Pollen Evidence of Late Holocene Mangrove Development in Bermuda

Joanna C. Ellison

Global Ecology and Biogeography Letters, Vol. 5, No. 6. (Nov., 1996), pp. 315-326.

Stable URL:
http://links.jstor.org/sici?sici=0960-7447%28199611%295%3A6%3C315%3APEOLHM%3E2.0.CO%3B2-M

Global Ecology and Biogeography Letters is currently published by Blackwell Publishing.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://uk.jstor.org/about/terms.html. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://uk.jstor.org/journals/black.html.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

http://uk.jstor.org/
Thu Jun 8 14:08:46 2006

Global Ecology and Biogeography Letters (1996) **5**, 315–326

RESEARCH ARTICLE

Pollen evidence of Late Holocene mangrove development in Bermuda

JOANNA C. ELLISON* *Department of Geography, University of California at Berkeley, Berkeley, CA 94720, U.S.A.*

Abstract. Bermuda is the northern latitudinal limit for mangroves, but communities are diverse and productive. Two pollen diagrams from the largest mangrove area show vegetation changes over the last 5000 years. From 5000 to 2100 years ago this was a marsh wetland, and pollen evidence is also shown of the dryland endemic forest before colonisation of Bermuda. Establishment of mangroves has only occurred in the last 3000 years, when sea-level rise slowed from 26 to 7 cm/100 years. Flotation experiments indicate that propagules could readily colonize from the Caribbean, and evidence both of cooler climate during the glacial and that none of Bermuda's many endemics utilize a mangrove habitat suggests that mangroves have had discontinuous presence in Bermuda through the Late Pleistocene. This study shows that mangrove ranges may be more plastic than was previously thought, subject to availability of habitats rather than dispersal capability.

Key words. Mangrove, Holocene, Bermuda, dispersal, pollen.

INTRODUCTION

Bermuda is a group of limestone islands located in the N.W. Atlantic Ocean (Fig. 1). At 32°N, Bermuda is the most northerly location in the world for mangroves as well as coral-algal reef communities, and owes its sub-tropical climate to eddies of the warm Gulf Stream that passes to the west and north. The climate is mild, with temperatures between 20°C and 30°C, and evenly distributed rainfall averaging 1470 mm per annum (Morris *et al.*, 1977).

The islands lie on the Bermuda Seamount, a volcanic peak rising 4000 m from the seafloor of the Sargasso Sea. Dating of basalt indicates that it began to form on, or near, the mid-Atlantic ridge approximately 110 million years ago, and has since drifted to the west, ceasing major volcanic activity about 30 million years ago (Rowe, 1990). Capping the volcanic pedestal is a layer of eolianite limestone of maximum depth 300 m, derived from lithified coral sand-dunes of Late Pleistocene interglacials (Land, Mackenzie & Gould, 1967). This gives the island a rolling hill topography, of maximum elevation 79 m.

The Holocene sea-level transgression has been shown by dating of basal peat deposits from the several marshes and ponds inland in Bermuda (Redfield, 1967; Neumann, 1971; Wanless, 1982). Between 8000 and 3000 years BP sea level rose at about 26 cm/100 years, and in the last 3000 years sea level rose at an average of 7 cm/100 years.

Bermuda has many small mangrove areas, mostly occurring in inland anachaline ponds, or narrow coastal fringes (Thomas, 1993). Despite the small area, mangroves of Bermuda are of interest owing to their latitude and isolation. There is a distance of 1070 km to the nearest land at Cape Hattaras, and 1600 km to the nearest mangrove community in NE Florida. Woodroffe & Grindrod (1991) suggested that contraction and expansion of mangrove ranges may have occurred with climate and sea-level changes of the Quaternary, although limited palynological or historical evidence exists.

Mangroves are also of significance to Bermuda, being the only remaining native forest areas. The unique native dryland forest composed largely of the endemics *Juniperus bermudiana* L. (Bermuda cedar), *Sabal bermudana* (Bailey) (Bermuda palmetto) and

*Present address: Australian Institute of Marine Science, PMB No. 3, Townsville, Queensland 4810, Australia.

