, 94: 213–237, 2011

Mangroves of the Kimberley Coast: ecological patterns in a tropical ria coast setting

I D Cresswell[1] & V Semeniuk[2]

[1] CSIRO Wealth from Oceans Flagship, GPO Box 1538, Hobart, Tasmania, 7001

[2] V & C Semeniuk Research Group, 21 Glenmere Rd., Warwick, W.A., 6024

Manuscript received November 2010; accepted April 2011

Abstract

Mangroves along the Kimberley Coast occupy an unparalleled position globally: they reside in a tropical humid to subhumid climate in the species-rich setting of the Old World Mangroves, and are located along a macrotidal ria shore. This setting provides a range of habitats for mangroves related to larger scale hinterland influences, coastal landforms, coastally expressed geological patterns, shoreline sedimentation patterns, and climate. The mangrove habitats of the Kimberley coast range from rocky (cliff) shores to classic ria shores with tidal flats, tidal creeks, spits, and high-tidal alluvial fans, to rocky-shore-dominated ravines, amongst others. Depending on coastal type, sedimentary setting, and the local species pool, the mangroves form habitat-specific assemblages and characteristic floristic and structural zones within the mangrove formations. The complexity of mangrove habitats and their relationship to the megascale coastal forms of this coastal setting is of international conservation significance.

Keywords: Kimberley Coast, mangroves, mangrove ecology, ria coast, mangrove habitats

Introduction

The Kimberley Coast (Fig. 1) presents a globally unique system of mangroves set in a tropical, (generally) macrotidal environment with variable wave energy. The mangroves therein form floristic, physiognomic, and structural formations that inhabit a wide range of coastal settings from rocky shores to beaches, to large tidal flat expanses, and range from relatively simple assemblages to complex systems. Spanning nearly 900 km from north to south, with ~ 4000 km of coast when measured in intricate detail (Brocx & Semeniuk 2011), the mangroves of the Kimberley Coast exhibit recurring patterns based on coastal form and mangrove habitat. The mangrove diversity within these patterns is determined by a climate that grades from humid in the central Kimberley Coast, to subhumid in a north-easterly direction to semiarid in a south-westerly direction.

There have been several studies that have recorded the mangroves floristically (Semeniuk *et al*. 1978, Bridgewater 1985, Duke 2006), as well as descriptions of mangrove formations in this region in biological surveys (Beard *et al*. 1984, Burbidge & McKenzie 1978; Hnatiuk & Kenneally 1981; Kabay & Burbidge 1977; Miles & Burbidge 1975), descriptions of local assemblages and ecology (Bridgewater 1989; Saenger 1996; Semeniuk 1983, 1985; Thom *et al*. 1975; Wells 1981, 1985, 2006), and descriptions of species distributions (Bridgewater 1982, 1985; Bridgewater & Cresswell 1999, 2003; Duke 1992, 2006; Duke *et al*. 1998; Saenger *et al.* 1977; Semeniuk *et al*. 1978; Semeniuk 1993; Specht 1981; Suzuki & Saenger 1996; Wells 1982). To date, however, there has not been a comprehensive and unifying study of the mangroves of the Kimberley region that explains their biogeographic and site-specific diversity.

This paper is an account of the mangroves of the Kimberley Coast, providing a description of their occurrence in relation to the regional species pool, coastal types, and, most importantly, the expression of habitat-specific assemblages along the coast. The Kimberley Coast has a relatively small regional species pool, a simple climate gradient, and a recurring pattern of coastal habitats, and thus provides an ideal setting to understand mangrove ecology, habitat relationships and biogeography.

To understand the ecological patterns of the mangroves of the Kimberleys it is necessary to examine the mangrove distributions at three hierarchical scales: at the broad regional 'coastal setting' scale; below this at the large scale of 'coastal habitat' within which there are assemblages of habitats; and below this at the finer site specific scale herein termed 'mangrove habitat'. The broadest scale (regional scale) is the form of the coast in the Kimberley region. Below that the 'large' intermediate scale is that at which assemblages of interrelated habitats occur in a given coastal setting. The finest scale is the site-specific mangrove habitat. For this paper, individual physiochemical zones within a mangrove habitat, which often produce the conspicuous zonation of mangrove species, are not treated as habitats. Semeniuk (2011) provides definitions and descriptions for the broad coastal settings that occur along the Kimberley Coast. This paper is structured to describe and explain the regional species pool of the Kimberley Coast from which will be drawn the species that may inhabit a given suite of habitats in the coastal and climate setting for a particular site at particular spatial scales. The scope of this paper and the objective is to provide a broad view of the variety of mangrove habitats and mangrove assemblages that occur in the Kimberley region and relate them to the main abiotic factors of climate, coastal setting, and habitat.

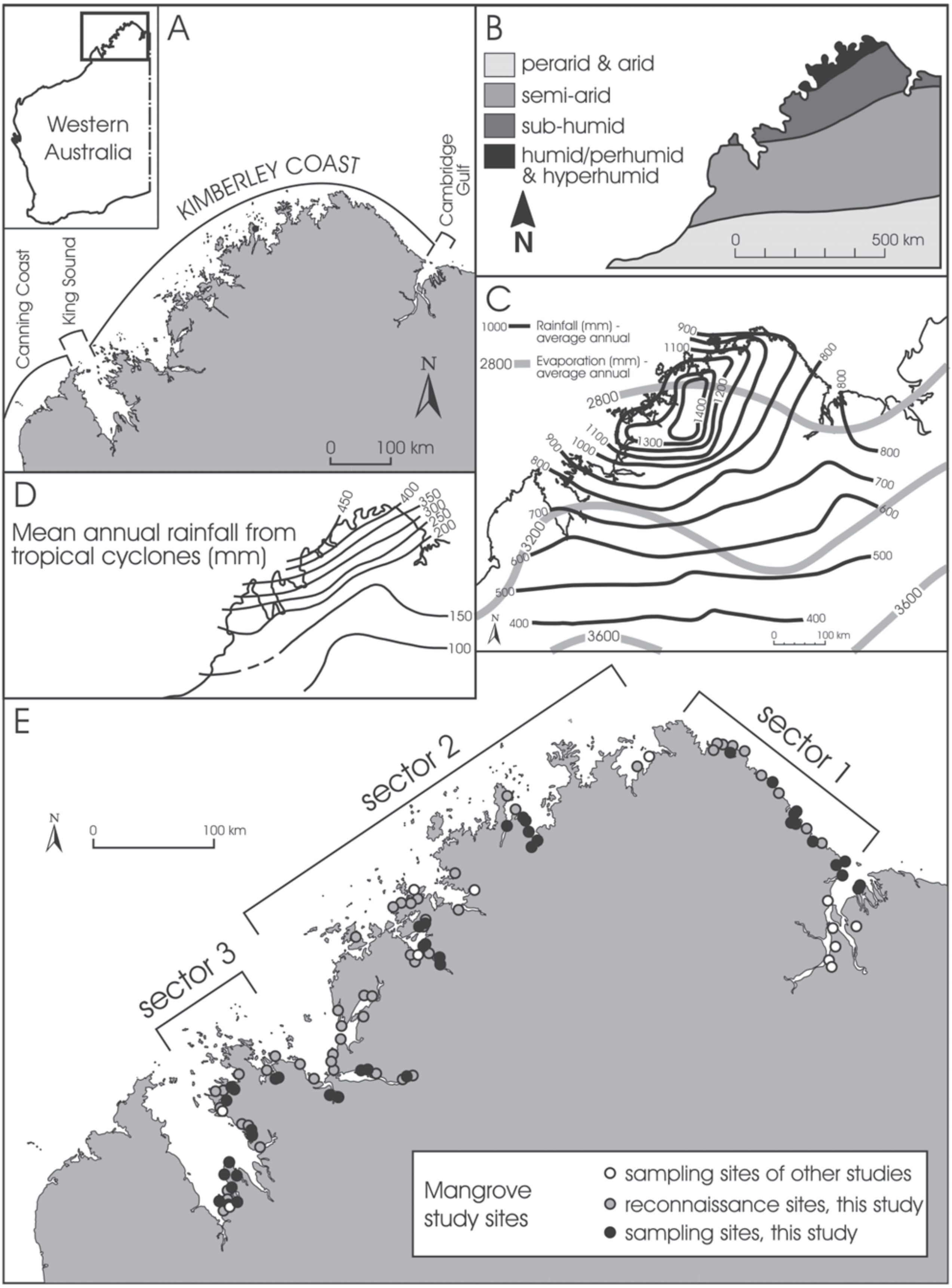


Figure 1. Location, climate and study sites. A. Location of the Kimberley Coast in north-western Australia. B. Climate map after Gentilli (1972). C. Map of rainfall and evaporation (from the Bureau of Meteorology 1973, 1975, 1988, 2010). D. Rainfall from tropical cyclones (after Lourenz 1981). E. Sampling sites this study, reconnaissance sites this study, and sampling sites from other studies.

Methods

The information presented in this paper derives from literature review and fieldwork. A description of the regional to local setting based on the geology, oceanography, tidal regime, climate, geomorphology and some mangrove ecology and biogeography was drawn from the literature and from fieldwork. The description of the geomorphic units and mangrove habitats has been based on extensive fieldwork over more than 40 years, and utilises the existing approach/terminology provided by Semeniuk (1986). In previous years, individual aerial photographs were used, which have been replaced in recent times with the use of satellite imagery and Google Earth, to identify large scale coastal types and finer scale mangrove settings. Field surveys were undertaken to investigate phototones and to describe habitats, substrate type, and mangrove associations and species. Field surveys were conducted over a number of years by road, helicopter, and boat. In general the approach adopted was to identify different "units" using remote sensing and to then ground truth and describe the physical setting and mangrove associations through site visits. At each site, substrate and salinity were noted and stratigraphy determined to ascertain broad compositions of mud, sand, gravel, and rock. Sampling sites in the Kimberley region are shown in Figure 1E.

Previous descriptions of the mangroves of the Kimberley Coast

Thom *et al*. (1975) were the first researchers to describe mangrove ecology in the Kimberley region. They noted the species in the southern Cambridge Gulf area, and described the relative abundance of mangrove species in a series of transects.

Saenger *et al*. (1977) noted the mangrove species across the subcontinent of Western Australia in terms of number of species and their decrease in species richness latitudinally. In describing mangrove distribution in Western Australia, Semeniuk *et al.* (1978) identified four biogeographic zones, assigning the Kimberley region to the zone 'tropic sub-humid'. Galloway (1982), in a description of the entire Australian mangrove coast, assigns the Kimberley area to a single "mangrove region" encompassing Cambridge Gulf, the Kimberley Coast and King Sound. Semeniuk (1983) described the relationship of mangroves to freshwater seepage, and recorded the species in the Kimberley region, and Semeniuk (1985) described mangrove habitats along the ria shorelines of northern Australia, including the Kimberley region, providing a habitat-oriented framework for understanding mangrove ecology. Wells (1985) undertook numerical analyses of mangroves along transects in the Port Warrender and Mitchell River areas, relating species and vegetation structure to riverine setting.

Bridgewater (1985) described the floristic variation along the Western Australia coast noting that "irrespective of local geomorphological differences, complexity of vegetation pattern in the mangal increases in a northerly direction, as a consequence of a greater species richness". He also attempted a phytogeographical analysis, based on the mangal plant communities. His analysis suggests three zones: temperate, extending north to Shark Bay; dry tropical, from Shark Bay to Cape Keraudren; and wet-dry tropical from Cape Bossut to Cape Hotham in the Kimberleys. Bridgewater noted the three zones correspond in some measure with those of Semeniuk *et al*. (1978). Johnstone (1990) in a study of avifauna habitats described the mangroves of the Kimberley region at 16 sites, noting species, some structure and associations.

Semeniuk (1993) described the mangrove systems of Western Australia, delimiting the Kimberley Coast as a tidally dominated coastal system bordered by two major elements, namely the tide-dominated deltaic systems of King Sound and Cambridge Gulf, and described the shoreline and fluvial inputs which control mangrove systems that occur there, providing examples of the mangrove settings and mangrove habitats present.

Saenger (1996), as part of a marine biological survey of the eastern Kimberley region, described the distribution of mangrove species and habitats. Following Thom *et al*. (1975), Semeniuk *et al*. (1978), Semeniuk (1983, 1985, 1993) and Semeniuk & Wurm (1987), Saenger (1996) described the mangroves and their setting at 17 sites.

Wells (2006) described a fringing vegetation survey of the mangroves undertaken opportunistically as part of another survey in 1977 of five tidal river systems, noting the presence and abundance of 14 vascular species, with some description of the vegetation formations and the salinity profiles of each river system. Following MacNae (1968), Wells (2006) described six habitat zones.

Definition of terms

It is important to define the use of the term "mangrove" to assess what to include or exclude in this paper, as it is a term variably used (MacNae 1968; Chapman 1977; Semeniuk *et al*. 1978; Hutchings & Saenger 1987; Tomlinson 1986, Duke *et al*. 1998). Duke *et al*. (1998), for instance, state that mangrove plants share a number of highly specialized adaptations to allow them to cope with regular inundation by salty waters, and list 39 species occurring in Australia and include ferns, creepers, and herbaceous plants. But use of the term in the literature is inconsistent, and some authors consider herbs in the tidal and shore environment to be mangroves, but exclude creepers and Chenopods. Others include Chenopods but not herbs and creepers/epiphytes. Yet others include all plants occurring in the tidal environment. No single definition has found consistent usage, and hence in this paper we elect to consider only the 'core set' of woody plants that are found within the tidal zone.

The term "mangrove" in this paper refers only to woody trees and shrubs that inhabit tidal environments between mean sea level (MSL) and the highest astronomical tide (HAT). The plants in this zone are anatomically adapted to deal with the tidal inundation, salt water, and anoxic substrate. We believe that in order to understand the biogeography of mangroves, it is necessary to exclude plants that fringe this environment such as samphires (Chenopods), herbaceous plants (*e.g.*, *Acanthus ebracteatus*), ferns (*e.g*. *Acrostichum speciosum*), strand plants (*e.g.*, *Hibiscus tilleaceus* and *Pemphis acidula*), as well as creepers and epiphytes that inhabit the trunks and foliage of any tidal woody plants. Thus we consider that not all plants that inhabit the tidal environment should be viewed as "mangroves". Also, in this paper, the term "mangrove" refers to individual plants inhabiting the tidal zone, while "mangal" refers to the assemblage or community of mangroves.

Definition of the Kimberley Coast based on geology and coastal landform

Following Semeniuk (1993), the Kimberley coastal region is divided into three natural geomorphic units, *viz.*, the Kimberley Coast (the subject area of this paper), King Sound (including Stokes Bay), and Cambridge Gulf (Fig. 1). The Kimberley Coast is the sector centred on the ria shores cut into the Precambrian massif of the Kimberley Basin and Halls Creek Orogen that (onshore) forms the Kimberley Plateau of (mainly) sandstone and (some) basalt (Griffin & Grey 1990a, 1990b). The Kimberley Coast is a rugged, dominantly rocky coastline with local sedimentary accumulations. Its geomorphology is dominated by fracture-controlled medium and short rivers that have incised deep valleys into the sandstone and basalt plateaux of the region. The geological grain, faults, and boundary between geological units (such as between Precambrian massifs and Phanerozoic rocks) have been selectively eroded to form major valley tracts such as the Fitzroy, May, and Meda Rivers.

