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MANGROVE SWAMPS IN BERMUDA

BY

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Abstract

Bermudian mangrove swamps at 32°N are floristically similar to those in the Gulf of Mexico at 23°N, both being composed of the red mangrove, *Rhizophora mangle*, the black mangrove, *Avicennia germinans* and the buttonwood, *Conocarpus erectus* with the Brazil pepper tree, *Schinus terebinthifolia* invading. The most frequent associated flora are the red alga, *Bostrychia montagnei* and green algae *Rhizoclonium riparium* and *R. kernerii* and the flowering plants, *Asparagus sprengeri*, *Borrchia frutescens* and *Sesuvium portulacastrum*. The faunal components are very diverse and vary greatly among swamps. Mangroves of coastal bays show typical plant zonation but the tree stands of inland saltwater ponds are typically monospecific with either *R. mangle* or *A. germinans*, and the associated flora and fauna very sporadic. Once established, red or black mangroves resist invasion and occupy a zone characteristic of both species.

INTRODUCTION

The mangroves of Bermuda at 32°N are the most northern in the Atlantic (Chapman 1977), their presence being fostered by the warm waters of the Gulf Stream which give the islands a warm, frost free climate (Anon. 1974, Morris *et al.* 1977). In the North Pacific, mangroves occur as far north as 35°N in Japan and on a world-wide basis those furthest from the equator are at 37°S in New Zealand (Walsh 1974). The Bermuda mangroves are isolated, generally small in size and confined to an archipelago of very small land area. The only large swamps are the so-called "Great Mangrove" of Hungry Bay and another around Mangrove Lake (Fig. 1). Bermuda mangroves like other isolated and outlying examples, for example in Japan and New Zealand (Walsh 1974) are low in tree diversity. Only three species occur, *Rhizophora mangle* L., the red mangrove, *Avicennia germinans* (L.) L., the black mangrove and *Conocarpus erectus* L., the buttonwood (Britton 1918). Early accounts that included the white mangrove, *Laguncularia racemosa* Gaertner (Lefroy, 1884) are probably in error (*C. erectus* being locally called the "white mangrove") even though more recent accounts still include it (Verrill 1902, Hanlon *et al.* 1975). The mangrove communities of Bermuda have never been described but aspects of plant components were mentioned by Verrill (1902), Harshberger (1905), Britton (1918) and Taylor (1960). Sterrer (1986) describes many of the commoner fauna and flora.

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An unusual feature of the mangrove swamps of Bermuda is that about one third of them are located around inland salt-water ponds, the majority of which are tidal and connected to the sea by submarine fissures. These are anchialine pools according to Por (1985).

Although mangrove communities in Bermuda have not been mapped before, there is no doubt that they were formerly much more widespread. They are mentioned in early writings (eg. Lefroy 1884, Verrill 1902) and place names, still currently used, reflect their former presence. For instance, there are now no longer any mangroves in "Mangrove Bay" on the west coast. Mangrove bark was used by early settlers in tanning as well as for fuel, additionally they were cleared for coastal development (Hayward *et al.* 1981). Once cleared, mangroves are generally slow to recover (Macnae 1968).

MATERIAL AND METHODS

The locations of mangrove swamps in the Bermuda Islands was determined by reference to 1:2500, Series E811 topographic maps of Bermuda, information from the Bermuda Dept. of Agriculture and Fisheries, and by personal inspection of likely locations. Fringing mangroves, on rocky shores, dominated by *C. erectus* were not considered as swamps.

At each location where there were more than 10 trees containing either or both of *R. mangle* and *A. germinans*, the perimeter of the swamp was mapped by measurement and the use of optical rangefinders, with reference to landmarks appearing on topographic maps. The edge was defined as the outer limit of the canopy of trees or the community of halophytic plants typical of mangroves, whichever extended further. Areas were determined from the maps produced. One to 25 line transects, depending on the size of the swamp were run at right angles to the general shoreline, at low tide, from the back of the mangrove to either, the seaward extent of the canopy, the centre of the main drainage channel, or the opposite side of the swamp, depending on site characteristics. On each transect, elevation levels were determined at points where the gradient changed or at 5 m intervals, whichever was less, by optical leveling and, beyond the water line, by depth. For bay and lagoonal tidal sites (Table 1), heights were corrected to chart datum, by the method of Anon. (1985). For anchialine ponds, tide readings were taken from staff gauges installed in each pond (Thomas *et al.* 1991) and corrected to a datum of mean low tide level. For non-tidal sites, datum was taken as the normal water level. Along each transect, the first and last occurrences of all macroscopic species were measured. For mangrove trees the following additional points were fixed: the start and end of *A. germinans* pneumatophores, canopy, trunks and seedlings; the start and end of *R. mangle* prop roots, canopy, trunks and seedlings; and for *C. erectus* and *Schinus terebinthifolia* (L.) the limits of the canopy. At five meter intervals, starting at the landward edge, for each tree species, the heights of the upper and lower canopies were measured. Mangrove abundance was counted in 9-25 m² plots at 3-9 m, intervals depending on the transect length. Maximum trunk diameters at 1.5 m above ground were measured on large specimens. The general character of the

substrate was noted. Frequency data herein is the percentage of sites at which the species were found.

The scientific names of species follow Sterrer (1986) wherever possible. Specimens are deposited in the collections of the University of New Brunswick, and the experts mentioned in the acknowledgements assisted with identifications.