© 1996 Blackwell Science Ltd

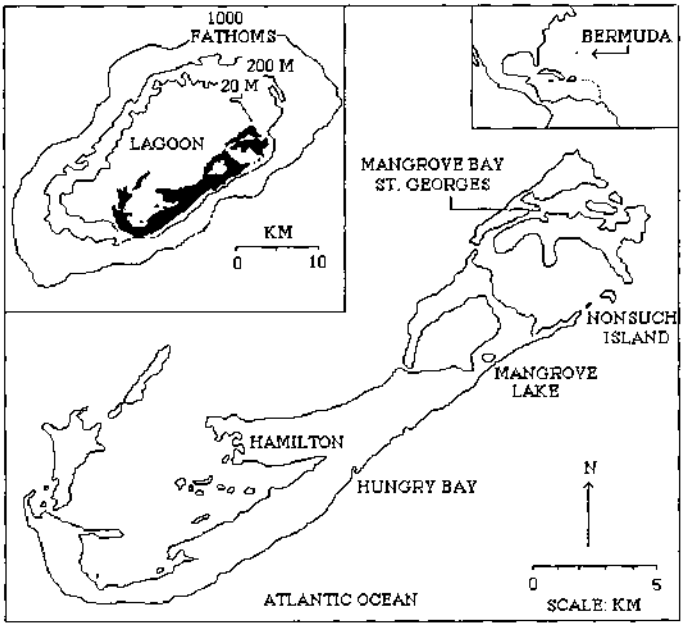

Fig. 1. Map of Bermuda, showing location in the Atlantic and on the Bermuda Platform, and locations mentioned in the text.

Elaeodendron laneanum A. H. Moore (Bermuda olivewood) has been entirely lost owing to high human population densities, introduction of aggressive exotics and the cedar blight of 1947 (Challinor & Wingate, 1971; Wingate, 1985).

This study investigates the Holocene history of mangroves in Bermuda from stratigraphic and pollen records of the largest mangrove area, and examines the dispersal capability of the mangroves by experimentation. Investigation is also made of pollen evidence of the natural dryland forest before colonization.

ECOLOGICAL DESCRIPTION OF HUNGRY BAY

Hungry Bay is the largest mangrove area in Bermuda, located on the south shore at 32°17′N, 64°45′W (Fig. 1). It is a peat-building swamp with direct exchange with the ocean, and supports diverse forest and shallow water communities.

The swamp is linear in shape, enclosed on three sides by limestone hills and open to oceanic exchange through one creek entrance. Bermuda has a microtidal range of 70–75 cm. The swamp is zoned as a Nature Reserve under the 1983 Development Plan, and a Tree Preservation Order protects the mangroves. Tomlinson (1986) described thirty-four species of mangroves in the world, of which eight occur in the Americas and West Africa, but only two species occur in Bermuda, *Rhizophora mangle* L. (red mangrove) and *Avicennia germinans* L. (L.) (black mangrove). *R. mangle* is the more common species, fringing lower elevations of creeks and the seaward edge, with a canopy of around 6 m. *A. germinans* is more common towards the dry land margins, and grows up to 10 m tall, shown on the left in Fig. 2. Lichens are very abundant on bark of mangrove trees, the most common are *Pyrenula aurantiaca* Fée and *Ramalina complanata* (Sw.) Ach.

Birds which occur in the mangrove swamp are *Ardea herodias* L. (great blue heron), the re-introduced *Nycticorax violacea* (L.) (yellow-crowned night heron), *Egretta thula* Molina (snowy egret), the introduced *Pitangus sulphuratus* (L.) (Kiskadee flycatcher) and *Anas platyrhinchos* L. (mallard).

Within the mangrove area, *Gecarcinus lateralis* Fréminville (red land crab) and *Goniopsis cruentata* Latreille (mangrove crab) occur, with burrows in the peat. *Ocypode quadrata* Fabricius (ghost crab) occurs at deeper locations in creeks, and *Clibanarius tricolor* Gibbes (hermit crab) on sandy ridges. Occasional

Fig. 2. Photograph of the eastern shore of Hungry Bay, showing mangroves dominated by *Avicennia* on the left, and strand vegetation of *Conocarpus*, *Coccoloba* and *Casuarina* on the right.

under upper intertidal leaf litter is *Melampus coffeus* (L.) (coffee bean shell). The land hermit *Coenibita clypeatus* (Fabricius) is found in sandy areas of Hungry Bay, and is now rare in Bermuda owing to lack of suitable shells, the whelk shells that they use being extinct since the 1800's (Sterrer, 1986). *Cardisoma guanhumi* Latreille (giant land crab) occurs in two colonies on the upper fringe of the mangrove swamp, which are the largest of the few remaining colonies in Bermuda.

Common fish in mangrove creeks are large schools of parrot fish (*Sparisoma viride* [Bonnaterre] and *Scarus coeruleus* [Bloch]), which feed on the abundant algal growth. Also occurring are *Holocanthus bermudensis* Goode (blue angel fish), *Abudefduf saxatilis* (L.) (sergeant majors), *Holocentrus rufus* (Walbaum) (longspine squirrel fish), *Pectrypops retrospinis* (Guichenot) (soldier fish), *Bothus lunatus* (L.) (peacock flounder) and juveniles of *Lutjanus griseus* (L.) (grey snapper), *Mugil trichodon* Poey (fantail mullet), *Kyphosus sectatrix* (L.) (Bermuda chub), *Sphyraena barracuda* (Walbaum) (great barracuda) and *Haemulon flavolineatum* Desmarest (yellow or French grunt). Occasional are *Octopus vulgaris* Cuvier (octopus), and *Lycodontis funebris* (Ranzani) (green moray).