The regional physical setting: climate, oceanography, and coastal processes underpinning the mangrove distribution and ecology

The Kimberley region is located in a tropical climate, with four climate subregions in terms of rainfall and evaporation (Fig. 1 modified after Gentilli 1972), subdivided into:

1. subhumid in the Cambridge Gulf area and north-eastern Kimberley Coast,
2. humid from Cape Londonderry to Prince Regent River, centred on Port Warrender,
3. subhumid between Prince Regent River and Yampi Sound,
4. semi-arid in the King Sound area.

Coastal rainfall influences local freshwater seepage, as well as the extent that saline high-tidal flats are developed. Evaporation is the other major co-determinant of the extent that high-tidal salt flats are developed. The overall climate, in particular the rainfall in the Kimberley Plateau, determines the extent of run-off into the rivers and the amount of freshwater and sediment delivered to the coastal zone.

The coastal zone of the Kimberley region is subject to four oceanographic processes: semi-diurnal tides, prevailing wind waves, swell, and cyclones.

Tidally, the Kimberley Coast is semi-diurnal, macrotidal with local areas being mesotidal. Tides are the major defining force along the coast in that they are pervasive regardless of coastal geometry, degree of shelter, and orientation (Semeniuk 2011). The next most important coastal process is wind waves. Where there is enough fetch (oriented in relation to wind directions), wind waves are effective in shaping coastal form and developing mangrove habitats. Wind waves are region-wide but have most influence where headland and coves face the wave direction, or where small islands act as foci for sedimentation. Though a year-round phenomenon, swell impinges on exposed coasts facing northerly to south-westerly sectors, but generally is dampened and refracted as it interacts with the shallowing near-shore shelf, and enters archipelago complexes and fracture-aligned deeply embayed rias. However, swell is not a major wave type in the region.

Cyclones regularly cross the Kimberley Coast on an inter-annual or seasonal basis. They result in highly localised but significant disturbance effects on shores from high seas, large waves and storm surges, and result in winnowing of existing sedimentary deposits, transport and emplacement of sediments at storm levels above and well above the high tide mark, and coastal erosion. They also result in major erosion into mangrove-vegetated tidal flats. The construction of sedimentary deposits above the high-tide mark creates aquifers for freshwater storage that can later discharge freshwater into the high tidal zone to influence vegetation. Also the massive influx of freshwater into the coastal zone during cyclones, results in physical transport of sediment from rivers/creeks to the high-tidal alluvial fans again creating new mangrove habitats, or maintaining high-tidal habitats.

The shores of the Kimberley Coast are highly indented and comprise south-facing, west-facing, and north-facing inlets and embayments, which apart from open gulfs, are mostly isolated from the open sea, being connected only by narrow channels. While most of the Coast is subject to inundation by high tides, storm surges and cyclone-induced high-water, there are many locations protected from swell, wind waves, and storm waves, and in these lower energy environments mangroves are best established.

The coastal processes of sedimentation, tidal erosion, wave action, storms and cyclones, combined with fluvial inputs create the complex habitats of the tidal zone. This region has a dynamic tidal zone not found in most other parts of the world, with massive erosion, or accumulation of sediments. Major cliffs can be cut into tidal mud, tidal channels incised, and sediment dumped into major shoals and creek-mouth fans. Superimposed on this is the longer time-frame of climatic variability in coastal processes, whereby erosion alternates with sedimentation. These processes and sedimentologic and geomorphic adjustments can occur on the small scale or large scale and over varying time frames (*cf.*, Thom *et al*. 1975; Semeniuk 1980; Fig. 2 this paper). The overall outcome of these processes is that mangrove habitats, rather than being an environment reflecting long term geomorphic, hydrologic, and hydrochemical stability, may locally be in flux. Consequently, the vegetation patterns in the mangal of the Kimberley Coast are complex with many differing expressions. For instance the mangal may be truncated, newly colonising recently adjusted surfaces, or in compositional chaos.

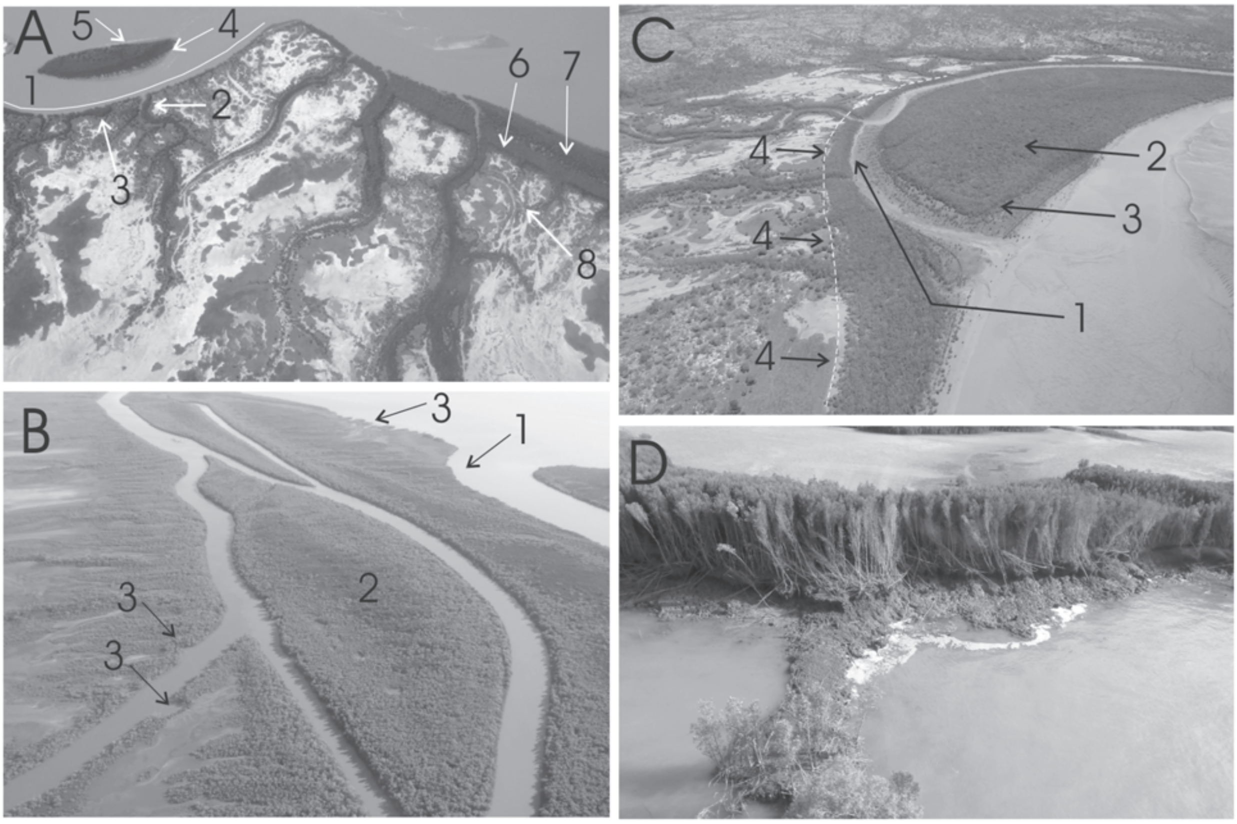


Figure 2. Aerial photographs showing evidence of the dynamic nature of the mangrove environments along the Kimberley Coast. A. Scour and fill and development of shoals: (1) large curvilinear eroded cliffed coast, here outlined by white line; (2) & (3) tidal creeks truncated by the cliffed coast; (4) accreted shoal with mangrove zones parallel to accreted margin; (5) accreted shoal with truncated mangrove zones; (6) former cliff cut into mud abutted by accreted ribbon of mud; (7) zoned mangrove parallel to accreted coast; (8) former history of accretion and erosion and (now) mud-filled tidal creek. B. Recent erosion and shoal development: (1) example of large scale active curvilinear erosion; (2) tidally oriented accreted mud shoal; and (3) examples of smaller scale erosion incising into the mangal. C. Large curvilinear erosional scar (1), with mangrove-vegetated accreted shoal to seaward (2), smaller more recent cliffs cut into the shoal and the mangal (3), and (4) former curvilinear erosional scar (outlined by white line) now stranded by accretion. D. Cliff cutting into mud, with truncation of *Ceriops* thickets.

Landscape, rivers and valleys as architecture to the mangrove habitats

Coastal forms in the Kimberley coastal region have been determined by the lithology and structure of regional geology, interfaces between major geological units, by marine inundation of onshore landforms, and by the sizes, shapes and configuration of rivers, creeks, their tributaries, and other valley tracts in the region, as controlled by geology. The horizontal nature of the lithologies, fault/fractures in the region, and the orogenic fold belts determine the underlying patterns to hinterland landforms and how these are expressed at the coast. Where they crop out along the shore, the rocks in the region define three main sectors of the Kimberley Coast (Fig. 1E):

Sector 1: sandstones of the north-eastern Kimberley coast, with fracture-controlled ravines and short rivers; this sector is the main landscape feature of the north-eastern coastal Kimberley region;

Sector 2: sandstones and basalt between Cape Londonderry and Collier Bay, with fracture-controlled ravines, and short river valleys cut into the sandstone, and more open embayments cut into basalt; this sector is the main landscape feature of the western coastal Kimberley region;

Sector 3: the extension of the King Leopold Orogenic WNW-oriented fold belt – which results in prominent WNW peninsulae (at various scales), inlets and embayments, lagoons, chains of islands, isolated or near-isolated linear high-tidal marine enclosures and, where fracture has influenced cross-oriented drainage, trellis-shaped inlets and embayments; this sector is the main landscape feature of the south-western coastal Kimberley region.

The sedimentary deposits along the Kimberley Coast have been described by Semeniuk (2011). The importance of these deposits is that, apart from rocky shores, a majority form the foundation to mangrove habitats in the region. The distribution of sediments along the Coast at the regional scale is shown in Figure 3. This provides an appreciation of the distribution of mangrove habitats along the Kimberley Coast showing those that are sand-dominated (portions of the coast that face open wave conditions) and that will be associated with barred lagoons, and those that are mud-dominated and occurring in the protected interior of large embayments, or deep embayments, or gulfs.

As noted earlier, an understanding of the distribution of mangroves along the Kimberley Coast requires viewing the system from a subcontinental perspective down to the local setting.

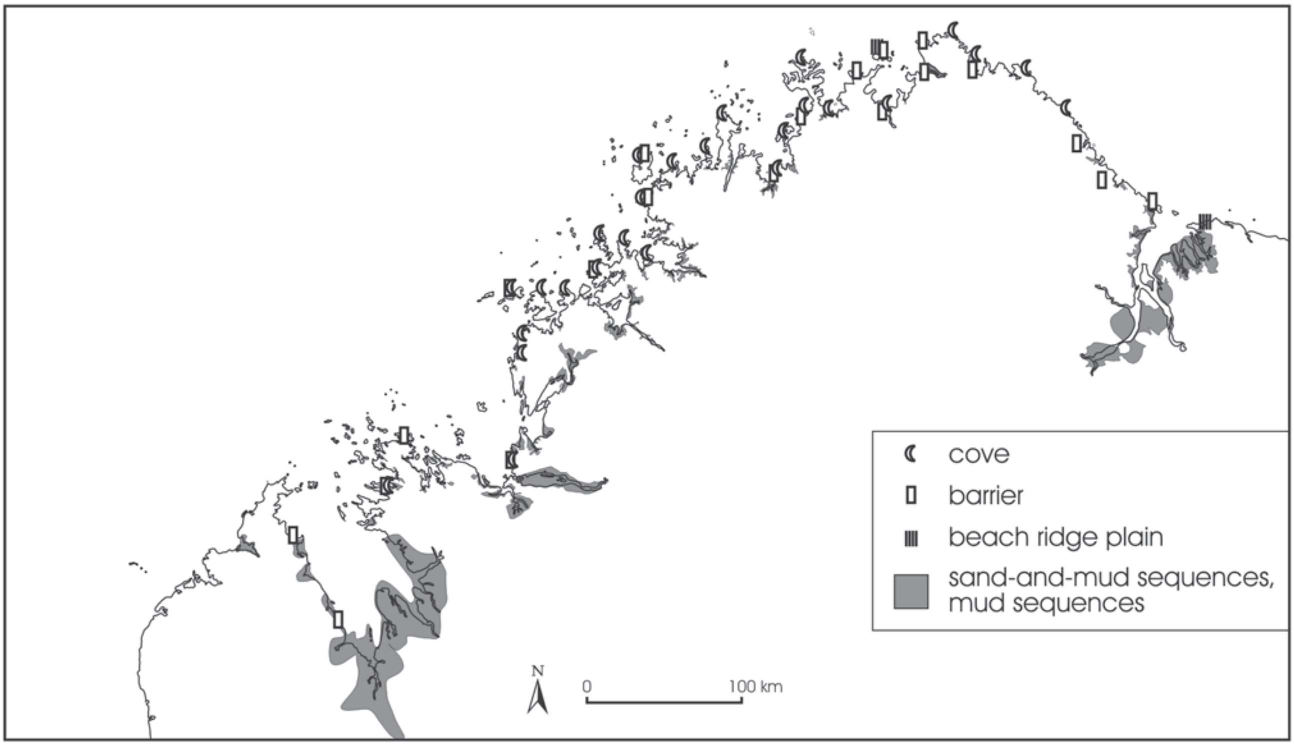


Figure 3. Coastal sediments along the Kimberley Coast (after Semeniuk 2011). The map shows the distribution of sandy coves, sandy barriers, beach ridge plains that are located on the wave exposed open coast, and the sand-and-mud deposits and mud deposits that occur in the interior of embayments and gulfs. The remainder of the coast is largely rocky shore or bouldery shores.

At the regional scale, Semeniuk (2011) describes eleven coastal settings that determine the oceanographic setting of the coast and the style of sedimentary accumulation, and hence which will differentially host mangroves; these are (Fig. 4): 1. large funnel shaped gulfs; 2. large narrow v-shaped gulfs; 3. large broad embayments; 4. medium-sized to small narrow v-shaped ravines and valleys; 5. medium-sized to small embayments and coves; 6. isolated inlets and lagoons; 7. rectilinear to rhomboidal intersecting embayment/inlet complexes; 8. archipelago-and-embayment complexes bordering the Kimberley Plateau; 9. archipelago-and-inlet complexes bordering the King Leopold Orogen; 10. straight rocky shores; and 11. scattered islands in an archipelago.

Depending on the orientation and the oceanographic aspect of these coastal forms, they experience a gradation of wave and tidal energy. They may be exposed to prevailing swell and wind waves and thus subject to high energy of waves and tides, or may be relatively protected from prevailing wave action and subject mainly to tidal currents, or may be fully protected from wave action and only inundated on the highest tide (slack-water, when mud settles from suspension on the high water). The coastal form, how much of it is subject to waves and tidal currents, and how much sediment is delivered to or generated at the site will determine the style of sedimentary accumulation and the nature of the mangrove habitat that will be developed.