RESULTS

The locations of the 33 mangrove swamps surveyed (Fig. 1) are listed together with their local names and areas along with the mangrove tree species present and whether the site is a coastal bay, lagoon, anchialine pond, non-tidal pond or landlocked and non-aquatic (Table 1). The species found and their frequency of occurrence among the 33 swamps and summaries of the vertical zonation of dominant species in bay and lagoonal (marine) sites found growing above chart datum are given in Tables 2 and 3 respectively. Pond mangroves are not included in this table because the very variable, and often much reduced tidal regime among ponds makes direct correlation difficult. A composite vertical profile of all marine mangroves is shown in Fig. 2a, while Figs 2b and c show Ireland Island Lagoon [#1 Fig. 1, Table 1] and Riddels Bay [#9] as examples of the range of profiles surveyed. Profiles from three pond sites (Fig. 3) include a "mixed" mangrove at Evans Pond (3a)[#7], a red mangrove dominated situation at Mangrove Lake (3b)[#18], and the black mangrove dominated Lovers Lake (3c)[#28]. Profiles of two unique mangrove swamps are the mangrove-salt marsh complex at Mill's Creek [#12] (Fig. 4a) and the "Great Mangrove" of Hungry Bay [#16] (Fig. 4b).

Table 1. Comparison of mangrove swamps of Bermuda: mangrove tree species present, type of habitat and area occupied.

Key to terms: R = *Rhizophora mangle*; B = *Avicennia germinans*; BU = *Conocarpus erectus*; Lagoon = marine with restricted connections with the sea; Pond = saline, non-tidal pond; An. Pond = anchialine (tidal) pond; Land = landlocked without pond.

Site #	Name	Trees	Type	Area(m ²)
1	Ireland Island	R,B,BU.	Lagoon	7109
2	Head of the Scour	R,B,BU.	Bay	189
3	Somerset Long Bay	R,B,BU.	Pond	2020
4	Elys Harbour	R,B.	Bay	5381
5	Pilchard Bay	R,B,BU.	Bay	9141
6	Whale Island	R,B,BU.	Bay	845
7	Evans Pond	R,B,BU.	An. Pond	4432
8	Jew's Bay	R,B,BU.	Bay	800
9	Riddels Bay	R,B,BU.	Bay	11568
10	Tom Wood's Bay	R,B,BU.	Bay	1781
11	Fairyland Creek	R,B,BU.	Bay	7989
12	Mill's Creek, Boss's Cove	R,B,BU.	Bay	10907

13	Paget Marsh	R.	Pond	12140
14	Foot of Crow Lane	R,B.	Bay	2336
15	Mangroville	R,B.	Pond	224
16	Hungry Bay	R,B,BU.	Bay	29717
17	Spittal Pond	B,BU.	Pond	229
18	Mangrove Lake	R,BU.	An. Pond	22597
19	Trotts Pond	R,BU.	An. Pond	8368
20	Compston Pond	R.	Pond	2900
21	Shelly Bay Mangrove	R,BU.	An. Pond	8500
22	Commonland Marsh	B,BU.	Land	800
23	Walsingham Pond	R,B,BU.	An. Pond	4933
24	Walsingham Bay	R,B,BU.	Bay	3776
25	Blue Hole	R,B,BU.	Bay	3003
26	Coney Island	R,B,BU.	Bay/Pond ¹	1755
27	Tuckers Town Bay	R,B,BU.	Bay	400
28	Lovers Lake	B,BU.	An. Pond	2288
29	Mangrove Bay	R,B,BU.	Bay	2837
30	Coot Pond	R,B,BU.	Bay	1643
31	Paget Island Pond	R,B,BU.	Bay ²	1594
32	Ferry Point	R,B,BU.	Bay	2200
33	U.S. Naval Air Base	R,B.	Pond ³	850
TOTAL				175252
Mean				5310±6495

¹ Former pond with channel cut to the sea.

² Former bay, now divided by causeway.

³ Former bay, now a pond.

Table 2. Check-list of plant and animal species and the percentage of localities at which they were collected in all Bermuda mangrove swamps.

SPECIES	%	SPECIES	%
CYANOBACTERIA			
<i>Entophysalis deusta</i>	3	<i>Scytonema hofmannii</i>	6

Oscillatoria lutea 12

CHLOROPHYTA

<i>Acetabularia crenulata</i>	9	<i>Cladophora expansa</i>	12
<i>Anadyomene stellata</i>	3	<i>Halimeda incrassata</i>	6
<i>Avrainvillea nigricans</i>	3	<i>Halimeda monile</i>	6
<i>Boodleopsis pusilla</i>	3	<i>Monostroma oxyspermum</i>	15
<i>Caulerpa mexicana</i>	3	<i>Penicillus capitatus</i>	6
<i>Caulerpa peltata</i>	3	<i>Rhizoclonium hookeri</i>	3
<i>Caulerpa racemosa</i>	3	<i>Rhizoclonium kernerii</i>	48
<i>Caulerpa sertularioides</i>	6	<i>Rhizoclonium riparium</i>	55
<i>Caulerpa verticillata</i>	3	<i>Udotea flabellum</i>	6
<i>Chaetomorpha linum</i>	12	<i>Valonia macrophysa</i>	3

RHODOPHYTA

<i>Acanthophora muscoides</i>	3	<i>Ceramium rubrum</i>	3
<i>Amphiroa fragilissima</i>	3	" <i>Falkenbergia hillebrandii</i> " stage of <i>Asparagopsis</i>	3
<i>Bostrychia binderi</i>	6	<i>Halymenia bermudensis</i>	3
<i>Bostrychia montagnei</i>	94	<i>Laurencia obtusa</i>	3
<i>Bostrychia tenella</i>	3	<i>Wurdemannia miniata</i>	3