The common algae on mangrove roots are the red algae *Bostrychia montagnei* Harv., the green algae *Caulerpa mexicana* (Sond.) J. Ag., *Chaetomorpha linum* (Müll.) Kütz., *Rhizoclonium hookeri* Kütz., and *Valonia macrophysa* Kütz. *Bugula neritina* (L.), an erect branching bryozoan, occurs on submerged objects such as mangrove roots. Deep mats of *C. linum* occur in landward margins of the swamp, possibly indicating cesspit seepage. Great rafts of *Sargassum natans* (L.) J. Meyen can be blown onto the swamp in winter storms.

On the SE edge of the mangrove swamp there are areas of marsh plants, with *Juncus acutus* L. (large marsh rush), *Sesuvium portulacastrum* L. (sea purslane), *Limonium carolinianum* (Walt.) Britton (sea lavender), *Paspalum vaginatum* Sw. (sheathed paspalum), *Salicornia perennis* Mill. (woody grasswort), and *Eustachys petraea* (Sw.) Desv. (West Indian grass). These areas are not extensive, but are of interest as they illustrate the position of Bermuda on the northern margins of tropical mangrove distributions and on the

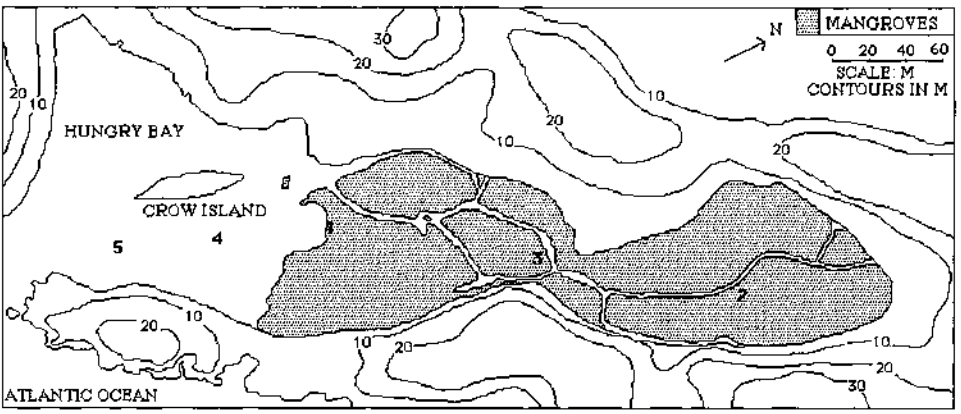

Fig. 3. Map of Hungry Bay mangrove swamp, showing core locations.

southern margins of temperate saltmarsh distributions.

Hungry Bay is a shallow bay (Fig. 3), fringed to the north and south by limestone rock, which outcrops in the centre of the bay as Crow Island, with the ocean entrance to the south west. There are sea anenome colonies of *Palythoa caribaea* Duch. & Mich. and *Zoanthus sociatus* (Ellis & Solander) on the north west rocky margin of the bay. In rock pools on the sea shore, and on the margins of Crow Island the chiton *Chiton tuberculatus* L. and the Gastropods *Tectarius muricatus* (L.) (beaded periwinkle), *Siphonaria alternata* (Say), *Nerita versicolor* (Gmelin) and *Fissurella barbadensis* (Gmelin) can be found. The Polychaete *Arenicola cristata* Stimpson burrows in sediment of the bay, its orange-coloured egg sacs can be seen.

Unmanaged coastal woodland occurs on the peninsula between the swamp and the ocean, giving examples of the invasion of aggressive introduced species into the small remaining forest areas of Bermuda.

Shown on the right in Fig. 2, clifftops are vegetated by the native trees *Conocarpus erectus* L. (buttonwood) and *Coccoloba uvifera* L. (bay grape), and emergent, introduced *Casuarina equisetifolia* L. Inland forest is dominated by the aggressive introduced trees *Casuarina*, *Livistona chinensis* R. Br. (Chinese fan palm), *Schinus terrebinthifolius* Raddi (Mexican pepper), and *Eugenia uniflora* L. (Surinam cherry). Also occurring are *Pittosporum undulatum* Vent., *Pimenta dioica* (L.) Merr. (Allspice), *Citharexylum spinosum* L. (fiddlewood), and *Tabebuia leucoxylon* D.C. (white cedar). The ground layer includes the herbs *Asparagus sprengeri* Regel (asparagus fern), *Jasminum simplicifolium* Forst. f. (jasmine), *Rhus radicans* L. (poison oak), *Bryophyllum pinnatum* (Lam.) Kurz. (life plant), *Sisyrinchium iridioides* Curtis (Bermudiana), *Euphorbia mesembrianthemifolia* Jacq. (coast spurge) and *Solidago sempervirens* L. (seaside goldenrod) and the fern *Adiatum bellum* T. Moore (maiden-hair fern).