At the large scale setting, the coastal habitats contain assemblages of finest scale mangrove habitats. The large scale coastal habitats identified are: 1. ria embayments; 2. bar-and-lagoon systems; 3. barred ravines; 4. gulfs; 5. tide-dominated deltas; 6. rocky coasts; and 7. beaches. The habitats present within these large scale settings are described in Table 1.

Table 1

Mangrove habitats developed within the large scale coastal habitats.

Large scale setting	Mangrove habitat in general order of abundance and extent
Ria embayments	muddy mid to high-tidal flats, tidal creeks, spits, cheniers, hinterland margin, high-tidal alluvial fan, rocky shore
Bar-and-lagoon systems	muddy high-tidal flats, sandy high-tidal flats, hinterland margin, high-tidal alluvial fan, rocky shore, sandy or gravelly barrier, dune margins
Barred ravines	muddy high-tidal flats, high-tidal alluvial fan, rocky shore, sandy or gravelly barrier
Gulfs	muddy tidal flats, tidal creeks, cheniers
Tide-dominated deltas	muddy tidal flats, tidal creeks, cheniers
Rocky coasts	rocky/bouldery shore, gravelly tidal flats
Beaches	sandy tidal flat, sandy slope

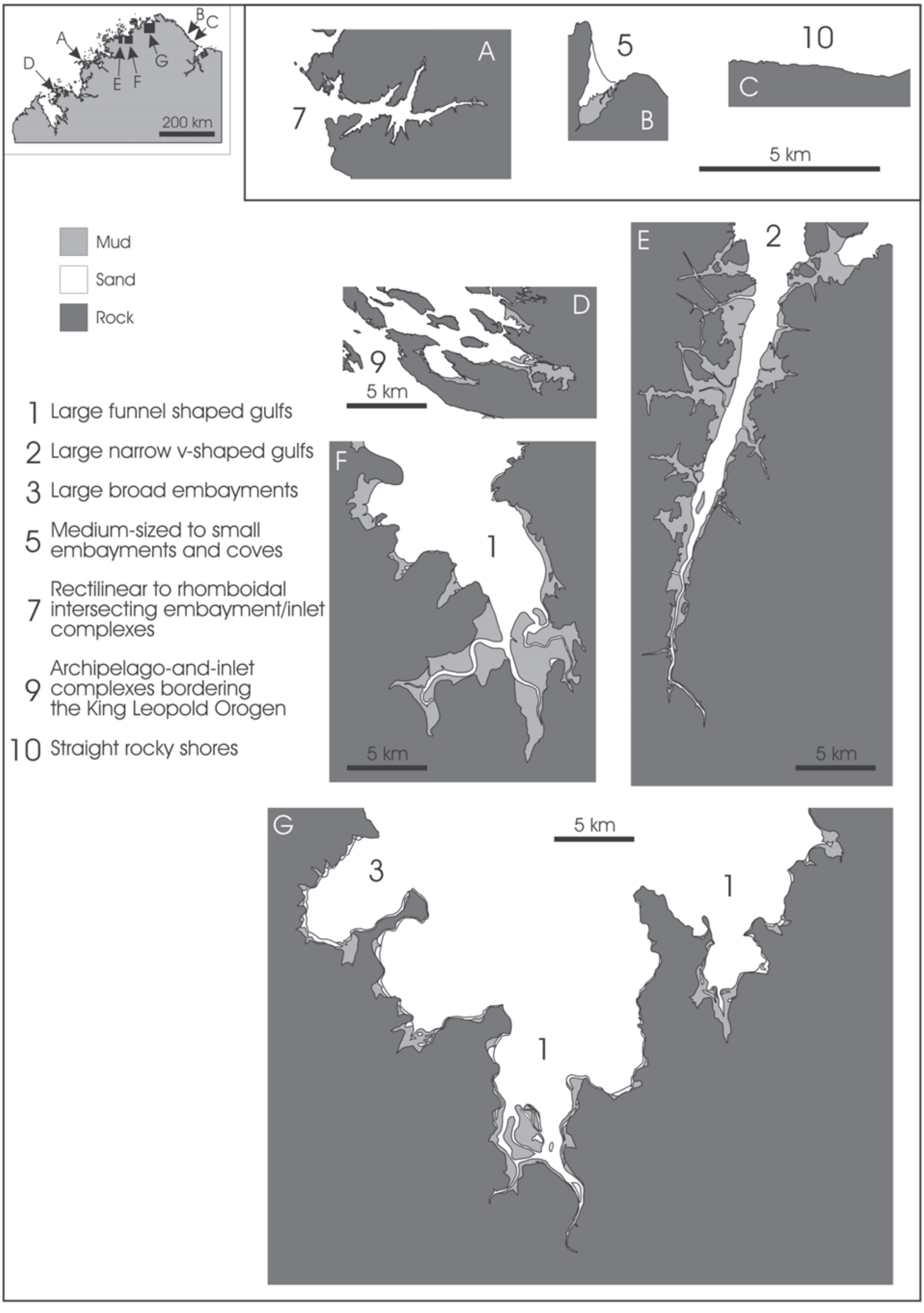


Figure 4. Coastal forms in the Kimberley region that determine (or influence) the nature and style of sedimentary accumulations and determine mangrove habitats (after Brocx & Semeniuk 2011). Bar scale for A, B, C, D, E, F & G is 5 km. The numbering reflects the eleven coastal forms mentioned in the text, and the letters A, B, C, etc. show the location of the example along the Kimberley Coast.

Table 2

Environmental characteristics of the mangrove habitat at the site-specific level

Habitat	Environmental characteristics of the mangrove habitat at the site-specific level
Tidal flat (muddy, sandy, or gravelly)	sloping low-gradient surface underlain mainly by mud, but also may be underlain by muddy sand or sand, or gravel; the surface is inundated by tides, with the mangrove seaward edge at ~ MSL and upper level at HAT; groundwater water salinity at ~ 40,000 ppm at MSL and increasing to 150,000–200,000 ppm at levels above MHWS; above ~ MHWS and salinity of 90,000 ppm, the surface is a salt flat; water table during neap tides usually shallow (< 50 cm); muddy tidal flats are slowly draining, while sandy tidal flats are more rapidly draining
Rocky/bouldery shore	generally moderately to steeply sloping rugged to vertical rocky surface, with shear surfaces, platforms, or fissured, variably covered in boulders, cobbles and pebbles, grading to bouldery shore that is a moderately to steeply sloping surface underlain by cobbles and pebbles; the surface is inundated by tides, with the mangrove seaward edge at ~ MSL and upper level at HAT; groundwater water salinity at ~ 40,000 ppm at MSL and increasing to 100,000 ppm at levels above MHWS; fissured rock is often a source of freshwater seepage discharging to sea and diluting the upper tidal level salinity; groundwater resides in its fracture porosity
Tidal creek bank	generally steeply sloping to vertical rocky surface cut into mud of tidal flat, and underlain by mud, with the mangrove seaward edge at ~ MSL and upper level at ~ MHWN; groundwater water salinity at ~ 40,000 ppm at MSL and increasing to 80,000 ppm at levels of MHWN; because of steep slope, the groundwater drains rapidly, and water table during neap tides is usually deep at bank edge (~ 1m, or > 1 m) grading to shallow (< 50 cm) upslope
Tidal creek point bar	generally low gradient moderately convex surface, underlain by sand, or muddy sand, or mud; mangrove seaward edge at ~ MSL and upper level at ~ MHWN; groundwater water salinity at ~ 40,000 ppm at MSL and increasing to 80,000 ppm at levels of MHWN; water table during neap tides usually shallow (< 50 cm)
Tidal creek shoal	generally low gradient hummocky or moderately convex surface, underlain by sand, or muddy sand, or mud; mangrove seaward edge at ~ MSL and upper level at ~ MHWN; groundwater water salinity at ~ 40,000 ppm at MSL and increasing to 80,000 ppm at levels of MHWN; water table during neap tides usually shallow (< 50 cm)
Hinterland margin	generally low gradient narrow habitat that adjoins the high tidal flat and the hinterland, underlain by muddy gravel, sandy gravel, sand, or muddy sand; mangroves at ~ HAT; groundwater water salinity at hinterland edge variable depending on freshwater seepage (10,000–90,000 ppm) to higher salinity towards salt flat; water table during neap tides usually shallow (< 50 cm); hinterland itself is usually fissured rock and is a source of freshwater seepage discharging to sea and diluting the upper tidal level salinity; groundwater resides in hinterland bedrock in its fracture porosity
High-tidal alluvial fan	generally low gradient triangular to fan shaped habitat that adjoins the high tidal flat and the hinterland in the headwaters of an embayment; underlain by muddy gravel, sandy gravel, sand, or muddy sand; mangroves at ~ HAT to MHWS; groundwater water salinity at hinterland edge variable depending on freshwater seepage (1000 10,000–90,000 ppm) with higher salinity towards salt flat; water table during neap tides usually shallow (< 10 cm); rivulet or small stream is the source of the sediment that underlies the alluvial fan and is the source of freshwater seepage discharging to sea and diluting the upper tidal level salinity; the habitat and its vegetation may grade upslope above HAT into freshwater wetland habitats
Beaches	moderately sloping surface underlain by sand or shelly sand; the sloping surface is inundated by tides, but the upslope part may be emergent above the level of HAT with development of dunes; mangrove seaward edge at ~ MSL and upper level at MHWS; groundwater water salinity at ~ 40,000 ppm at MSL and increasing to 60,000 or 70,000 ppm at levels above MHWS; the dune hinterland or the bedrock hinterland that adjoins the beach, occurring above HAT, stores freshwater or brackish water that discharges to seaward and dilutes the groundwater salinity that is under the tidally inundated beach slope; water table during neap tides on slopes of beach usually shallow (< 50 cm), but may be up to 1 m deep
Spits	Convex bar or finger of sediment underlain by sand or gravel, or gravelly sand, emanating from a headland; margins of the spit are sloping low-gradient surfaces; the sloping surfaces are inundated by tides, but the crest may be emergent above the level of HAT; mangrove seaward edge at ~ MSL and upper level at MHWS; groundwater water salinity at ~ 40,000 ppm at MSL and increasing to 60,000 – 70,000 ppm at levels above MHWS; the core of the spit, particularly if emergent above HAT, stores freshwater or brackish water that discharges to seaward and dilutes the groundwater salinity that is under the tidally inundated spit margin; water table during neap tides on slopes of spit usually shallow (< 50 cm)
Cheniers	convex bar or finger of sediment underlain by sand or gravel, or gravelly sand, but isolated on the tidal flat, often surrounded by salt flat; margins of the chenier are sloping low-gradient surfaces; the sloping surfaces are inundated by tides, but the crest is emergent above the level of HAT; mangrove seaward edge at ~ MHWS and upper level at HAT where there is fresher-water discharge; groundwater water salinity at ~ 70,000– 90,000 ppm at MHWS and decreasing to 10,000 ppm at levels above MHWS; the core of the chenier, particularly if emergent above HAT, stores freshwater or brackish water that discharges to seaward and dilutes the groundwater salinity that is under the tidally inundated chenier margin; water table on slopes and margins of chenier during neap tides usually shallow (< 50 cm)

Table 2 (cont.)

Habitat	Environmental characteristics of the mangrove habitat at the site-specific level
Barriers	similar to a spit, but the sedimentary body fully bars the entrance to an embayment; the barrier is a convex bar or finger of sediment underlain by sand or gravel, or gravelly sand, bridging the headland of an embayment; margins of the barrier are sloping low-gradient surfaces; the sloping surfaces are inundated by tides, but the crest is emergent above the level of HAT; mangrove seaward edge at ~ MSL and upper level at MHWS; groundwater water salinity at ~ 40,000 ppm at MSL and increasing to 60,000 or 70,000 ppm at levels above MHWS; the core of the barrier stores freshwater or brackish water that discharges to seaward and dilutes the groundwater salinity that is under the tidally inundated spit margin; water table on slopes of barrier during neap tides usually shallow (< 50 cm)
Dune margin	generally low gradient narrow habitat that adjoins supratidal sand dunes, underlain by sand or muddy sand; mangroves at ~ HAT; groundwater water salinity at dune edge variable depending on freshwater seepage (10,000–90,000 ppm) increasing to higher salinity towards salt flat; water table during neap tides usually shallow (< 50 cm); dune sands are a source of freshwater seepage discharging to sea and diluting the upper tidal level salinity

The finest site-specific mangrove habitat scale (after Semeniuk 1985, 1993) in general order of abundance and extent of mangrove cover, are: 1. tidal flat; 2. rocky/bouldery shore; 3. tidal creek bank; 4. tidal creek point bar; 5. tidal creek shoal; 6. hinterland margin; 7. high-tidal alluvial fans; 8. beaches; 9. spits; 10. cheniers; 11. barriers; and 12. dune margin.

Within each habitat there are gradients of environmental conditions (decreasing tidal inundation, increasing groundwater salinity, decreasing groundwater salinity towards sources of freshwater, or progressive change in sediment grainsize). In response to these gradients and their combinations along the habitat slope, zonation of mangrove species takes place across a given habitat. Environmental characteristics that are important to mangroves at the site-specific habitat level are described in Table 2.

Distribution of mangroves in the Kimberley region (the regional species pool)

Determining the occurrence and distribution of mangrove species in the Kimberley region, whether through the literature, herbaria records, or field work (in order to determine what might be present in a given coastal sector) is difficult for several reasons:

1. species do not occur consistently within an environmental setting;
2. not all species will be present in a given locality even if (apparently) appropriate habitats are present;
3. species richness progressively decreases along the coast from the species-rich northern Australia to the Kimberley Coast, and locally increases in the Kimberley region in relation to subregional increase in rainfall; and
4. the "regional species pool" is not well delineated or determined due to incomplete literature both in terms of geographic scope and sampling.

In the first instance, use of the literature to determine where mangroves occur is not reliable, as the records of species occurrences are related to type and effort of sampling. For example, consider the species recorded to date in the Point Walsh, Port Warrender area: Semeniuk (1985) records thirteen species of mangrove (*Avicennia marina*, *Aegialitis annulata*, *Aegiceras corniculatum*, *Bruguiera exaristata*, *Bruguiera parviflora*, *Camptostemon schultzii*, *Ceriops tagal*, *Excoecaria agallocha*, *Lumnitzera racemosa*, *Osbornia octodonta*, *Rhizophora stylosa*, *Sonneratia alba*, and *Xylocarpus* sp) while Johnstone (1990) records only eleven species (with *Bruguiera parviflora* and *Lumnitzera racemosa* not recorded). The mangroves recorded by Semeniuk (1980, 1983) at Stokes Bay and at Derby total eleven and ten species, respectively (*viz*., *Avicennia marina*, *Aegialitis annulata*, *Aegiceras corniculatum*, *Bruguiera exaristata*, *Camptostemon schultzii*, *Ceriops tagal*, *Excoecaria agallocha*, *Osbornia octodonta*, *Rhizophora stylosa*, and *Xylocarpus moluccensis*; with *Bruguiera parviflora* at Stokes Bay only) while Johnstone records only six species. Using the information in Johnstone (1990) would distort the picture of the regional species pool in that the local biodiversity at Port Warrender would be underestimated and the southern extensions of key species (such as the occurrence of *Bruguiera parviflora* at Stokes Bay) would be missing.