PHAEOPHYTA

Sargassum bermudense 3

MAGNOLIOPHYTA

<i>Akebia quinata</i>	3	<i>Nerium oleander</i>	6
<i>Asparagus plumosus</i>	9	<i>Opuntia dilleni</i>	3
<i>Asparagus sprengeri</i>	36	<i>Pittosporum undulatum</i>	9
<i>Avicennia germinans</i>	73	<i>Rhizophora mangle</i>	85
<i>Borrchia arborescens</i>	12	<i>Ruppia maritima</i>	3
<i>Borrchia frutescens</i>	30	<i>Sabal bermudana</i>	6
<i>Carpobrotus chilensis</i>	3	<i>Salicornia perennis</i>	21
<i>Casuarina equisetifolia</i>	6	<i>Schinus terebinthifolia</i>	42

<i>Coccoloba uvifera</i>	6	<i>Sesuvium portulacastrum</i>	33
<i>Conocarpus erectus</i>	22	<i>Syringodium filiforme</i>	15
<i>Ficus lentiginosa</i>	3	<i>Tamarix gallica</i>	12
<i>Foeniculum foeniculum</i>	3	<i>Tamarix hispida</i>	6
<i>Halodule bermudensis</i>	6	<i>Thalassia testudinum</i>	15
<i>Ipomoea</i> sp.	6	<i>Typha angustifolia</i>	3
<i>Leucaena glauca</i>	3	<i>Wedelia perfoliata</i>	33
<i>Musa cavendishii</i>	3		

PORIFERA

<i>Acervochalina molitba</i>	3	<i>Leucetta imberbis</i>	3
<i>Acervochalina crassiloba</i>	3	<i>Lissodendoryx isodictyalis</i>	3
<i>Aplysilla longispina</i>	3	<i>Megalopastas nux</i>	3
<i>Biemna microstyla</i>	3	<i>Mycale microsigmatosa</i>	3
<i>Chondrilla nucula</i>	3	<i>Niphates erecta</i>	3
<i>Cinachyrella apion</i>	5	<i>Oceanapia coela</i>	3
<i>Desmascula desdemona</i>	3	<i>Suberites</i> sp.	6
<i>Dysidea etheria</i>	3	<i>Tedania ignis</i>	3
<i>Eurypon clavatum</i>	3	<i>Terpios aurantiaca</i>	6
<i>Geodia gibberosa</i>	3	<i>Tethya actinia</i>	6
<i>Hymeniacidon</i> sp.	3	<i>Ulosa ruetzleri</i>	6
<i>Leucandra aspersa</i>	3		

CNIDARIA

<i>Aiptasia pallida</i>	9	<i>Cassiopea xamachana</i>	21
<i>Bartholomea annulata</i>	6	<i>Palythoa mammilosa</i>	3

ANNELIDA

<i>Arenicola cristata</i>	9	Sabellidae	6
Spirorbidae	9		

MOLLUSCA

<i>Assiminea succinea</i>	6	<i>Littorina angulifera</i>	15
<i>Batillaria minima</i>	15	<i>Melampus coffeus</i>	9

<i>Brachydontes domingensis</i>	3	<i>Mitrella ocellata</i>	15
<i>Cerithium lutosum</i>	15	<i>Ovatella myosotis</i>	3
<i>Hydrobia bermudae</i>	6	<i>Pedipes mirabilis</i>	3
<i>Isognomon alatus</i>	6	<i>Truncatella caribaeensis</i>	6
<i>Lasaea adansoni</i>	6		

BRYOZOA

<i>Amathia vidovici</i>	3	<i>Watersiporia subovoidea</i>	6
<i>Bugula neritina</i>	6	<i>Zoobotryon verticillatum</i>	3
<i>Schizoporella serialis</i>	6		

ARTHROPODA

<i>Alpheus</i> sp.	3	<i>Ligia baudiniana</i>	15
<i>Callianassa branneri</i>	3	<i>Mithrax forceps</i>	3
<i>Callinectes sapidus</i>	3	<i>Nephila clavipes</i>	33
<i>Cardisoma guanhumii</i>	6	<i>Pachygrapsus gracilis</i>	33
<i>Clibanarius tricolor</i>	6	<i>Panopeus herbstii</i>	3
<i>Garteracantha</i> sp.	30	<i>Sesarma ricordi</i>	6
<i>Gecarcinus lateralis</i>	9	<i>Stenopus hispidus</i>	3
<i>Goniopsis cruentata</i>	33		

ECHINODERMATA

<i>Synaptula hydriformis</i>	6
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TUNICATA

<i>Aplidium bermudae</i>	3	<i>Ecteinascidia conklini</i>	6
<i>Aplidium exile</i>	3	<i>Ecteinascidia turbinata</i>	6
<i>Botrylloides nigrum</i>	3	<i>Leptoclinum macdonaldi</i>	3
<i>Clavelina oblonga</i>	3	<i>Perophora viridis</i>	3
<i>Clavelina picta</i>	3	<i>Phallusia nigra</i>	3
<i>Cystodytes dellechiaiei</i>	3	<i>Polycitor capsulatus</i>	3
<i>Didemnum candidum</i>	6	<i>Styela plicata</i>	3
<i>Distaplia bermudensis</i>	3		

CHORDATA

<i>Anolis grahami</i>	24	<i>Eleutherodactylus johnstoni</i>	33
<i>Bufo marinus</i>	12	<i>Malaclemys terrapin</i>	6
<i>Chelonia mydas</i>	3		

Table 3. Mean vertical zones above low-water level and their standard deviations, of the dominant plant species in Bermudian bay and lagoon mangrove swamps. Tidal heights are in cm above chart datum.