METHODS

The Hungry Bay mangrove swamp and creek system was mapped by point-to-point survey. Results were plotted at 1:200 to produce Fig. 3.

Stratigraphy and pollen analysis

Cores were taken along a transect up the centre of the swamp (Fig. 3), and elevation of coring stations was determined by detailed survey (Ellison, 1993). Hiller corers were used, for ease of penetration through sand facies and wood. The corers were of 0.5 m and 1 m sample chamber length, and of 3 cm diameter. Cores were taken at low tide on rainless days, and sub-sampled at 10 cm intervals. Sample contamination was prevented by washing the corer each time with tap water carried into the swamp, and by wiping the spatulas used for sub-sampling. To avoid contamination from upper layers, the sampler was washed off before opening the cylinder. While coring, air bubbles rose through the hole, indicating that the chamber was air tight before opening. Colour of stratigraphic units was determined in the field by comparison with Munsell Soil Colour Charts. Samples

for dating were submitted to Beta Analytic for radiocarbon and carbon-13 analyses.

Subsamples from cores were concentrated for pollen analysis, by standard chemical treatments as described by Faegri & Iverson (1975). In addition, samples were filtered through a 250 μm mesh for extraction of larger peat fragments. The HF treatment for silicate sediments was not necessary owing to the limestone geology of Bermuda, allowing also for preservation of sponge spicule and diatom microfossils.

A pollen key was generated from a reference collection of pollen and spores of Bermuda flora, using flowers, herbarium samples, and the collection of B. Rueger. Pollen and spores were identified and counted on exclusive transects on each slide until a total of 200 fossil pollen and spores was exceeded for each level. Sponge spicules exceeding 20 m in length were also counted, and concentration determined by comparison with a known number of exotic *Lycopodium* spores added to the sample (Benninghoff, 1962).

Subsamples from cores were analysed for organic fraction, by loss on ignition techniques.

Propagule experiment

To investigate the hypothesis that the mangroves in Bermuda could readily colonise from Florida and the NE Caribbean, the flotation properties of *Rhizophora mangle* were tested. Propagules of *Avicennia germinans* were not available. 100 newly fallen hypocotyls were collected from a dry beach area in Hungry Bay, and placed in a salt water flow tank for 3 months. Numbers floating (horizontal, inclined and vertical) and sunk (horizontal and vertical) were counted over the period, as well as appearance of roots. The experiment was replicated using 100 hypocotyls from Mangrove Bay, St George's.

RESULTS

Survey produced the map of the mangrove swamp and creeks shown in Fig. 3, reduced from a 1:200 original plot. This indicated that the area of mangrove trees was 23,616 m^2 (5.83 acres), the area of creeks within the mangrove swamp was 1744 m^2 (0.43 acres), giving a total area for the mangrove swamp of 25,360 m^2 (6.26 acres).

Stratigraphy

Stratigraphic and dating results from cores are shown in Fig. 4, and core locations in Fig. 3.

Core HB-2 is located in the centre of the landward basin of the mangrove swamp, 10 m south of the creek. Above the rock base from 550 to 620 cm was a reduced clay (5Y 4/1), 15–20% organic. From 90 to 550 cm was black fibrous peat (7.5 YR 2/0), around 70% organic. Peat above the basal clay was dated at 4940 ± 100 yr BP, and peat from 80–90 cm depth was dated at 730 ± 80 yr BP. Above 90 cm depth was red-black fibrous peat (10 YR 2/1), with red wood chips, 60–70% organic.

Core HB-3 is between cores 1 and 2, where the mangrove swamp narrows between the seaward and landward basins. This provided 95 cm depth of reddish brown peat (10 YR 2/1), 47–68% organic. The creek close to core HB-3 is 1 m deep, and the base at this point is limestone rock.

Core HB-1 is located in the centre of the seaward margin of the mangroves. Above the rock base from 575 to 620 cm was a reduced clay (5YR 4/1), 20–30% organic. From 575 to 260 cm depth was black fibrous peat (7.5 YR 2/0), 50–65% organic. Peat above the basal clay, from 550 to 560 cm depth, was dated at 4870 ± 90 yr BP, and peat from 240 to 250 cm was dated at 2090 ± 90 yr BP. From 260 to 250 cm depth was a calcareous sandy layer, 26% organic, with a high concentration of ostracods. From 65 to 245 cm was red-black fibrous peat (10 YR 2/1), with red wood chips, 45–60% organic, and peat from 65 to 70 cm was dated at 390 ± 90 yr BP. From 65 cm depth to the surface was a mixture of organic mud and calcareous silt, 4–30% organic.