Similarly a comparison between Thom *et al*. (1975), Johnstone (1990) and Saenger (1996) of the number of mangrove species in the general Cambridge Gulf region, shows variation in species richness due to sites visited, taxonomic changes, habitats sampled, and sampling effort. Thom *et al*. (1975), in the general Cambridge Gulf region record seven species, Johnstone (1990) in the southern Cambridge Gulf region records nine species, and Saenger (1996) in the northern Cambridge Gulf region records eleven species. In the Cape Domett area of northern Cambridge Gulf, Thom *et al*. (1975) record three species, while Saenger (1996) in the northern Cambridge Gulf region records ten species.

The variation in survey results, in part, reflects ecological variation. *Sonneratia alba*, for example, a mangrove that commonly occupies the seaward fringe, does not always occur in this seaward location/habitat, rendering difficult the characterisation of the regional species pool by literature review and herbaria records. Similarly, the preferred habitats for some species are not consistently developed from site to site and the species will be locally absent, again rendering difficult the characterisation of the regional species pool by literature review and herbaria records.

Surveys of mangroves often concentrate on the main shore-parallel stands of mangroves, with documentation of zonation, and here *Sonneratia alba*, *Avicennia marina*, *Rhizophora stylosa* and *Ceriops tagal* will be the most obvious, and thus recorded. But unless the researchers have traversed the mangroves in a number of transects, any understorey of low abundance and scattered species, *Aegialitis annulata*, for instance, may be missed, and if there is no focus specifically on shore-transverse tidal creeks, *Aegialitis annulata*, *Aegiceras corniculatum* and *Camptostemon schultzii* may also be missed.

Figure 5 illustrates the principle of variability of mangal composition depending on sampling location and habitat complexity. In this example a shore-normal, elongate, small island (with a seaward bouldery shore) acts as an anchor for a sandy tombolo. There are several mangrove habitats present: a rocky shore, bouldery shore, a shore-normal sandy tombolo (equivalent to a high-tidal spit), a gravelly tidal flat, muddy tidal flat, hinterland margin, and a sand spit (located in the middle extreme right of the image). The mangrove habitat at approximately MSL varies from right to left, which is reflected in a change in mangal composition from a *Sonneratia* and *Avicennia* association and an upper slope occurrence of *Rhizophora* on right and left flanks to dominantly an *Avicennia* stand in the central seaward area. *Rhizophora* is most abundant and forms a dense copse on the left side of the tombolo. The mangal fringing the tombolo is asymmetric in its composition, with *Avicennia*, *Ceriops*, and *Bruguiera* forming denser formations on the left flank. There is mangal fringing the sand spit. The sand spit also is a reservoir for freshwater, which discharges in a series of (six) small "rivulets" that are inhabited by mangrove shrubs.

As mentioned above, researchers tend to focus on the main mangrove stand, documenting the species in the shore-parallel zonation, but the minor landward fringe comprised of scattered shrubs, the headwaters of ria embayments, and margins of spits and cheniers (where again there are only fringing narrow stands of scattered shrubs) may not be examined. It is in these latter locations that *Ceriops tagal*, *Excoecaria agallocha*, *Lumnitzera racemosa*, *Scyphiphora hydrophylacea* and *Xylocarpus moluccensis* occur (as well as the other species considered by other authors to be mangroves, *viz*., *Acanthus ebracteatus* and *Pemphis acidula*), and if there is to be a robust analysis of the progressive change in the regional species pool against climate gradients and local habitats, these latter habitats would need to be systematically examined.

The records of mangrove species along the Kimberley Coast in the literature, and indeed the sparse records lodged as specimens in herbaria (see Fig. 6) are not reliable sources of information to establish occurrences of species in the region, or even whether a given species occurs at a given site, due to the limited sampling effort

Figure 5. Oblique aerial photograph illustrating the variability of mangal composition along and across the shore in relation to habitat type, substrates, tidal levels, and freshwater seepage (see text for more detailed description).

and method carried out along the Kimberley coastal region to date, the patchiness of species occurrence, the serendipitous nature of the occurrence of some species, and the habitat-specific nature of other species. Yet, this type of information is fundamental to assessing change in biodiversity of mangroves gauged against various parameters of the climate gradient and freshwater seepage. The surveys of mangroves in the northern and north-eastern Kimberley area by Saenger (1996) illustrate the problems of opportunistic and *ad hoc* collecting, sampling without a habitat framework (as distinct from identifying the habitat type at the sampling site), and the difficulties in determining an inventory of the regional species pool that would form the foundation to determining and predicting the habitat-specific biodiversity. Notwithstanding logistic difficulties such as the pressure of lack of time as a factor in sampling effort, variations in records of species can result from how the mangrove surveys are approached. Researchers surveying by boat tend to access the mangroves from the seaward edge, usually on a mid-tide, and have to traverse thick stands of mangroves to sample within the mangal and to sample the hinterland fringe or the high-tidal alluvial fans. As a result, usually only one traverse might be made, and the hinterland fringe is often not fully surveyed. Researchers accessing the shore by road tend to access the mangroves from the landward edge, and may have to traverse thick stands of mangroves to sample the seaward fringe. As a result, for land-based surveys, the hinterland fringe, high-tidal alluvial fans, rocky shores, and spits may be reasonably sampled, but variations in the main mangrove stand, especially the occurrence of understorey species, such as *Aegialitis annulata*, or patchy copses of *Osbornia octodonta*, may be missed.

Remote sensing (aerial surveys, aerial photography, satellite imagery) enables researchers to note the general zonation and distribution of species in a mangrove system. Low-altitude aerial surveys allow, at best, identification of key species such as *Sonneratia alba*, *Avicennia marina*, *Rhizophora stylosa*, *Ceriops tagal*, *Lumnitzera racemosa*, *Camptostemon schultzii*, and *Xylocarpus moluccensis*, but do not allow for identification of understorey species or between species of *Bruguiera*. Helicopter surveys allow for closer-to-ground flight paths, and hovering, and hence clearer identification of key species from low-altitudes, and also allow for landings whereby specific trees of a given height, physiognomy, or canopy colour can be differentiated (*e.g.*, the species of *Bruguiera*, or the species of *Xylocarpus*). Generally the similar morphology and leaf 'greenness' makes it very difficult to accurately attribute species with remote sensing.

The habitat-directed approach adopted by Semeniuk (1985) and Semeniuk & Wurm (1987), wherein every habitat is identified and sampled, provides a systematic method of determining the species pool at a given site because species often form assemblages related to habitat, or tend to prefer specific habitats (e.g., *Osbornia octodonta* is commonly found on sandy beaches where there is beach rock, *Lumnitzera racemosa* is commonly found along the hinterland fringe, and *Camptostemon schultzii*, *Aegialitis annulata*, and *Aegiceras corniculatum*, singularly or collectively, are commonly found along tidal creek banks). With this approach, sampling all habitats in a given locality is likely to capture all the mangrove species occurring at that locality and the absence or presence of a given species can be assessed in context.

While sampling style and effort will determine whether a given species is recorded in an area, in some locations habitats may not be developed, so particular species will be absent from the site. Conversely, other natural processes may preclude some species even though their preferred habitat is present. Also, very local and recent coastal history of erosion and sedimentation may result in the elimination of characteristic zonation and predicable occurrence of species and, instead, is replaced with an (erosionally) truncated zonation (Fig. 2D), or with a chaotic mixture of species (as the environment adjusts to an altered and dynamic hydrology and hydrochemistry).

Given these complications, nonetheless, we have endeavoured to provide an overview of the mangroves of the Kimberley region from a perspective of species distribution to determine what species are available locally to colonise the various habitats of the Kimberley Coast. To achieve this, we note the occurrence of a given species in tropical humid northern Australia as recorded in the literature, and its most southern occurrence in Western Australia. We have then presumed that the biogeographic range of the target species will encompass the most northern localities in Western Australia as well as its most southern localities, with confirmation of sites between these two extremes from records in the literature. Following this, site-specific occurrences and habitat-specific occurrences of any given species, and habitat-specific assemblages are drawn from this "regional species pool". If a species is absent at a given location, but is within its biogeographic range, this may be due to climate setting, lack of habitat, or the local history of erosion and sedimentation, amongst other factors.

Overall, with the exclusion of *Acanthus ebracteatus* and *Pemphis acidula,* there are 15 species of mangroves along the Kimberley coast, though they are not present consistently and ubiquitously throughout the region. For this paper, the entire Kimberley region is treated as the one regional species pool, with local climate and habitat factors selecting for mangroves species that will occur at a given site. In order of general abundance and relatively consistent occurrence through the region, the species are placed in three groups: generally abundant and consistently present; generally present, though not abundant and consistently present; generally not abundant nor consistently present). The composition of these groups are:

1. Generally abundant and consistently present: *Avicennia marina*, *Rhizophora stylosa*, *Ceriops tagal*, *Sonneratia alba*, *Camptostemon schultzii*, *Aegialitis annulata*, *Aegiceras corniculatum*, *Bruguiera exaristata*, *Lumnitzera racemosa*, and *Excoecaria agallocha*.

2. Generally present, though not abundant and consistently present: *Bruguiera parviflora*, *Osbornia octodonta*, and *Xylocarpus moluccensis*.

3. Generally not abundant nor consistently present: *Scyphiphora hydrophylacea* and *Xylocarpus granatum.*

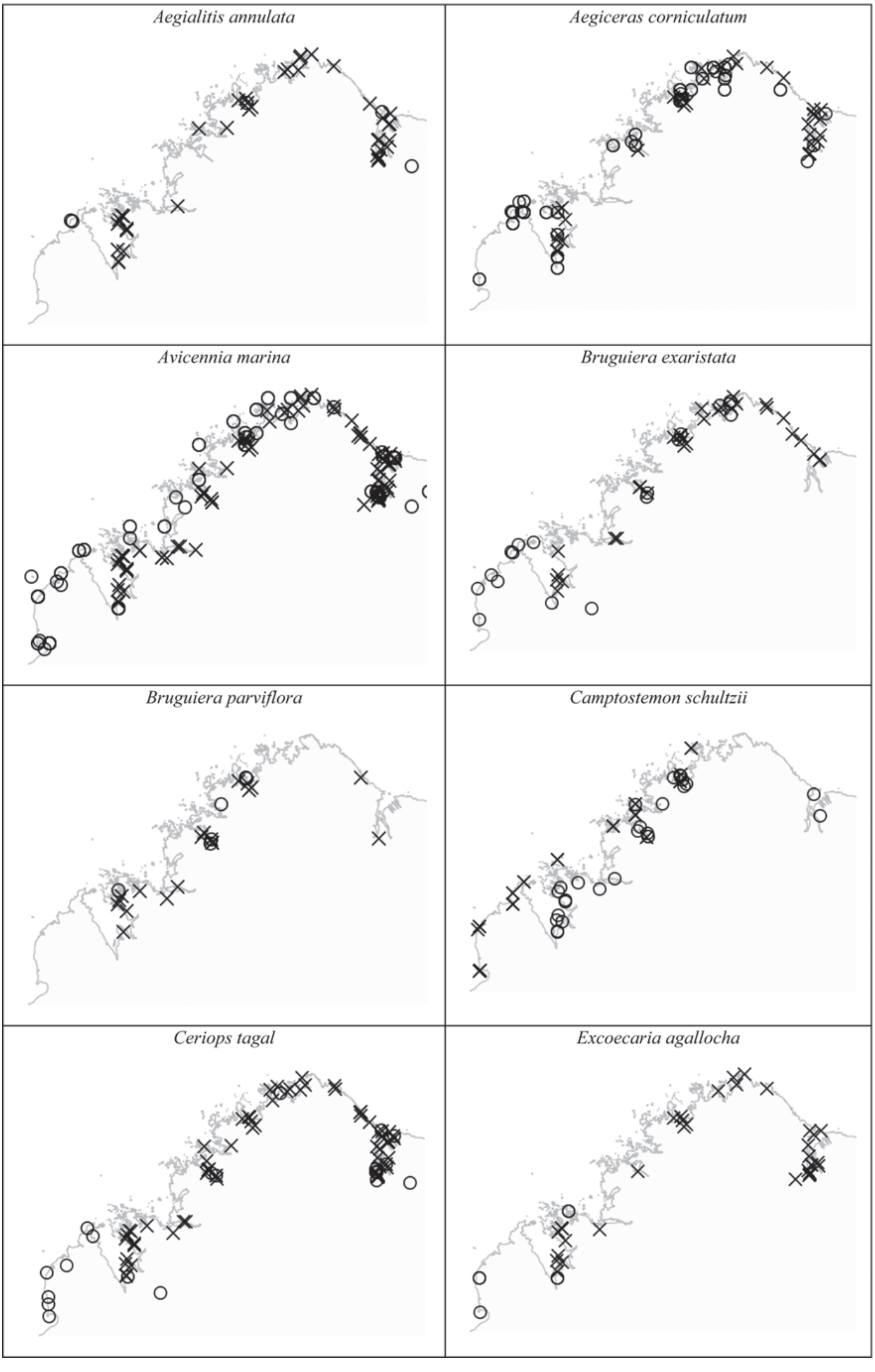


Figure 6. Distribution of the key species of mangroves according to herbaria records (via Atlas of Living Australia), studies by other authors as mentioned in the text, and our studies.