Species	Part of plant	Tidal Heights	
		Lower Limit	Upper Limit
<i>Rhizophora mangle</i>	Prop Roots	22.0 ±16.9	80.7 ±25.7
<i>Rhizophora mangle</i>	Canopy ¹	11.3 ±14.6	110.7 ±66.2
<i>Rhizophora mangle</i>	Trunks ¹	33.0 ±16.3	70.0 ±17.8
<i>Avicennia germinans</i>	Pneumat.	34.7 ±13.0	85.3 ±26.8
<i>Avicennia germinans</i>	Canopy ¹	26.0 ±22.5	148.3 ±76.7
<i>Avicennia germinans</i>	Trunks ¹	48.7 ±14.1	84.7 ±29.4
<i>Conocarpus erectus</i>	Canopy ¹	82.5 ±53.0	307.5 ±145.0
<i>Conocarpus erectus</i>	Trunks ¹	125.0 ±7.1	267.5 ±109.6
<i>Schinus terebinthifolia</i>	Canopy ¹	116.7 ±37.9	150.0 ±60.6
<i>Schinus terebinthifolia</i>	Trunks ¹	140.0 ±52.2	151.7 ±47.3
<i>Bostrychia montagnei</i>	Entire	25.0 ±22.3	71.0 ±17.1
<i>Rhizoclonium kernerii</i>	Entire	38.8 ±24.9	68.8 ±17.5
<i>Rhizoclonium riparium</i>	Entire	31.3 ±20.7	96.3 ±25.1
<i>Borrchia frutescens</i>	Entire	85.0 ±24.5	133.8 ±40.9

<i>Sesuvium portulacastrum</i>	Entire	68.0 ±20.8	106.0 ±47.2
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¹At sediment surface vertically below limit.

For comparison, tidal levels are: Mean Low Tide Level 30 cm, Mean Tide Level 70 cm, Mean High Tide Level 105 cm and Extreme High Tide Level 150 cm.

The average bay or lagoonal mangrove in Bermuda is about 25m wide, dominated intertidally by *R. mangle* and *A. germinans*, the former forming the seaward fringe and the latter the mid-portion of the community, but usually with considerable overlap. Above the high-tide mark, *C. erecta* and *S. terebinthifolia* intermingle on rising drier ground. The height of the canopy top for these four species lies between 5 and 6 m. On prop-roots and pneumatophores in the lower to mid-intertidal, the red alga *Bostrychia montagnei* Harvey is ubiquitous together with the green filamentous alga *Rhizoclonium kernerii* Stockmeyer, whereas *R. riparium* Harvey occurs in patches throughout the intertidal but not generally on the mangroves. *Sesuvium portulacastrum* L. is scattered above mean tidal level, giving way to an irregular band of *Borrchia frutescens* (L.) A. P. de Candolle around high tide mark. A wide variety of associated fauna and flora were found but none were regular and many were at a single location only (Table 2). The best developed and most diverse mangrove is at Hungry Bay on the south shore (Fig. 4a). This is the only Bermuda mangrove with a well developed drainage channel. The width of the swamp reaches 90 m, the canopy height exceeds 10 m in places, and there is no zonation among red and black mangroves, which are completely intermingled. The giant land crab, *Cardisoma guanhumi* Latreille, rare in Bermuda is common on the landward fringe, and the coffee-bean marsh snail, *Melampus coffeus* (L.), is found at only three locations, abundant in the upper intertidal. Trunk diameters of mangrove trees were largest here, with *A. germinans* reaching 36 cm and *R. mangle* to 27 cm.

The structure of pond mangroves (Fig. 3) differs considerably from that of bay mangroves. They are narrower, only 14.8 ± 11.2 m wide compared to 30.6 ± 20.1 for bay mangroves, but have a similar canopy height and are more varied. Mono-specific stands of either *R. mangle* or *A. germinans*, are typical (Table 2) in Bermuda ponds, but red and black mangroves are sympatric in Evans pond and Walsingham Pond. However, in Evans Pond, black mangroves dominate and red mangroves are scattered individuals except at the eastern end (see profile Fig. 3a). In the largest pond mangroves of Mangrove Lake and Trotts Pond, black mangroves are absent, as they are at the smaller Compston Pond and they are not abundant at Walsingham Pond. In contrast at Lovers Lake, red mangroves are absent. In the former pond (now connected to the sea) at Paget Island, red mangroves are confined to a few young trees at the seaward margin of the swamp, suggesting an earlier monospecific stand of *A. germinans*.