Two cores were taken from the open water of Hungry Bay, extending the transect to the south of Crow Island, with corresponding stratigraphy to HB-1. Both had a reduced clay above bedrock, from 290 to 404 cm in HB-4 and 227 to 250 cm depth in HB-5. A basal peat sample from HB-5 gave a date of 3990 ± 100. Above the clay was dark brown peat, from 150 to 290 cm depth in HB-4 and 160 to 227 cm depth in HB-5. Above this was red-brown peat from 25 to 140 cm depth in HB-4, where the transition was marked by a calcareous sand layer, and 25 to 160 cm depth in HB-5. Above the peat was calcareous shelly sand of 25 cm depth in both cores. Peat from beneath the capping sand layer gave a date of 750 ± 60 yr BP in HB-4 and 1460 ± 60 yr BP in HB-5.

Pollen analysis

Results from pollen analysis of cores HB-1 and HB-2 are given in Figs 5 and 6. Both cores show a record

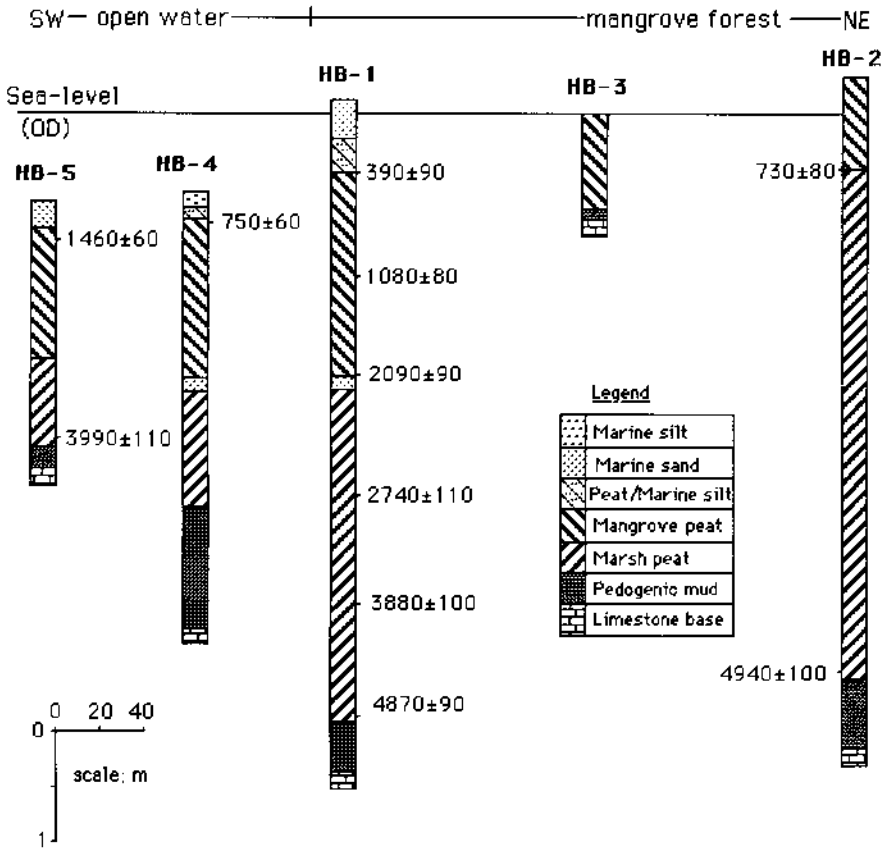

Fig. 4. Stratigraphy and radiocarbon dates of Hungry Bay.

for the last 5000 years, and have four corresponding pollen zones.

In core HB-1, zone 1 extends from 575 to 250 cm depth, 4870 ± 90 to 2090 ± 90 yr BP. This is dominated by forest pollen, particularly *Juniperus bermudiana* and *Sabal bermudana*. *Elaeodendron laneatum* is consistently present, and there is occasional occurrence of spores of the fern *Adiatum bellum*, common on shaded rocks. There is evidence of the local wetland, with consistent occurrence of Cyperaceae, also occasional *Acrostichum aureum* L., *Osmunda cinnamomea* L., and *Scirpus validus* Vahl. Zone 2 extends from 240 to 80 cm depth, 2090 ± 90 yr BP to 390 ± 90 yr BP, and is dominated by mangrove pollen. Between 240 and 220 cm depth pollen of *Rhizophora mangle* rises from 2 to 32.5%, and maintains high representation through zone 2. Pollen of *Avicennia germinans* increases towards the top of zone 2. The dry forest species that dominated zone 1, *Juniperus bermudiana*, *Sabal bermudana* and *Elaeodendron laneatum*, continue to be present.