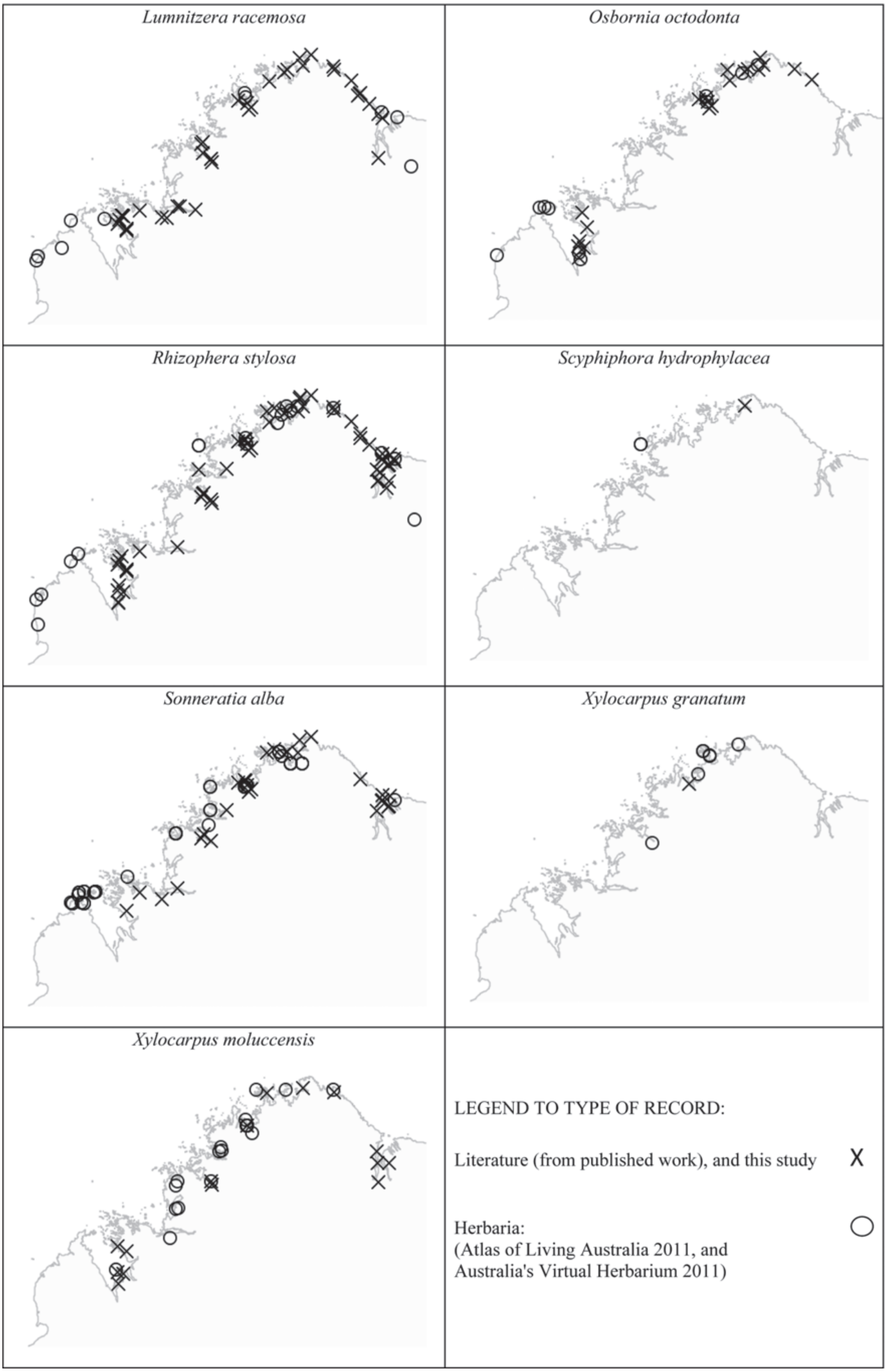


Figure 6 (cont.)

Avicennia marina, *Rhizophora stylosa*, and *Ceriops tagal* are the most common and ubiquitous species in the region. [*Avicennia eucalyptifolia* listed in Thom *et al*. (1975) and Semeniuk *et al*. (1978) has been taxonomically re-assigned to a variety of *Avicennia marina* (Duke 2006). The varieties of *Avicennia marina* are not distinguished in this paper.]

Overview of the distribution of mangrove species in the Kimberley region determined by regional abiotic factors

There are two major gradients that determine species richness along the Kimberley Coast: 1. the general decline in species richness towards the Kimberley from the species-rich humid northern Australian region; and 2. the climate gradient *within* the Kimberley region.

In the first instance, mangrove species richness decreases from the species-rich humid northern Queensland coast and the humid Darwin area (where there are some 39 species and 31 species of mangroves, respectively (Duke (2006)) to the Kimberley region, where there are less than 20 species (using our definition there are only 15 species). As noted earlier, there is a climate gradient *within* the Kimberley region from subhumid and semiarid in the Cambridge Gulf and King Sound areas, respectively, to humid in the central Kimberley Coast, with an increase in mangrove diversity towards this humid centre. From humid northern Australia to mid-western Western Australia, the limits of key species are listed in Table 3.

Of these 15 "core" species of mangroves in the Kimberley Coast region, *Xylocarpus granatum* is localised in the humid Port Warrender region, and *Scyphiphora hydrophylacea* extends from northern Australia to the Drysdale River region only. The distribution of mangrove species in the Kimberley region is shown in Figure 6.

Mangrove assemblages along the Kimberley Coast with respect to habitats

As noted above, 15 mangrove species are regionally widespread and available to inhabit the various coastal types and appropriate habitats. Thus habitats will, to a large extent, determine the species of mangrove that will occur in a site-specific area, with colonisation underpinned by the driving factors of tidal level, substrate types, hydrology, prevailing soil moisture, salinity, freshwater seepage, and air temperature. Aspects of habitats and the occurrence of habitats as suites within a coastal setting are illustrated and explained in Figures 7–10. Figure 7 shows the most common coastal settings in the region and the suites of habitats that occur within them. Figures 8 and 9 show the habitat elements of ria embayments and the mangroves inhabiting them. Figure 10 shows a suite of habitats within a ria embayment and the hydrological/hydrochemical mechanisms maintaining the mangroves. Aerial photographs of typical habitats and mangals along the Kimberley Coast are illustrated in Figures 11 and 12.

While species such as *Avicennia marina* can be inundated for up to 6 hours a day, survive salinities of up to 90,000 ppm, and inhabit substrates of rocky shores, sand, or mud (as such, it is the species that is most widespread across a variety of habitats), various other mangrove species clearly are adapted to different and specific environments in the tidal zone. *Scyphiphora hydrophylacea*, for instance, inhabits the highest tidal zone along hinterland margins with freshwater seepage, and is not found in the main belt of mangroves, and certainly not at the seaward fringe. *Camptostemon schultzii* preferentially inhabits muddy tidal creek banks, where it is inundated for several hours a day, but where tidal creek banks rapidly drain tidal groundwater.

While the combination of environmental conditions suitable for a given species to survive can be created in a

Table 3

Limits of mangrove species latitudinally/longitudinally in Western Australia

Species	Most southern or western occurrence	Coordinates
Scyphiphora hydrophylacea	Drysdale River	14°12'28.99"S 126°38'36.23"E
Xylocarpus granatum	Port Warrender	15°17'54.65"S 127°17'24.57"E
Bruguiera parviflora	Stokes Bay	35°37'46.44"S 137°12'12.55"E
Camptostemon schultzii	Broome	17°57'43.62"S 122°14'10.05"E
Lumnitzera racemosa	Broome	17°57'43.62"S 122°14'10.05"E
Xylocarpus moluccensis	Broome	17°57'43.62"S 122°14'10.05"E
Sonneratia alba	Cape Bossut	18°43'0.00"S 121°37'60.00"E
Excoecaria agallocha	De Grey River delta	20°18'7.53"S 119°15'58.50"E
Osbornia octodonta	Cossack	20°18'7.53"S 119°15'58.50"E
Aegiceras corniculatum	Maitland River delta	21°13'40.84"S 116°53'6.77"E
Bruguiera exaristata	Maitland River delta	21°13'40.84"S 116°53'6.77"E
Ceriops tagal	Exmouth Gulf	22°53'34.40"S 114°31'22.27"E
Aegialitis annulata	Exmouth Gulf	21°13'40.84"S 116°53'6.77"E
Rhizophora stylosa	Yardie Creek and Exmouth Gulf	22°28'32.22"S 113°57'9.07"E
Avicennia marina	Bunbury	33°19'37.44"S 115°38'21.03"E

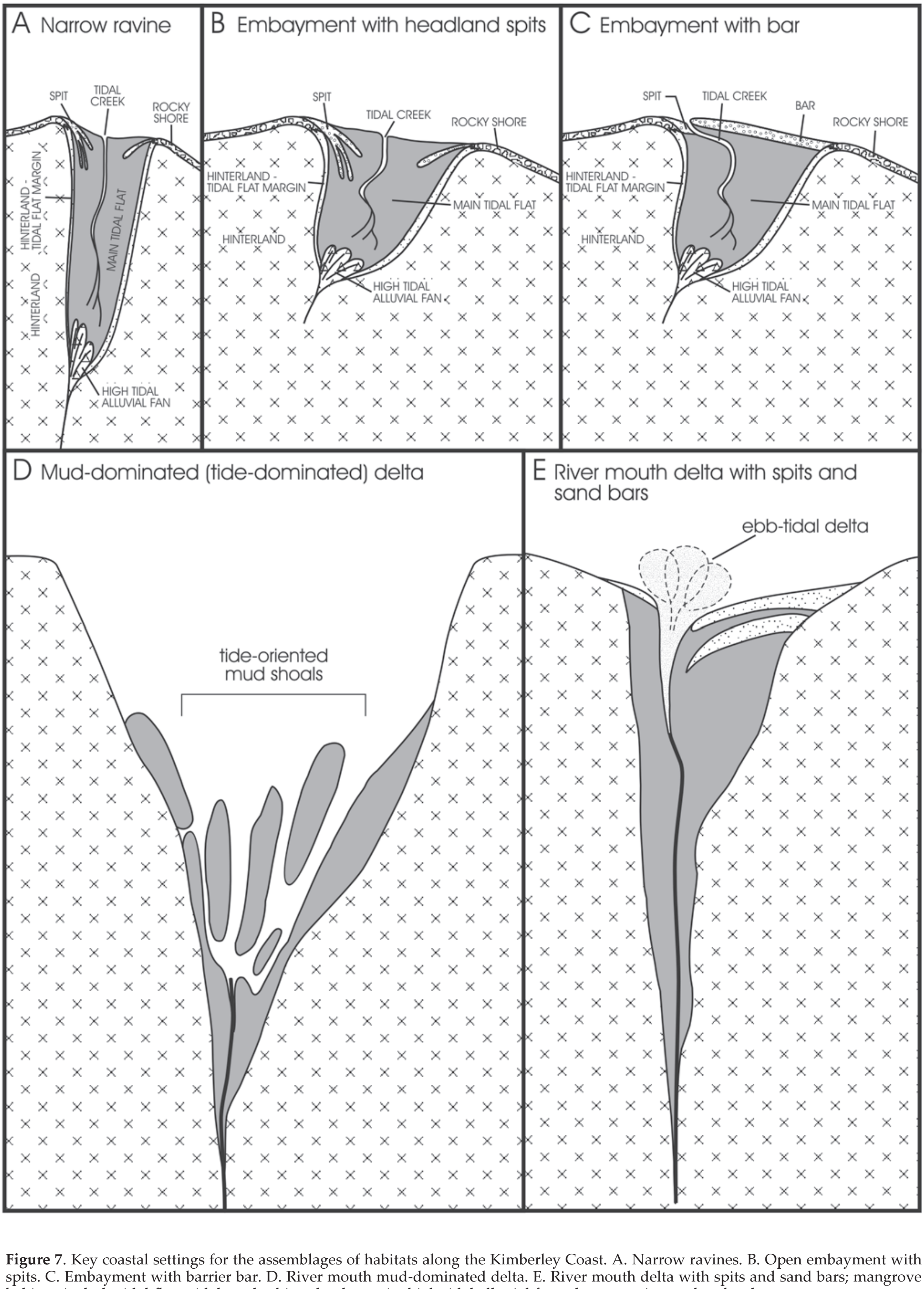


Figure 7. Key coastal settings for the assemblages of habitats along the Kimberley Coast. A. Narrow ravines. B. Open embayment with spits. C. Embayment with barrier bar. D. River mouth mud-dominated delta. E. River mouth delta with spits and sand bars; mangrove habitats include tidal flats, tidal creeks, hinterland margin, high-tidal alluvial fans, dune margins, and rocky shores.

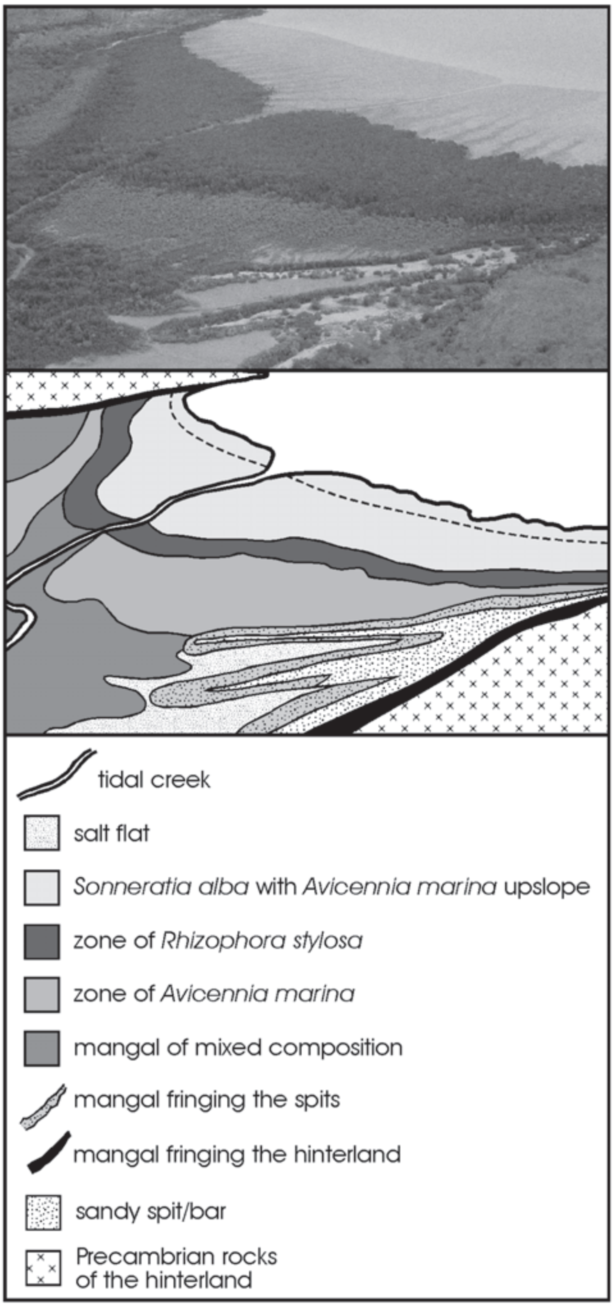


Figure 8. Mangrove habitats in a ria coastal setting: an embayment with tidal flat, tidal creek, spits, and hinterland margin. The mangal across the tidal flat is clearly zoned.