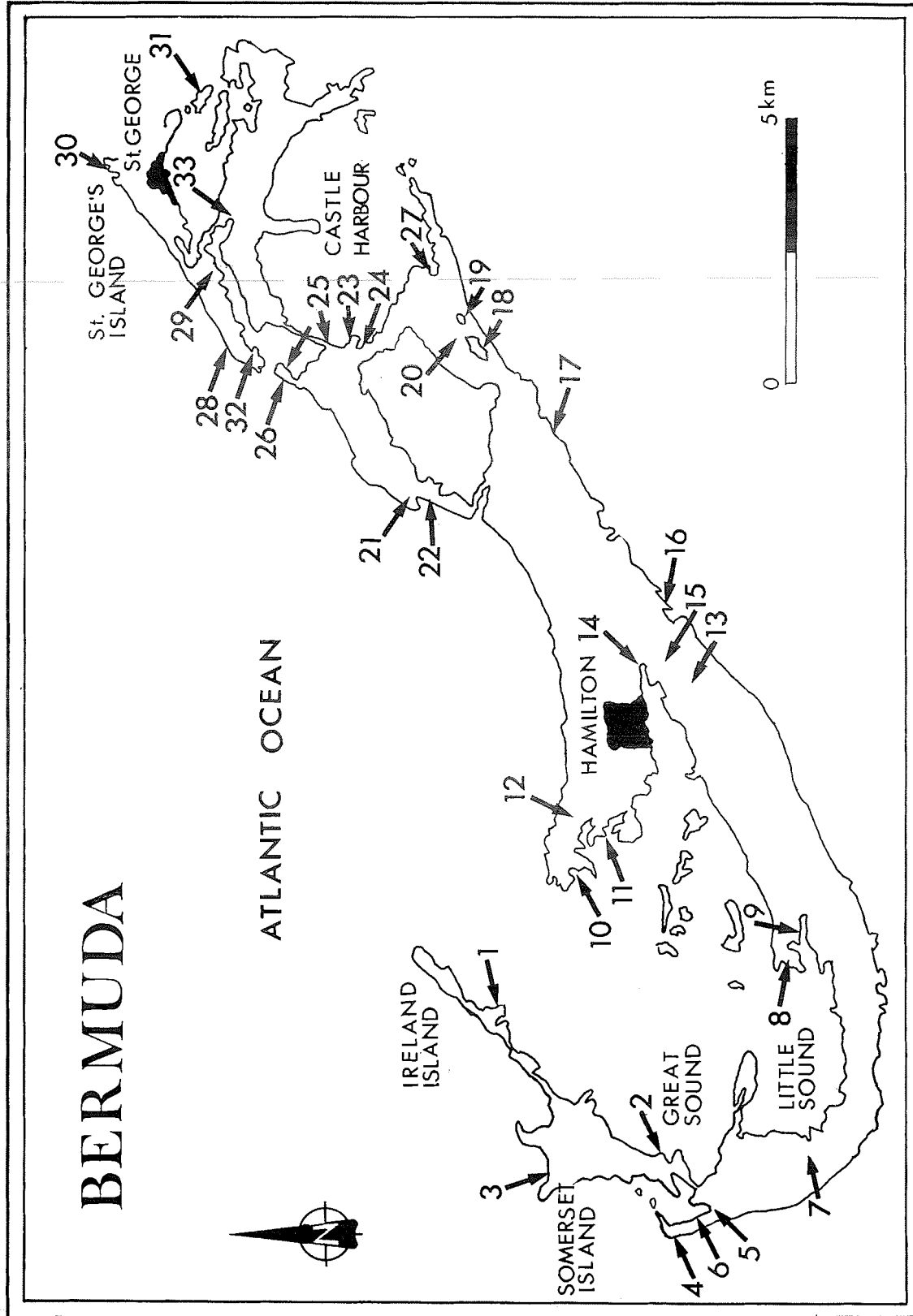


Figure 1. The Bermuda Islands showing the locations of the mangrove swamps surveyed. For locality names see Table 1.