Zone 3 extends from 80 to 30 cm depth, from 390 ± 90 yr BP towards the present, and is characterized by the appearance of pollen of introduced species, *Plantago lanceolata* L., *Casuarina equisetifolia* and *Apium leptophyllum* F. Muell., and an increase in Graminae. *Juniperus bermudiana* continues to be present, but pollen of *Sabal bermudana* and *Elaeodendron laneatum* becomes rare. The pollen assemblages continue to be dominated by the mangroves *Rhizophora mangle* and *Avicennia germinans*. There is a great increase in concentrations of siliceous sponge spicules in this zone.

Zone 4 extends from 20 cm depth to the surface, and is characterized by a sudden decline in pollen of *Juniperus bermudiana* at 20 cm depth, and an increase in pollen of *Casuarina equisetifolia*. The pollen

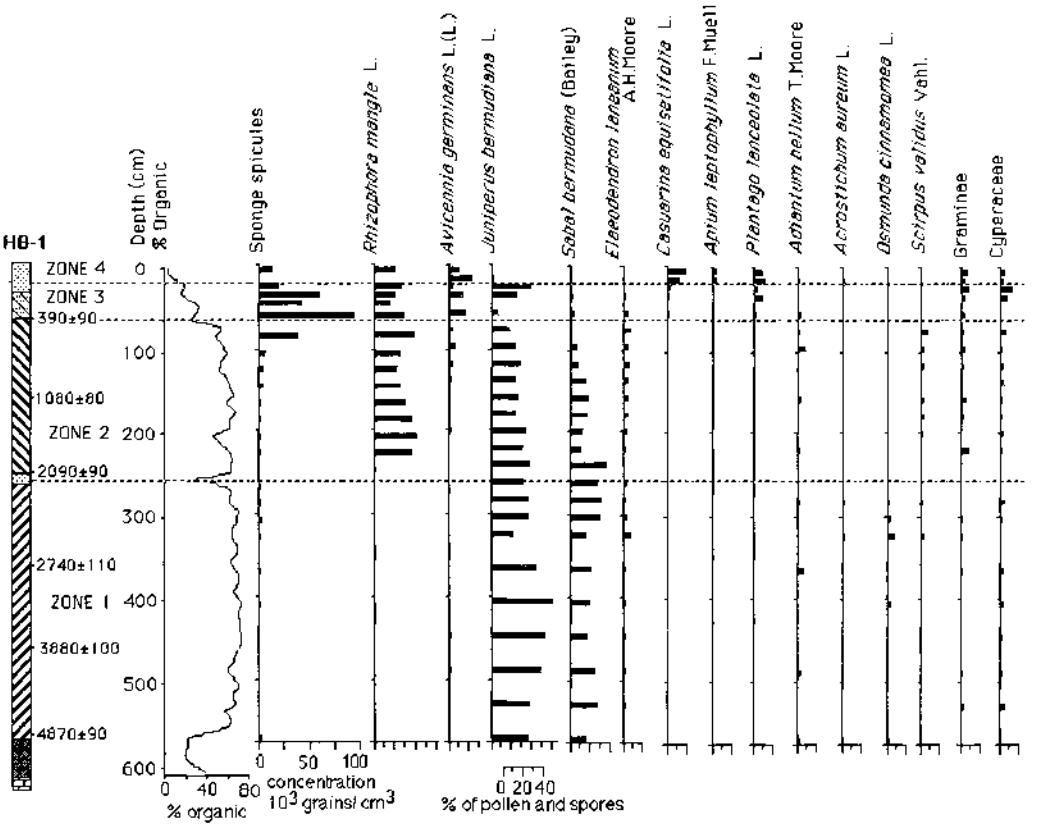

Fig. 5. Pollen diagram of core HB-1, also showing sponge spicule concentration and percent organic of sediment.

assemblages continue to be dominated by mangrove pollen of *Rhizophora mangle* and *Avicennia germinans*, and the introduced species *Plantago lanceolata* and *Apium leptophyllum* continue to be present.

In core HB-2, zone 1 extends from 550 to 100 cm depth, 4940 ± 100 yr BP to 730 ± 80 yr BP (Fig. 6). This is dominated by forest pollen, *Juniperus bermudiana* and *Sabal bermudana*. There is consistent presence of *Elaeodendron laneatum* and spores of *Adiatum bellum*. There is evidence of the local wetland, with consistent occurrence of Cyperaceae, also occasional *Acrostichum aureum* and *Scirpus validus*.