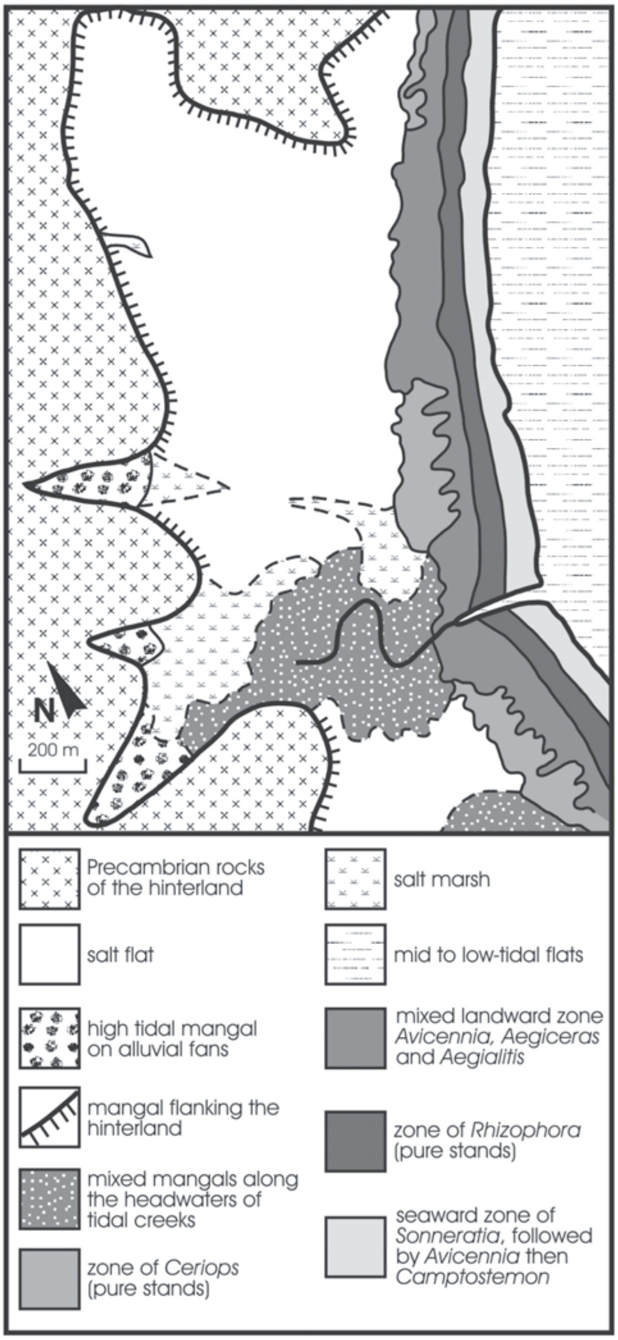


Figure 9. Embayment along ria coast in the Port Warrender area showing the mangrove habitats and species (modified from Semeniuk 1983).

number of habitats, often there is a preferred habitat for a species or an association of species, and each habitat is suitable for only a limited range of species. The high-tidal alluvial fan, tidally inundated infrequently, with fresh water seepage illustrates this. With low seepage rates, it is the habitat of *Avicennia marina*, *Excoecaria agallocha* and *Lumnitzera racemosa*; with high seepage rates, it is the habitat of *Avicennia marina*, *Xylocarpus sp*, *Excoecaria agallocha* and *Lumnitzera racemosa*, and can also support *Bruguiera exaristata*, *Bruguiera parviflora*, and *Ceriops tagal*. The seaward edge of mangal inhabiting muddy tidal flats is the habitat of *Avicennia marina* and/or *Sonneratia alba*. Table 4 presents for each mangrove habitat along the Kimberley Coast the species that occur (*i.e.*, supported by that habitat). Some typical mangrove formations, in terms of their assemblage composition, structure, and physiognomy, in various habitats along the Kimberley Coast are shown in Figure 13.

Table 4 presents a generalised description of species that occur with the habitats along the Kimberley Coast, but because of local climate factors or because of more pronounced freshwater seepage (due to hinterland drainage), there is subregional variation in mangrove assemblages within habitats. The key habitats that

Table 4

Mangrove species and species associations inhabiting the various habitats along the Kimberley Coast

Habitat	Species and species associations
Tidal flat (muddy tidal flats)	zoned mangroves, with seaward *Avicennia marina* and/or *Sonneratia alba*, followed to landward by *Rhizophora stylosa*, then *Bruguiera exaristata* (and *Bruguiera parviflora*), *Ceriops tagal* and to landward *Avicennia marina*
Rocky/bouldery shore	zoned mangroves, with seaward *Avicennia marina* followed to landward by *Rhizophora stylosa*, then *Ceriops tagal* and *Avicennia marina*
Tidal creek bank	zoned mangroves, with seaward *Avicennia marina* and/or *Camptostemon schultzii*, with *Aegialitis annulata* and *Aegiceras corniculatum*, followed to landward by *Rhizophora stylosa*
Tidal creek point bar	zoned mangroves, with *Avicennia marina* and/or *Aegialitis annulata* and *Aegiceras corniculatum*, followed upslope by *Rhizophora stylosa*
Tidal creek shoal	zoned mangroves, with *Avicennia marina* and/or *Aegialitis annulata* and *Aegiceras corniculatum* Hinterland margin zoned mangroves, with *Avicennia marina*, *Aegialitis annulata*, *Ceriops tagal*, *Excoecaria agallocha*, *Lumnitzera racemosa*, and locally scattered *Xylocarpus moluccensis*; in more northern warmer environments, rare *Scyphiphora hydrophylacea*
High-tidal alluvial fan	with low freshwater seepage, zoned mangroves, with *Avicennia marina*, *Excoecaria agallocha*, and *Lumnitzera racemosa*, and rare *Ceriops tagal*; with marked freshwater seepage, zoned mangroves, with *Avicennia marina*, *Bruguiera exaristata*, *Bruguiera parviflora*, *Ceriops tagal*, *Excoecaria agallocha*, and *Lumnitzera racemosa*, and locally scattered *Xylocarpus moluccensis*; in more humid environments, locally scattered *Xylocarpus granatum*
Beaches	zoned mangroves, with seaward *Avicennia marina* (and sometimes *Sonneratia alba*) followed to landward by *Rhizophora stylosa*, then *Bruguiera exaristata*, *Ceriops tagal* and to landward *Avicennia marina*; this habitat also supports *Aegialitis annulata*, and (especially where underlain by beach rock) *Osbornia octodonta*
Spits	zoned mangroves, with seaward *Avicennia marina* (and sometimes *Sonneratia alba*) followed to landward by *Rhizophora stylosa*, then *Bruguiera exaristata*, *Ceriops tagal* and to landward *Avicennia marina*; spits in drier subregions are fringed by *Avicennia marina* and/or *Ceriops tagal* and/or *Excoecaria agallocha* and *Lumnitzera racemosa*
Cheniers	a fringe of *Avicennia marina* and/or *Ceriops tagal*; in drier subregions are fringed by *Avicennia marina* and/or *Ceriops tagal* and/or *Excoecaria agallocha* and *Lumnitzera racemosa*
Barriers	zoned mangroves, with seaward *Avicennia marina* (and sometimes *Sonneratia alba*) followed to landward by *Rhizophora stylosa*, then *Bruguiera exaristata*, *Ceriops tagal* and to landward *Avicennia marina*
Dune margin	a fringe of *Avicennia marina* and/or *Ceriops tagal*; in drier subregions are fringed by *Avicennia marina* and/or *Ceriops tagal* and/or *Excoecaria agallocha* and *Lumnitzera racemosa*

express variation in mangal composition, structure, and physiognomy across a climate gradient are: the hinterland margin where freshwater seepage is expressed; the high tidal alluvial fans where freshwater seepage is best expressed; beaches where freshwater is stored under the upper beach; spits and cheniers where freshwater is stored under the sand body; and the high-tidal parts of muddy tidal flats that are subject to evaporation and (in more arid areas) develop into salt flats.

The reason for the variation in mangal composition, structure, and physiognomy is that not all habitats respond equally to climatic or hinterland-physiographic setting because of their location along the tidal gradient and their proximity to hinterland terrestrial influences. It is possible to separate mangrove systems into dominantly marine-influenced and dominantly terrestrial-influenced zones (Figure 10 provides an idealised picture of decreasing marine influence across a tidal flat). Following Semeniuk (1983), these zones are:

1. from MSL to Mean High Water Neap Tide (MHWN), a zone dominated by marine influences; being inundated daily by tides; while air temperatures and sea temperatures play a part in determining regional species distribution sub-continentally, there is not enough differentiation in these climate parameters in the Kimberley region to markedly affect species composition in this zone, hence the species such as *Avicennia marina*, *Sonneratia alba*, *Rhizophora stylosa*, *Bruguiera exaristata*, and *Aegialitis annulata* are generally widespread and cosmopolitan in this tidal interval, particularly on muddy tidal flats;

2. from MHWN to HAT, a zone progressively dominated more by terrestrial influences, with terrestrial effects increasing from Mean High Water Spring (MHWS) to HAT; being inundated less frequently by tides and affected by evaporation (through solar radiation, air temperatures and wind), and rainfall (expressed as rain directly falling on saline high tidal flats, run-off, freshwater seepage, and base-flow of creeks, streams and rivulets); in these environments, changes in rainfall, and the extent the hinterland can deliver freshwater to the high-tidal zone through creeks, streams and rivulets or through freshwater seepage, determine species composition, structure and physiognomy; there are specific species associations, and

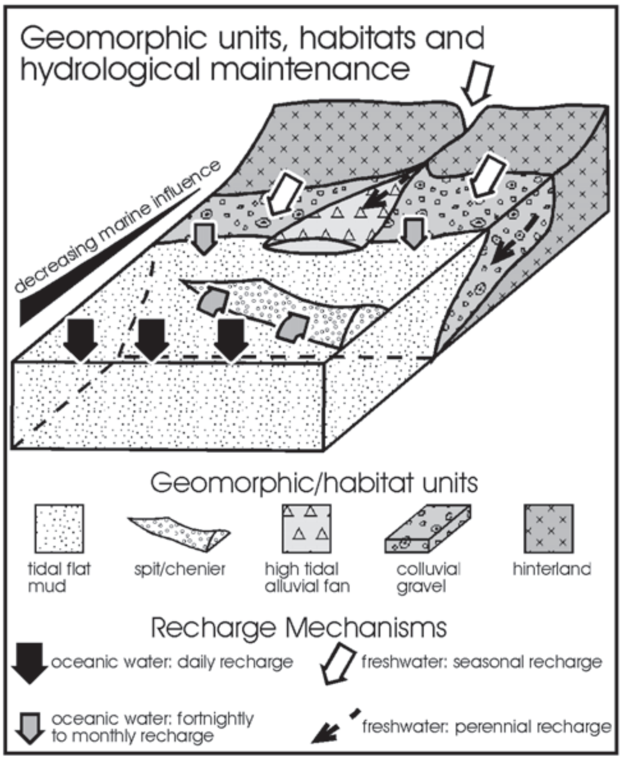


Figure 10. Suite of habitats with diverse substrate types within a ria coast embayment, and the various hydrological/hydrochemical mechanisms maintaining the mangroves. From MSL to the edge of the tidal flat along the edge of the hinterland, there is a decreasing marine influence.

expressions of mangrove structure and physiognomy in relation to substrate, tidal zone aquifers (*e.g.*, emergent cheniers) or terrestrial aquifers that store and deliver freshwater (*e.g.*, dunes bordering beaches, or fractured rock hinterland, or valley-tract alluvial ribbons), as well as the style by which freshwater is delivered to the high-tidal zone, and tidal level.

The freshwater input into the marine environment occurs through river/creek discharge after rainfall as well as sheet flooding during the frequent high rainfall events, and subterranean groundwater seepage into the coastal zone is important during the wet and dry seasons. Semeniuk (1983) documents the regional climatic differences in north-western Australia and the importance of subsurface seepage in the north-west of Australia and postulates its importance for mangrove distribution. Bridgewater & Cresswell (2003) note differences in mangal phytogeography between the east and west coasts of Australia suggesting the more restricted western Australian groupings are determined by the amount of groundwater flow, which enables only the highly halophytic mangrove species to persist. The effect of rainfall on the habitat, and mangrove species occurrences in the critical freshwater-influenced habitats is presented in Table 5 below. There are also changes in vegetation structure, physiognomy, and density changes within the habitat with increased rainfall, but we focus here only on floristic changes.

A model to explain mangrove distribution and diversity along the Kimberley Coast

The mangrove habitats of the Kimberley Coast draw their species from the regional species pool. While there is some variation in species richness across the region (such as the loss of *Scyphiphora hydrophylacea* and *Xylocarpus granatum*) the Kimberley Coast can be broadly considered to be one pool of 15 core species. Subregionally local factors determine those species that will inhabit the twelve mangrove habitats in the region (Table 2) to form mangal with variable composition and variable structure and physiognomy. The 'selection' of species from the regional species pool (and the variable expression of these species by habitat factors) creates the mosaics of species assemblages evident along the coast within the twelve habitats described above. The distribution of the main mangrove species within each of these twelve habitats is then further determined by regional climate and local freshwater input. Figure 14 summarises the main patterns determining distribution and diversity. It illustrates the progressive forcing factors in decreasing scale acting on the global species pool

Table 5

Effect of increased rainfall or increased seepage, or run-off on habitat and occurrences of species

Habitat	Effect of increased rainfall or increased seepage, or run-off
Hinterland margin	increased freshwater seepage from fracture rock aquifer; with increased seepage *Avicennia marina* and scattered *Ceriops tagal* changes to complex association of *Avicennia marina*, *Ceriops tagal*, *Lumnitzera racemosa*, *Bruguiera exaristata*, *Excoecaria agallocha*, and in the wettest areas *Xylocarpus granatum*
High tidal alluvial fan	increased freshwater run-off, alluvial base-flow, and seepage; with increased seepage *Avicennia marina*, *Lumnitzera racemosa* and scattered *Ceriops tagal* changes to complex association of *Avicennia marina*, *Ceriops tagal*, *Lumnitzera racemosa*, *Bruguiera exaristata*, *Excoecaria agallocha*, *Rhizophora stylosa*, and in the wettest areas *Xylocarpus granatum*
Beaches, spits, chenier	increased storage of freshwater in sandy aquifer landward of mangrove habitats, and increased seepage from aquifer; with increased seepage *Avicennia marina*, *Ceriops tagal* and *Bruguiera exaristata* changes to complex association of *Avicennia marina*, *Ceriops tagal*, *Bruguiera exaristata*, *Rhizophora stylosa*, and *Osbornia octodonta*
High-tidal muddy tidal flat	decreased evaporation of the salt flats, and increased freshwater dilution of saline flats; with increased rainfall, thickets of *Ceriops tagal* and salt flats change to forests of *Ceriops tagal*, *Bruguiera exaristata*, *Bruguiera parviflora*, *Osbornia octodonta*, and *Lumnitzera racemosa*