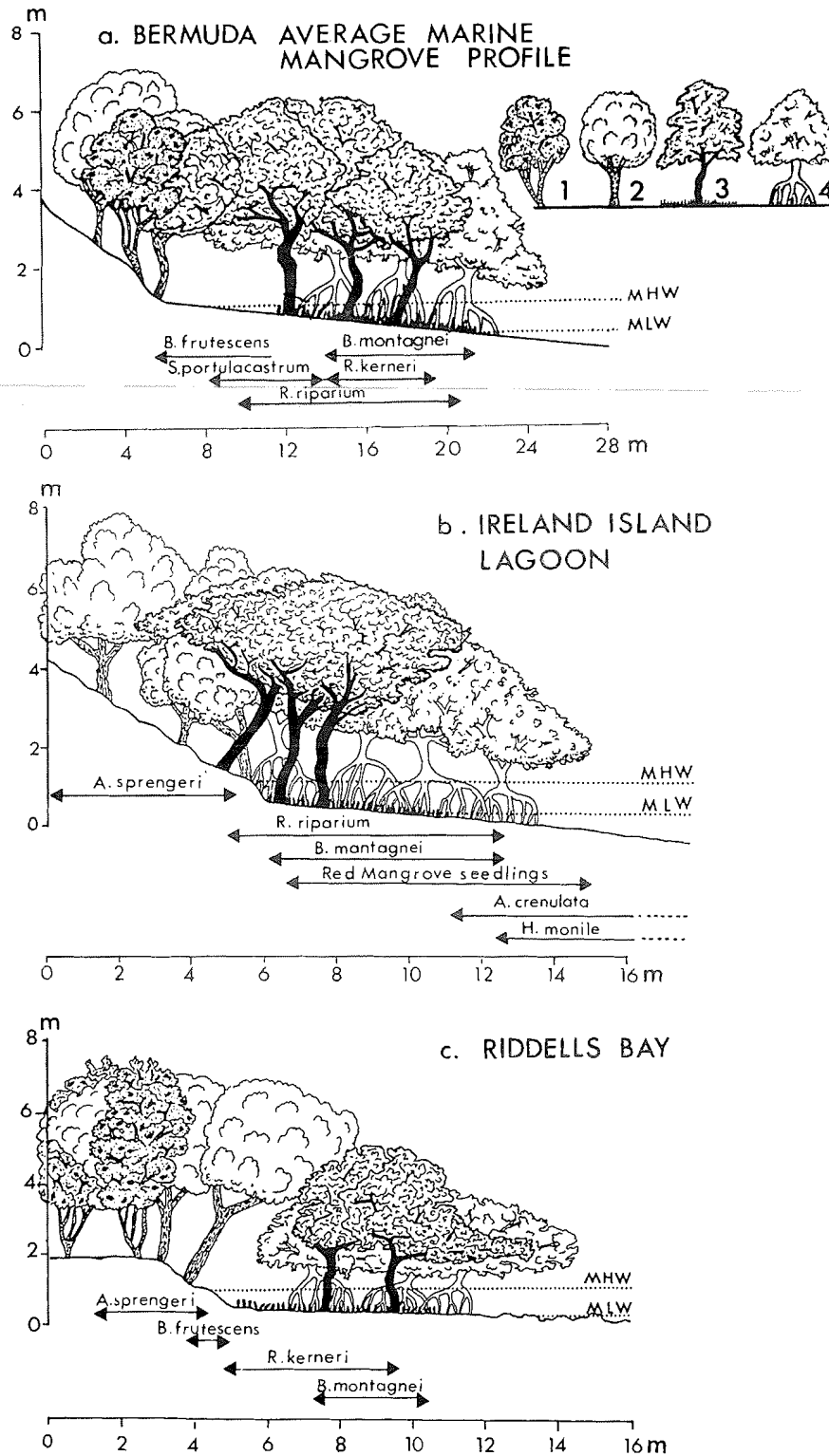


Figure 2. Profiles of Bermudian marine mangrove swamps: 2a, Profile for the average marine mangrove and key. 1=*Schinus terebinthifolia*, 2=*Conocarpus erectus*, 3=*Avicennia geminans*, 4=*Rhizophora mangle*; 2b, Ireland Island Lagoon; and 2c, Riddells Bay.

Species are as in Table 2. MHW = Mean high water. MLW = Mean low water.

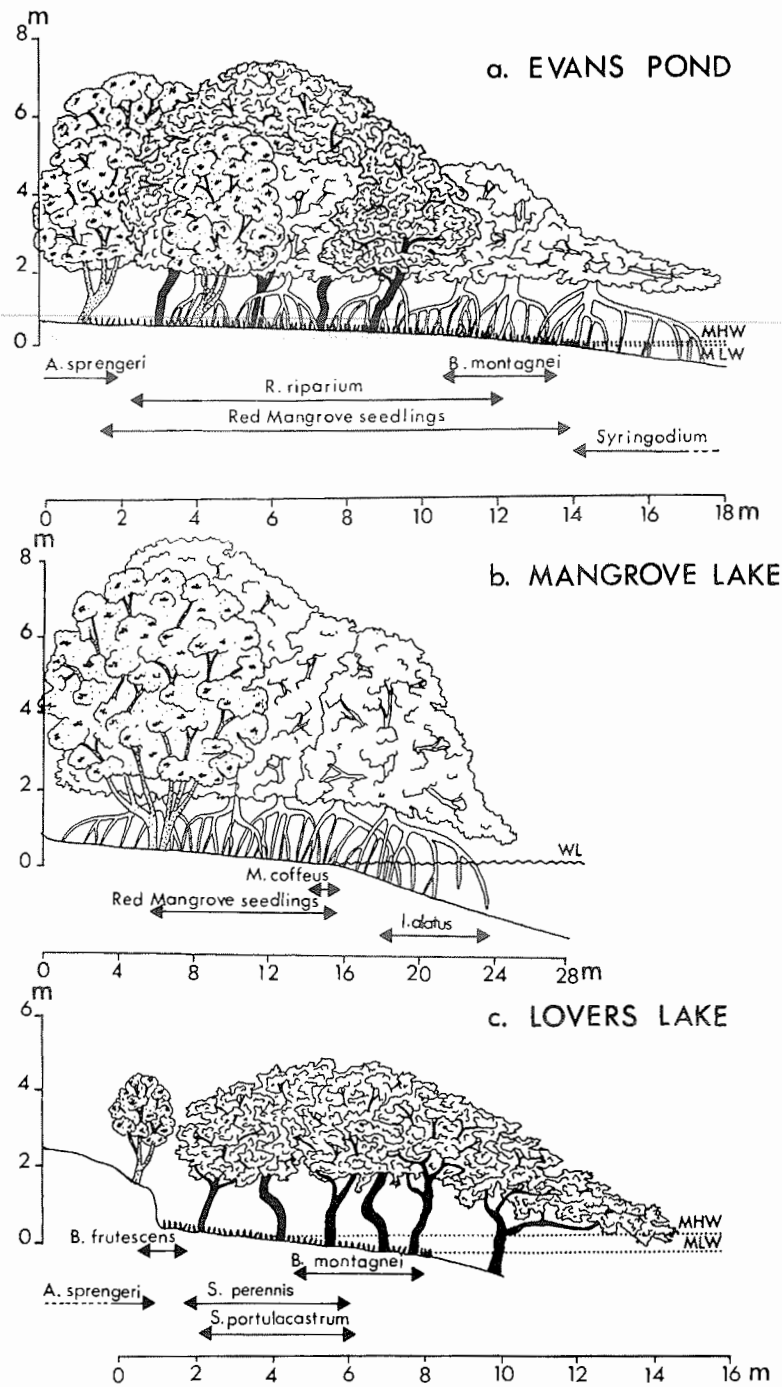


Figure 3. Profiles of Bermudian pond mangroves swamps: 3a, Evans Pond; 3b, Mangrove Lake; and 3c, Lovers Lake. Key and abbreviations as in Figure 2.