Zone 2 extends from 100 to 50 cm depth, 730 ± 80 yr BP towards the present, and is dominated by mangrove pollen of *Rhizophora mangle* and *Avicennia germinans*. Pollen of the dry forest species of zone 1, *Juniperus bermudiana*, *Sabal bermudana* and *Elaeodendron laneatum* remain high.

Zone 3 extends from 50 to 20 cm depth, and is characterized by the appearance of introduced species, particularly *Plantago lanceolata* and *Apium leptophyllum*. Pollen of the dry forest species *Sabal bermudana* and *Elaeodendron laneatum* decline, although *Juniperus bermudiana* is still common. Pollen assemblages of this zone continue to be dominated by the mangrove pollen of *Rhizophora mangle* and *Avicennia germinans*.

Zone 4 extends from 20 cm depth to the surface, and is characterized by sudden decline in pollen of *Juniperus bermudiana*, and increase in pollen of *Casuarina equisetifolia*. Pollen assemblages of this zone continue to be dominated by the mangrove pollen of *Rhizophora mangle* and *Avicennia germinans*, and there is an increase in concentrations of sponge spicules.

Propagule experiment

Results on flotation capabilities of Bermuda's *Rhizophora mangle* propagules are plotted in Fig. 7.

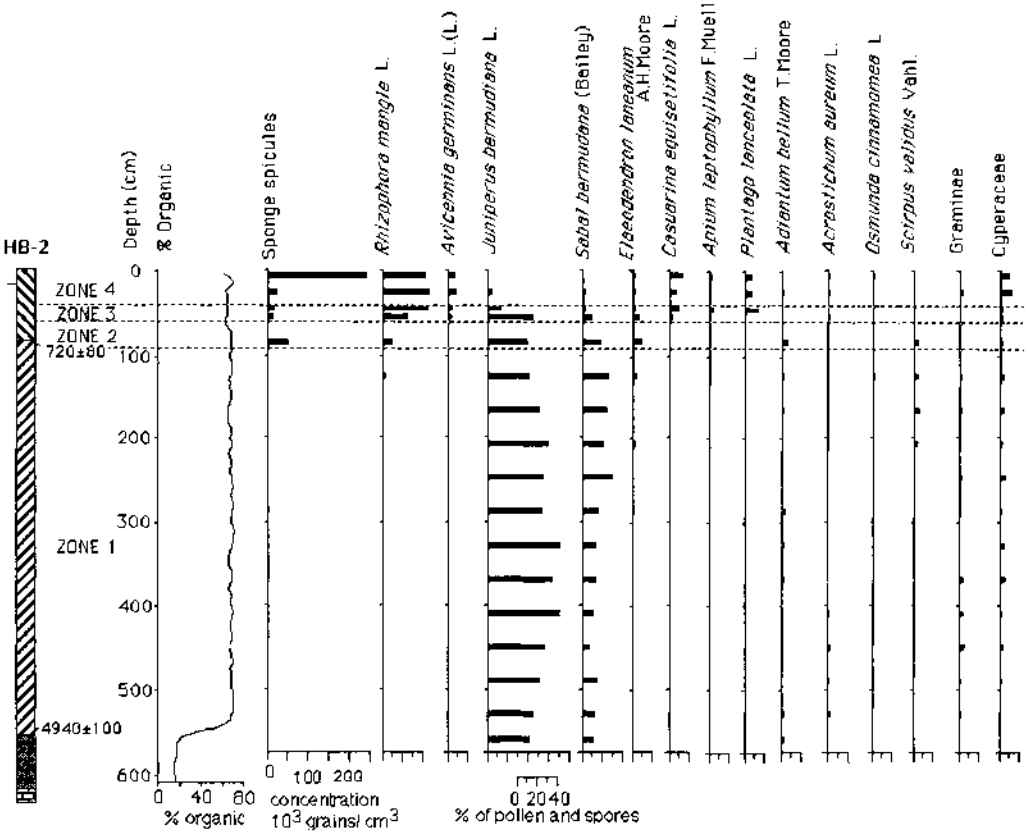

Fig. 6. Pollen diagram of core HB-2, also showing sponge spicule concentration and percent organic of sediment.

Most floated throughout the 3 month period, more floating vertically the first month and then more floating horizontally. However, nearly 50% sank for the first week and then became buoyant. Roots started to appear on floating and sunk hypocotyls towards the end of the second month. Results from the replicated experiment were very similar.

INTERPRETATION

Analysis of stratigraphy and palynology of Hungry Bay cores shows the evolution of the bay from the mid-Holocene from a brackish marsh to an oceanic mangrove swamp. The more recent dieback of seaward margins of the mangroves is examined in another paper (Ellison, 1993).

In cores HB-1 and HB-2, pollen zone 1 records the native forest of Bermuda before settlement, dominated by *Juniperus bermudiana* and *Sabal bermudana* with *Elaeodendron laneatum*, forming a dense evergreen forest over much of the island (Britton, 1918; Wingate, 1985). Results from zone 1 indicate the validity of the reconstruction of Bermuda's native forest on Nonsuch Island (Wingate, 1985) from the evidence of early records.