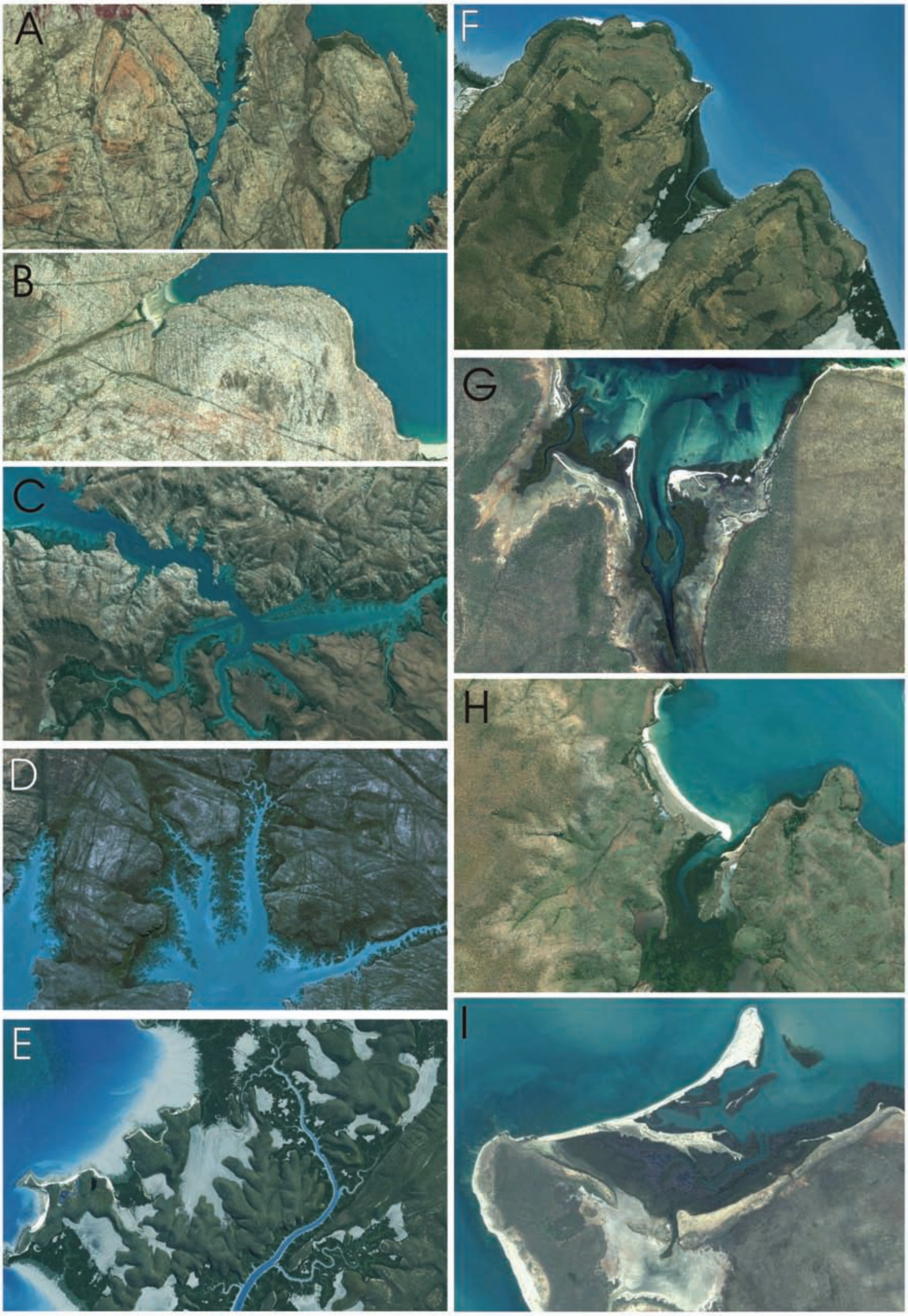


Figure 11. Aerial photographs of mangrove coastal settings and mangrove habitats. A. Large, narrow v-shaped gulf, and subsidiary fracture-controlled narrow ravines. B. Fracture-controlled narrow ravine barred by a sand barrier. C. Mangrove-lined branching, dendritic embayments (rias). D. Mangrove-lined branching small gulfs (rias). E. Network of dendritic drainage and associated landforms with mangrove vegetated muddy tidal flats in sheltered areas and in embayments, and sandy coves, beaches, and rocky shores on the wave-exposed open coast. F. Open embayment with spits at the headlands. G. Spits and tidal creek point bars at the front of a mangrove-vegetated delta, comprised of sand and mud, and tidally oriented shoals. H. Barrier of beach ridges barring a small mangrove-fringed lagoon at the front of a mangrove-vegetated delta. I. Sandy spit complex protecting a mangrove-vegetated lagoon and embayment.

Figure 12. Oblique photographs of mangrove coastal settings and habitats. A. Rocky shore along the Buccaneer Archipelago with thin fringe of mangroves. B. Mangroves (zoned) inhabiting a low gradient gravelly shore. C. Mangroves inhabiting the tidal parts of (fracture-controlled) narrow ravines. D. Mangrove-vegetated tidal flat and meandering tidal creek (located inside a narrow, elongate v-shaped embayment). E. Gravelly spit partially protecting an open embayment, with zoned mangal within the embayment; chenier in the interior of the embayment is fringed by narrow mangal; mangrove-vegetated high-tidal alluvial fan is developed where a small ravine has debouched onto the high-tidal part of the salt flat. F. Narrow ravine, with sandy barrier across a mangrove-vegetated lagoon. G. Interface of rocky hinterland and salt flat, with mangroves fringing the hinterland margin and the alluvial fans. H. Mangroves inhabiting a sandy beach cove. I. Sandy spits and associated protected mangrove-vegetated lagoons. J. Broad muddy tidal flats with zoned mangroves along the seaward edge, and thin fringe of mangroves inhabiting the hinterland margin.

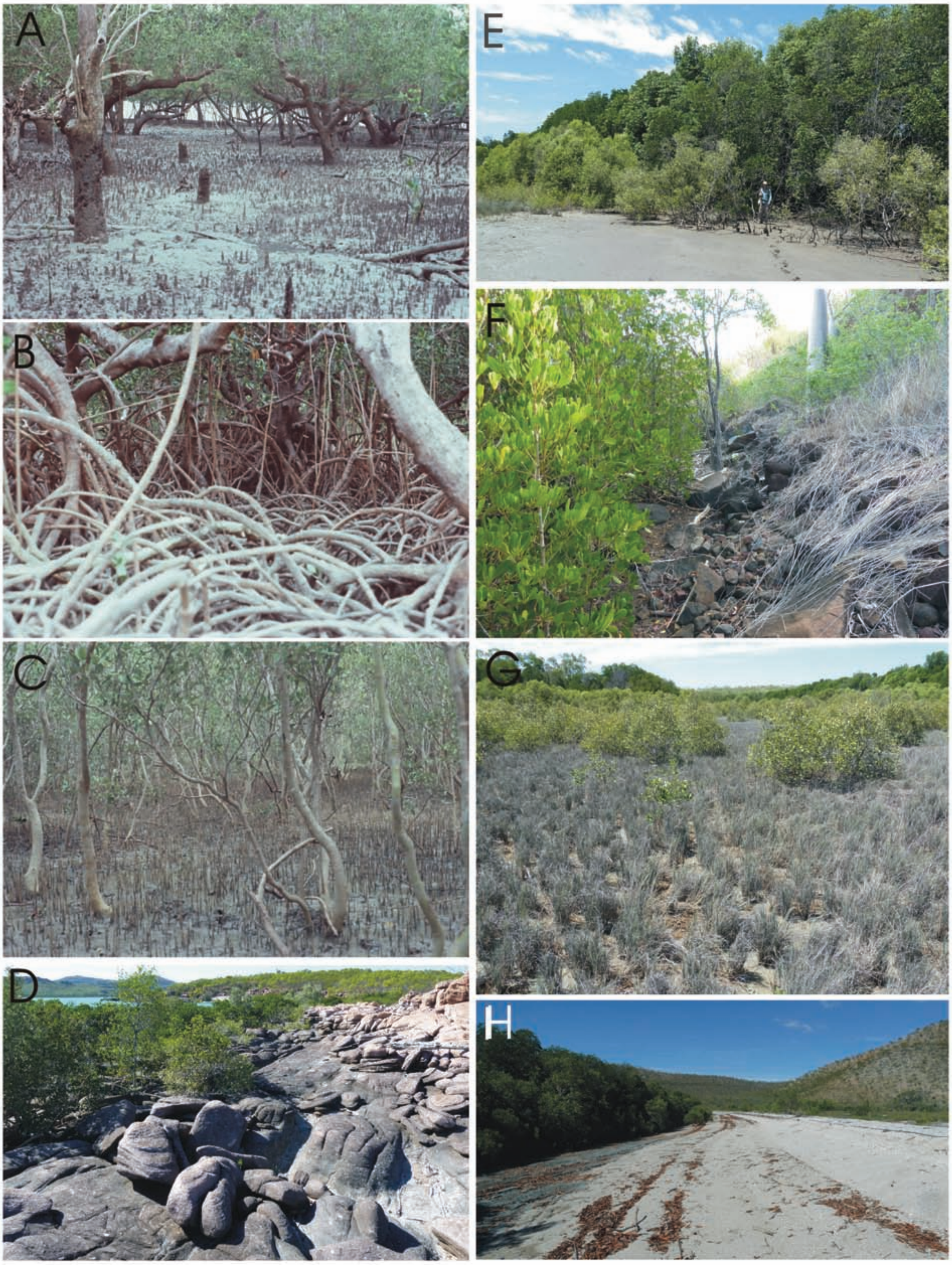
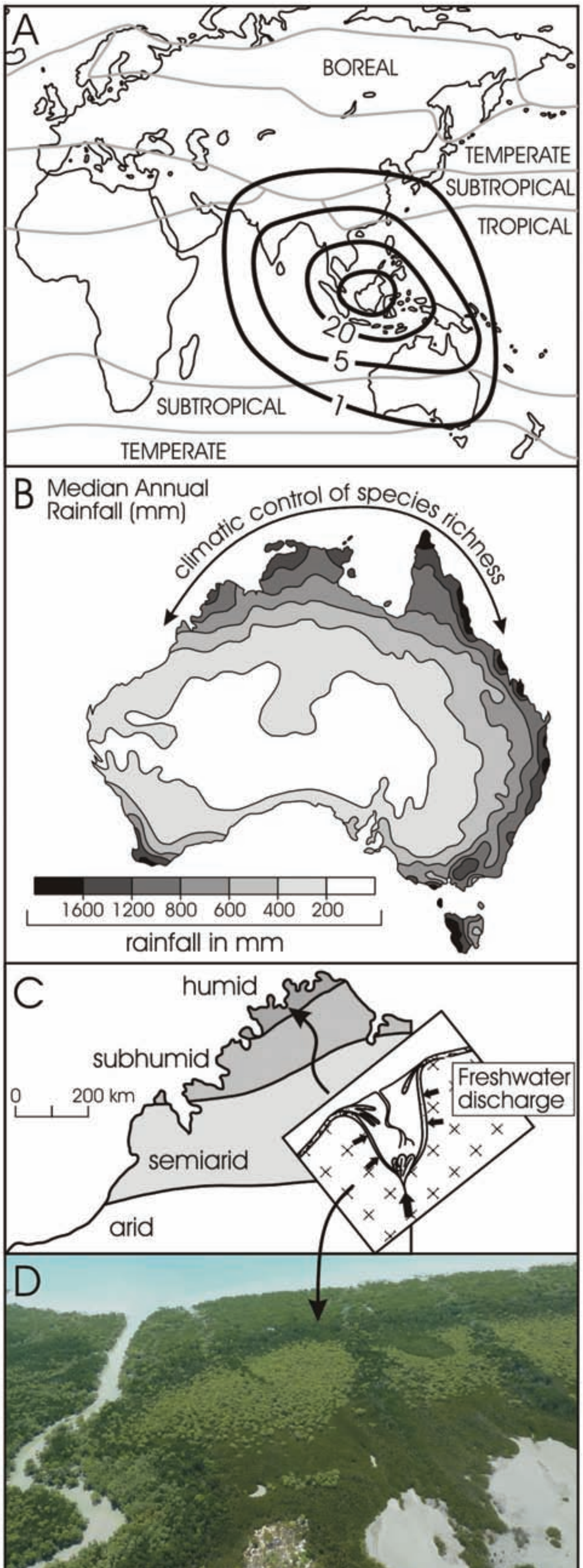


Figure 13. Features of the mangroves of the Kimberley Coast. A. Closed low forest of *Sonneratia alba* in the seaward front of the mangal. B. Closed low forest of *Rhizophora stylosa* of the mangal interior. C. Closed low forest of *Avicennia marina* of the mangal interior. D. Mangal inhabiting terraced rocky shore. E. Zoned mangal inhabiting a high-tidal alluvial fan, composed of an outer fringe of shrubs of *Avicennia marina*, and an interior tall forest of *Rhizophora stylosa*, *Bruguiera parviflora*, *Bruguiera exaristata*, and *Ceriops tagal*. F. Mangroves (*Ceriops tagal*, *Bruguiera exaristata*, and *Avicennia marina*) inhabiting the bouldery hinterland margin – boab trees and grasses to the right on the terrestrial slope; and G. Seaward margin of a high-tidal alluvial fan, with shrub of *Avicennia marina* and graminoid ground cover. H. Closed low forest of *Avicennia marina*, *Rhizophora stylosa*, *Bruguiera exaristata*, *Ceriops tagal*, and *Osbornia octodonta* along a sandy slope (beach) in front of a beach rock pavement.



leading to the species richness, assemblages, structure and physiognomy of mangroves along the Kimberley Coast. From a global species pool of Old World Mangroves in excess of 30 species centred on the Malaysian Archipelago, the progressive change in climate towards northern and north-western Australia results in a regional species pool of some 10–20 species across the Northern Territory and the Kimberley region. Smaller scale climate variation and local habitat characteristics along the Kimberley Coast further selects species from the regional pool to develop the habitat-specific assemblages and the climate-specific and habitat-specific species occurrence.

The main factors involved in determining species diversity at the fine mangrove habitat scale are: 1. oceanographic processes determining accumulation and maintenance of sediment bodies to develop as habitats; 2. the terrestrial sedimentary processes that determine accumulation and maintenance of sediment bodies, such as alluvial fans; 3. the marine hydrological and hydrochemical processes that determine accumulation and maintenance of mangrove habitats; and 4. the amount of freshwater delivered to the high-tidal zone. These factors result in the expression of species in distinct habitat-related assemblages, often zoned across the habitat in relationship to environmental gradients developed within the habitat (Fig. 14D). Variations also occur in relation to the dynamic nature of the coastal environments. Long-term stable habitats result in long-term assemblages and in stable mangal zonation. Dynamic environments, or those where there have been geomorphic or hydrologic adjustments will result in floristically and structurally less stable assemblages.

Some general patterns emerge:

1. The rocky shores are mangrove-depauperate.
2. The high-energy sandy shores also are mangrove-depauperate.
3. On moderate energy sandy shores, *e.g.*, beaches, spits, and cheniers which support mangroves, species composition is determined by grainsize, sediment composition, hydrological factors such as internal drainage and freshwater storage and seepage, hydrochemistry, and tidal level.

Figure 14. Diagram illustrating the progressive forcing factors, in decreasing scale, acting on the global species pool leading to the regional species pool along northern Australia and the Kimberley region then to the habitat-specific assemblages and the climate-specific and habitat-specific species occurrence. A. The species richness of the Old World mangroves (isopleths denote the general numbers of mangrove species). B. The mean annual rainfall across north-western, northern and eastern Australia that influences the species richness at the sub-continental scale. C. The climate of the Kimberley region that determines which species from the sub-continental species pool are available to generate a regional species pool, as well as the further selection of species by habitat factors (the generalised ria embayment shown here (inset) with array of habitats and with locations of freshwater seepage). D. Gradients within the habitats force species into zones of composition, structure and physiognomy; in this example, compositional and structural zonation of species is following tidal flat gradients, and the effects of shore-normal tidal creeks.

4. The muddy tidal flats where there is protection from high energy conditions are mangrove-rich zones, and if the environment is stable geomorphically and hydrologically/ hydrochemically then the full complement of mangrove species are zoned according to gradients of environmental conditions.
5. In tidal creeks there is a subset of habitats which are relatively mangrove-rich; these subsets of habitats include steep creek banks, point bars, and mid channel shoals.
6. Where there is freshwater seepage, such as along the margin of the hinterland, and from high-tidal alluvial fans, the habitats, though generally mangrove-depauperate, increase in species richness with increased freshwater seepage.