a. HUNGRY BAY

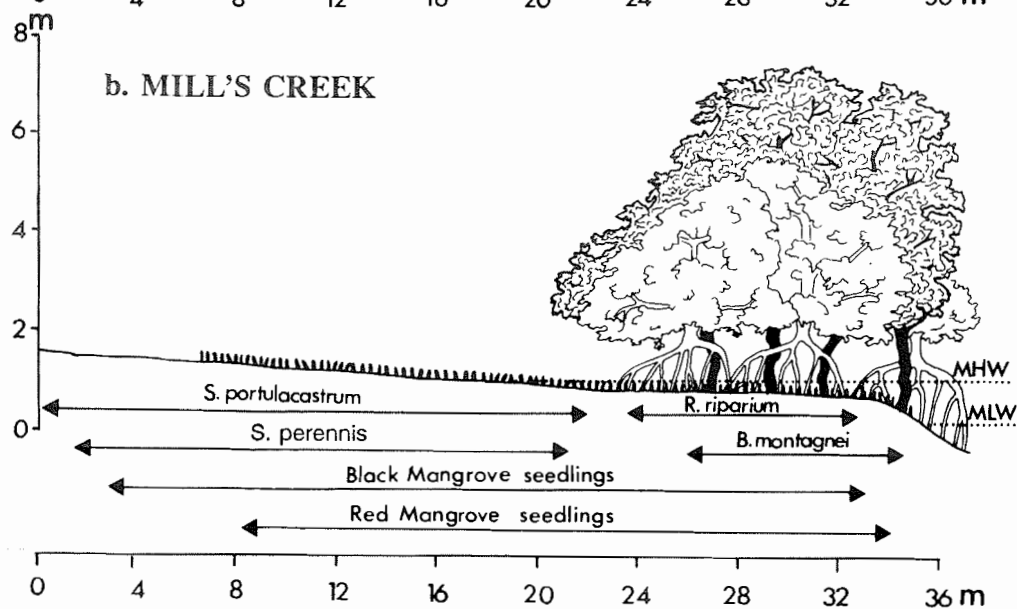
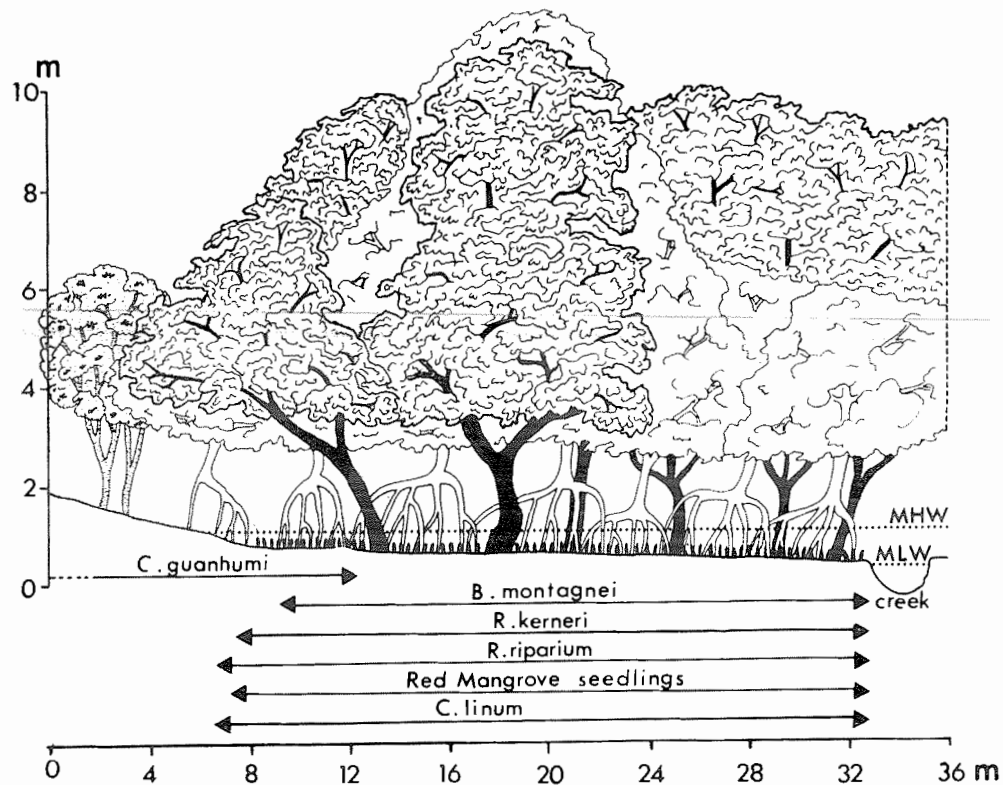


Figure 4. Comparison of two profiles: 4a, Profile of the "Great Mangrove" at Hungry Bay; and 4b, Profile of a mangrove swamp-salt marsh complex at Mill's Creek. Key and abbreviations as in Fig. 2.