The finest scale manifestation of diversity in mangroves is the physiognomic, structural and floral expression at the habitat level. Here, salinity, inter-species competition, intra-species competition, type of substrate and nutrients, and amount of hydrological through-flow, are the major factors that determine how individual species manifest various structural and physiognomic forms. For instance (reflecting habitat differences in terms of substrate, tidal level, and salinity), the structure and physiognomy of a *Ceriops tagal* low forest or a *Bruguiera exaristata* low forest on a muddy tidal flat will be structurally and physiognomically different to a *Ceriops tagal* thicket or a *Bruguiera exaristata* scrub fringing a sand spit and, similarly, a formation of scattered *Lumnitzera racemosa* as multi-stemmed shrubs along a high-tidal alluvial fan will be different to a single-trunked stand of *Lumnitzera racemosa* co-associated with *Avicennia marina* along a landward fringe adjoining a salt flat.

Thus, the environmental conditions of the habitat, and the resulting zoning of the habitat drive the different expressions of the structure and physiognomy of individual species which provide the finest scale expression of biodiversity in the region. These expressions represent physico-chemical differences in the environment which may also host significant variations in more cryptic fauna and micro-biota. Therefore to truly capture the physiognomic and structural expression in relation to mangrove flora, it is not sufficient to simply note which mangrove species are present. It is at this finer scale of mangrove expression that a more fulsome analysis of biodiversity must be explored.

Discussion

The Kimberley Coast occupies a unique position globally in terms of its tropical latitude, ria coast setting, and rainfall, within a mostly macrotidal regime, and the mangroves therein also acquire global significance.

The mangroves along the Kimberley Coast reside in a tropical humid to subhumid climate in the species-rich setting of the Old World Mangroves, and are located along a macrotidal ria shore, a setting that is unusual around the Globe. For instance, the areas of mangrove-species-rich Queensland, and the Malaysian Archipelago are not ria coasts and do not have the rich range of ria coast settings wherein species can express themselves variably in different associations, and in different structural and physiognomic forms responding to habitat and hydrology/hydrochemistry. Globally ria coasts are not common (Brocx & Semeniuk 2011), and most are not mangrove coasts. Where mangroves and (small scale) ria coasts coincide on other continents, the mangroves are New World Mangroves. The Kimberley Coast uniquely carries the Old World Mangroves into a ria coastal environment.

The mangroves of the Kimberley region belong to the Indo-Malesian group of Old World Mangroves centred in the Indian-Pacific area (Tomlinson 1986, Chapman 1977), which is the most species-rich region of the world. Spalding *et al*. (1997) describe the overall global distribution of mangroves with the most species occurring in tropical climates, and a reduction in species in higher latitudes. Suzuki and Saenger (1996) in a comparison of mangrove vegetation at similar latitudes between eastern Australia and Japan note that the Australian mangrove flora is one of the richest in the world, and Duke *et al*. (1998) document the species diversity within the Indo-Malesian group also noting that the mangrove flora of the Australasian region is one of the richest in the world, with Australia recording 39 of the 58 taxa found in the 'Indo West Pacific' hemisphere. Duke (1992) relates latitudinal (temperature) and rainfall patterns to the number of mangrove species present, with a decrease in species from the tropical north southwards.

The Kimberley Coast is the largest laterally extensive ria coast in the World and, in this context, it presents a range of coastal forms variable in shape, size, and orientation but developed on a regionally relatively consistent bedrock template, *viz*., the rocks of the Kimberley Basin and the seaward expression of the Kimberley Plateau. The ensemble of coasts along the Kimberley Basin and adjoining King Leopold Orogen present a global example of the range of fracture-and-fault controlled ria coasts that can be developed, and has been recognised as such in the preliminary assessment of the heritage values of the West Kimberley (Australian Heritage Council 2010). The mangrove habitats exhibit a recurring pattern across the length of the Kimberley region.

One of the important features of the region is the freshwater seepage and the freshwater storage in spits and cheniers. The fracture-dominated bedrock that forms the hinterland to the mangrove-lined coast provides a globally unique expression of the phenomenon of freshwater seepage into hinterland margin habitats and into high-tidal alluvial fans. The region is located in a climate that alternates between dry season and wet season, and the freshwater residing in a fractured bedrock (fractured aquifer) discharges into the tidal zone during the wet and into the dry season. This controls the occurrence and maintenance of mangroves in the high-tidal zone and is a feature unique globally and of international significance in mangrove ecology. Similarly, the spits and cheniers, in a monsoonal setting, provide specific hydrological and hydrochemical function to the mangroves. With freshwater discharge along the edges of the sand bodies into adjoining tidal flats, there are specific mangrove ecological processes operating within this ria coast setting.

The Kimberley Coast manifests a range of habitats for mangroves related to larger scale hinterland influences, coastal landforms, coastally expressed geological patterns, shoreline sedimentation patterns, and climate; varying from rocky (cliff) shores to classic ria shores with tidal flats, tidal creeks, spits, and high-tidal alluvial fans, to rocky-shore-dominated ravines, amongst others. The mangroves form habitat-specific assemblages and characteristic floristic and structural zones within the mangal. The complexity of mangrove habitats and their relationship to the megascale coastal forms of this regional coastal setting is of international conservation significance.

The approach adopted in this paper, involving scale of coastal setting for mangroves, identification of habitats, explanation of mangrove diversity (floristically, structurally and physiognomically) in relation to habitat, and the stratified scalar approach integrating global species richness to local species richness with climate gradients and habitats, is applicable elsewhere in Australia and globally. This approach provides a framework for studies at the next level of mangrove ecology involving transect work describing species zonation, abiotic factors underpinning the zonation, inter-species competition, species tolerance levels to physiochemical gradients, changes in plant physiognomy across habitats in relation to physicochemical gradients, and density between habitats.

Acknowledgements: For VS, this study is part of VCSRG's R&D endeavour registered as Project #3 with AusIndustry. Drafting carried out by CAM Graphics. Specimen location records from all of Australia's herbaria for each species noted in Figure 6 were accessed from Australia's Virtual Herbarium (AVH 2011), and mapped using the Atlas of Living Australia (ALA 2011). The Australian Plant Name Index has been used for current species nomenclature (APNI 2011).

References

ALA 2011 Atlas of Living Australia website at http://www.ala.org.au/. Accessed 27 March 2011.

APNI 2011 Australian Plant Names Index website at http://www.anbg.gov.au/apni/. Accessed 27 March 2011.

AVH 2011 Australia's Virtual Herbarium website at http://avh.rbg.vic.gov.au/avh/. Accessed 27 March 2011.

Australian Heritage Council 2010 Summary of the Australian Heritage Council's Preliminary Assessment of Possible National Heritage Values in the West Kimberley. Department of Sustainability, Environment, Water, Population and Communities, Canberra, viewed 12 February 2011 <http://www.environment.gov.au/heritage/ahc/national-assessments/kimberley/values.html>.

Beard J S Clayton-Greene K A & Kenneally K F 1984 Notes on the Vegetation of the Bougainville Peninsula, Osborn and Institut Islands, North Kimberley District, Western Australia, Vegetatio 57: 3–13.

Bridgewater P B 1982 Mangrove vegetation of the southern and western Australian coastline. *In*: B F Clough (ed) Mangrove Ecosystems in Australia: structure, function and management. AIMS & ANU Press, Canberra. 111–120.

Bridgewater P B 1985 Variation in the mangal along the western coastline of Australia. Proceedings of the Ecological Society of Australia 13: 243–255.

Bridgewater P B 1989 Syntaxonomy of the Australian mangal refined through iterative ordination. Vegetatio 81: 159–168.

Bridgewater P B & Cresswell I D 1999 Biogeography of Mangrove and Saltmarsh Vegetation: Implications for Conservation and Management in Australia. Mangrove and Saltmarsh. 3: 117–125.

Bridgewater P B & Cresswell I D 2003 Identifying biogeographic patterns in Australian saltmarsh and mangal systems: a phytogeographic analysis. Phytocoenologia 33: 231–250.

Brocx M & Semeniuk V 2011 The global geoheritage significance of the Kimberley coast. Journal of the Royal Society of Western Australia 94: 57–88.

Burbidge A A & McKenzie NL (eds) 1978 The Islands of The North-West Kimberley Western Australia. Wildlife and Research Western Australia Bulletin No. 7.

Bureau of Meteorology 1973 Climatic averages and meteorology of West Australia. *In*: West Australian Yearbook 12, Melbourne.

Bureau of Meteorology 1975 Climatic averages Western Australia. Australian Government Publishing Services, Canberra.

Bureau of Meteorology 1988 Climatic Atlas of Australia. Bureau of Meteorology, Department of Administrative Services, Australian Government Publishing Services, Canberra.

Bureau of Meteorology 2010 Tropical cyclones. Commonwealth of Australia 2010, Bureau of Meteorology, Canberra.

Chapman V J 1977 Introduction. *In*: Ecosystems of the World. 1. Wet coastal ecosystems. Elsevier, Amsterdam.

Duke N C 1992 Mangrove floristics and biogeography. *In*: A I Robertson & D M Alongi (eds) Tropical mangrove ecosystems. American Geophysical Union, Washington D.C. 63–100.

Duke N C, Ball M C & Ellison J C 1998 Factors influencing biodiversity and distributional gradients in mangroves. Global Ecology and Biogeography Letters 7: 27–47.

Duke N C 2006 Australia's mangroves – the authorative guide to Australia's mangrove plants. University of Queensland, Brisbane. 200pp.

Galloway R W 1982 Distribution and Physiographic Patterns of Australian Mangroves. *In:* B F Clough (ed) Mangrove Ecosystems in Australia: structure, function and management. AIMS & ANU Press, Canberra. 31–54.

Gentilli J 1972 Australian climate patterns. Nelson Academic Press, Melbourne, 285 pp.

Griffin T J & Grey K 1990a King Leopold and Halls Creek Orogens. Western Australia Geological Survey Memoir 3, 232–234.

Griffin T J & Grey K 1990b Kimberley Basin. Western Australia Geological Survey Memoir 3, 293–304.

Hnatuik R J & Kenneally K F 1981 A survey of the vegetation and flora of Mitchell Plateau, Kimberley, Western Australia. *In*: Biological Survey of Mitchell Plateau and Admiralty Gulf, Kimberley, Western Australia. Western Australian Museum, Perth. 13–94.

Hutchings P & Saenger P 1987 Ecology of mangroves. Queensland University Press St Lucia.

Kabay E D & Burbidge A A (eds) 1977 A Biological Survey of The Drysdale River National Park North Kimberley, Western Australia in August, 1975. Wildlife and Research Bulletin WA No.6.

Johnstone R E 1990 Mangroves and Mangrove Birds. Records of the Western Australian Museum Supplement 32. Western Australian Museum, Perth.

Lourensz R S 1981 Tropical cyclones in the Australian region, July 1909 to June 1980. Department of Science & Technology, Bureau of Meteorology, Australian Government Publishing Service, Canberra.

Macnae W 1968 A general account of the fauna and flora of mangrove swamps and forests in the Indo-West-Pacific region. Advances in Marine Biology 6: 73–270.

Miles J M & Burbidge AA (eds) 1975 A biological survey of the Prince Regent River Reserve North-west Kimberley, Western Australia in August 1974. Wildlife and Research Bulletin WA No.3.

Saenger P Specht M M Specht R L & Chapman V J 1977 Mangal and coastal salt marsh communities in Australasia. *In*: V J Chapman (ed) Ecosystems of the World. I. Wet Coastal Ecosystems. 293–345.

Saenger P 1996 Part 6. Mangrove Flora: Distribution of species and habitat descriptions. *In*: D I Walker, F E Wells & J Russell Hanley (eds) Marine Biological Survey of the Eastern Kimberley, Western Australia, Heritage Council of Western Australia, West Perth, WA.

Semeniuk V, Kenneally K F and Wilson P 1978 Mangroves of Western Australia. WA Naturalists Handbook No. 12.

Semeniuk V 1980 Mangrove zonation along an eroding coastline in King Sound, North-western Australia. Journal of Ecology 68: 789–812.

Semeniuk V 1983 Regional and local mangrove distribution in Northwestern Australia in relationship to freshwater seepage. Vegetatio 53: 11–31.

Semeniuk V 1985 Development of mangrove habitats along ria shorelines in north and northwestern tropical Australia. Vegetatio 60: 3–23.

Semeniuk V 1986 Terminology for geomorphic units and habitats along the tropical coast of Western Australia. Journal of the Royal Society of Western Australia 68: 53–79.

Semeniuk V 1993 The mangrove systems of Western Australia: 1993 Presidential Address. Journal of the Royal Society of Western Australia, 76: 99–122.

Semeniuk V 2011 Stratigraphic patterns in coastal sediment sequences in the Kimberley region: products of coastal form, oceanographic setting, sedimentary suites, sediment supply, and biogenesis. Journal of the Royal Society of Western Australia 94: 133–150.

Semeniuk V & Wurm P 1987 Mangroves of Dampier Archipelago, Western Australia. Journal of the Royal Society of Western Australia 69: 29–87.

Spalding M D Blasco F Field C D (eds) 1997 World Mangrove Atlas. World Conservation Monitoring Centre & International Society for Mangrove Ecosystems. Okinawa Japan 178pp.

Specht R L 1981 Biography of halophytic angiosperms (saltmarsh, mangrove and seagrass). *In*: A Keast (ed) Ecological Biogeography of Australia. The Hague: Dr W Junk. 577–589.

Suzuki K & Saenger P 1996 A phytosociological study of mangrove vegetation in Australia with a latitudinal comparison of East Asia. Mangrove Science 1: 9–27.

Thom B G, Wright L D & Coleman J M 1975 Mangrove ecology and deltaic-estuarine geomorphology: Cambridge Gulf – Ord River, Western Australia. Journal of Ecology 63: 203–232.

Tomlinson P B 1986 The botany of mangroves. Cambridge University Press, Cambridge UK.

Wells A G 1981 A survey of riverside mangrove vegetation fringing tidal river systems of Kimberley, Western Australia. *In*: Biological Survey of Mitchell Plateau and Admiralty Gulf, Kimberley, Western Australia. Western Australian Museum, Perth, 95–121.

Wells AG 1982 Mangrove Vegetation of Northern Australia. *In:* B F Clough (ed) Mangrove Ecosystems in Australia: structure, function and management. AIMS & ANU Press, Canberra, 57–78.

Wells A G 1985 Grouping of tidal systems in the Northern Territory and Kimberley Region of Western Australia on presence/absence of mangroves species. *In*: K N Bardsley, J D S Davie & C D Woodroffe, Coasts and tidal wetlands of the Australian monsoon region: a collection of papers presented at a conference held in Darwin 4–11 November 1984. North Australia Research Unit, Mangrove Monograph No. 1.

Wells A G 2006 A survey of riverside mangrove vegetation fringing tidal river systems of Kimberley, Western Australia. Biological Survey of Mitchell Plateau and Admiralty Gulf, W.A. Western Australian Museum Supplement No. 3 95–121.