About 150 species of macrobiota (Table 1) have been identified from the Bermuda mangroves but only a few species have wide distribution among the mangrove swamps. Seventy-three species (48.7%) were found at a single locality, while only 16 species (10.7%) occurred at 10 or more sites and only four species were present in over 50% of the mangroves. This unexplained discontinuity of distribution generally obscures correlations with obvious physical environmental factors but, the pond mangroves tend to have unique assemblages of associated species. For example, *B. montagnei*, ubiquitous in the bay mangroves, occurs only in the mangrove ponds Walsingham Pond and Lovers Lake. The mangrove oyster, *Isognomon alatus* (Gmelin), and the sponges, *Terpios aurantiaca* Duchassaing & Michelotti and *Chondrilla nucula* Schmidt, occur only in Mangrove Lake and Trotts Pond, the ascidian *Styela plicata* (Lesueur) only in Evans Pond, the holothurian *Synaptula hydriformis* (Lesueur) only in Evans Pond and Lovers Lake, and a host of species, including the endemic *Sargassum bermudae* Grunow, is unique to Walsingham Pond.

In a few locations, mangrove swamps adjoin small salt marshes dominated by *Sesuvium portulacastrum* and/or *Salicornia perennis* Miller with associated *Borrhchia arborescens* (L.) A. P. de Candolle. At Mill Creek (Fig. 3b) the salt marsh lies landward of the mangrove whereas at Foot of Crow Lane it fringes the mangrove to the seaward.

The abundance of trees is highly variable among the swamps, the overall mean for *R. mangle* being $3842 \pm 2415 \text{ ha}^{-1}$ and for *A. germinans* $2044 \pm 2200 \text{ ha}^{-1}$. The high standard deviations prevent any correlations with physical or biotic factors.

DISCUSSION

Bay and lagoonal mangrove swamps in Bermuda, although they are smaller, are structurally and floristically similar to those of Florida (Davis 1940, Lugo and Snedaker 1975, Ball 1980), except that overall plant diversity is lower, a situation normal in oceanic islands where opportunities of immigration and colonisation are reduced (Mac Arthur and Wilson 1967). Lot-Helgueras *et al.* (1975) have described floristic characteristics of mangroves at their northern limit in the Gulf of Mexico, a situation comparable to Bermuda, except for latitude and the significant rainfall change within the transitional belt in Mexico. In the Gulf of Mexico, *A. germinans* extends furthest north to 27.3°N, followed by *C. erectus* to 25.7°N; *R. mangle* and *L. racemosa* both stop at about 24°N, however, north of about 23°N, *R. mangle* trees are stunted and poorly developed; at this latitude the floristic composition of the swamp and tree size is similar to Bermuda, except that *Batis maritima* L., very common in the Gulf of Mexico, is absent in Bermuda. South of this latitude in the Gulf of Mexico the mangrove swamps have many more plant species than in Bermuda (Lot-Helgueras *et al.* 1975).

Monospecific stands of either *A. germinans* or *R. mangle* are common in Bermudian pond mangroves at different locations (Table 1). All the Bermudian ponds are relatively close to the sea and the anchialine ones are very close, thus

opportunities for colonisation via the sea may not differ greatly among the ponds. It might be expected that the smaller propagules of *A. germinans* would be transported overland more readily than the larger ones of *R. mangle*, however, several of the more inland swamps such as Mangroville, Paget Marsh and Compston Pond, are colonised by *R. mangle*, while only one, Commonland Marsh supports *A. germinans*. Three of the anchialine ponds have large connections to the sea through which propagules could pass. Of these, Lovers Lake has a monospecific black mangrove stand, Evans Pond supports a community strongly dominated by black mangroves, and Walsingham Pond is principally a red mangrove forest with a few black mangroves. There is no evidence that the presence of either species is related to tidal range or salinity. Both red and black mangroves appear to be equally capable of colonising marine ponds, however, once either alone is established, it appears to be able to occupy the entire zone colonised by both species in Bermudian bay mangroves, resulting in the essentially monospecific stands in inland mangroves. Even where the black mangrove has become established, either through man-made connections as in Paget Island, human introduction as in Evans Pond or natural processes as in Walsingham Pond, typical zonation never develops and the red mangrove characteristically exists as scattered trees or in small clumps.

The times of colonisation of the Bermuda ponds by mangroves are not known, most were basically as they are now when the first settlers arrived (Lefroy 1884), however, Paget Island pond was connected to the sea about 1950 and red mangrove embryos were introduced into Evans pond in the 1970's (D. Wingate *pers. com.*). In the latter case, it is likely that there were a few red mangroves present prior to the introduction since the examination of a few old trunks showed greatly in excess of 20 annual rings, however, a noticeable increase in red mangrove abundance has occurred near to the introduction site but not elsewhere.

The high overall, but low site, total species diversity in the Bermudian mangroves is difficult to explain. Opportunities for colonisation in all but a few isolated inland stands appear not to differ greatly. It seems probable that environmental differences between sites may result in differential rates of settlement, mortality and growth. Some species may have had their distributions reduced by coastal pollution, since it is known that this has happened in the case of *I. alatus*, the mangrove oyster, formerly common in coastal mangroves (Sterrer 1986).

There is no evidence of active succession in Bermudian mangroves most are remarkably stable, reductions being mainly attributable to man's activities. *Schinus terebinthifolia*, a fairly recent introduction is invading the drier, landward fringe of the mangroves. Ball (1980), in studying secondary succession, found long-term stability in Florida mangroves. In fact active succession in mangroves is mostly confined to areas of active sediment accretion (e.g., Davis 1940, Chapman 1944, 1977). West's (1977) observation that there is such great variation in zonation patterns that they do not form a good model for succession, is borne out in the Bermudian mangroves. Mangrove tree abundances are very similar to those cited for Florida by Lugo and Snedaker (1975).

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