At this time Hungry Bay was probably a brackish enclosed marsh, the sea-level being 3–5 m lower (Neumann, 1971), so that it did not have direct connection with the ocean. Sea-level rise since flooding of the valley *c.* 5000 BP was sufficiently slow to allow marsh peat buildup to keep pace with the rate of rise of the water table. This interpretation is supported by the presence of pollen of *Sabal bermudana*, in higher proportions than has been shown from the pollen record of Mangrove Lake (Watts & Hansen, 1986). Mangrove Lake was a brackish lake during the period,

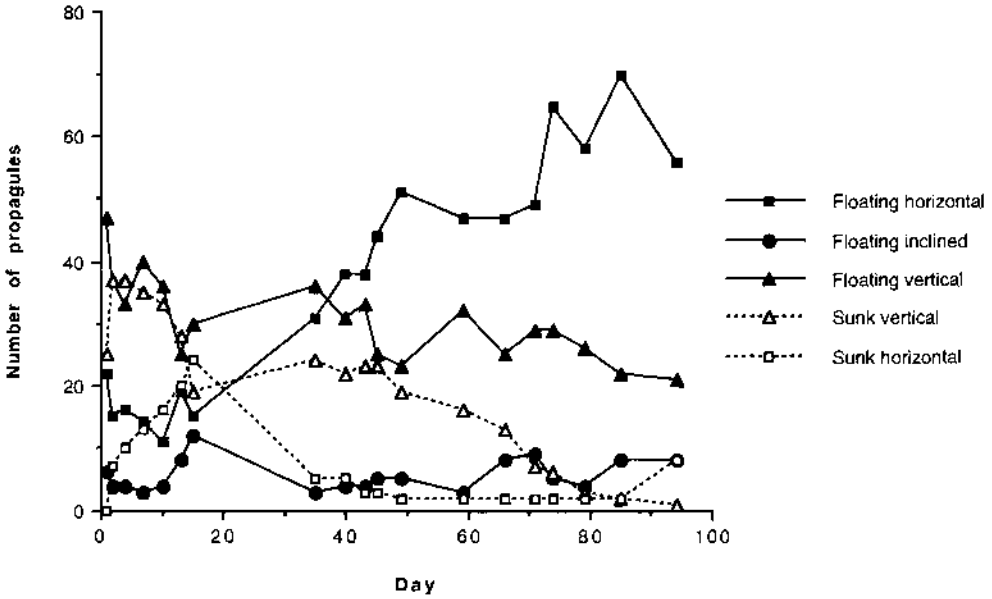

Fig. 7. Flotation properties of Bermuda's *Rhizophora mangle* propagules.

hence pollen assemblages better reflect the island vegetation as opposed to local communities.

Zone 2 records a local event, the conversion of the brackish marsh to a mangrove swamp. This occurred as sea-level rose to cause a direct connection with the ocean, and colonisation of the marsh by mangrove propagules. In core HB-1 this occurred at 245 cm depth, 2090 ± 90 yr BP, and in core HB-4 at 150 cm depth, which are corresponding elevations of 230 cm below OD (Ordnance Datum, set at MSL in 1964). The present depth of the ocean opening to Hungry Bay is just over 2 m. In both of these cores, a sand lens rich in marine ostracods occurs at this level, indicating that the sea broke through during an extreme event such as a hurricane, and subsequently the new bay was colonized by mangrove propagules.

In core HB-2 the transition from a brackish marsh to an ocean-exchanging mangrove swamp occurred at 90 cm depth, 720 ± 80 yr BP, with appearance of mangrove pollen and sponge spicules. The depth of the bedrock lip that separates the front and back basins of Hungry Bay mangrove swamp is 1 m below MSL, as shown by core 3 (Fig. 4).

Zone 3 records the permanent settlement of Bermuda, which commenced in 1612, bringing extensive deforestation for tobacco plantations, and introductions of species (Wingate, 1985), shown in the pollen diagrams by *Plantago lanceolata*, for example. *Juniperus bermudiana* remained dominant, its excellent wood and resilience in high winds leading to a monoculture.

Zone 4 records the cedar blight, which commenced in 1946 when two accidentally introduced scale insect pests destroyed 96% of the cedar before 1951 (Challinor & Wingate, 1971). This disaster stimulated a major reafforestation program by the government, favouring the fast growing *Casuarina equisetifolia*. This had been introduced earlier, being planted for ornament (Britton, 1918), but became commonly planted as wind-break. The pollen diagrams show presence of *Casuarina* in zone 3, but great increase in zone 4.

In core HB-2, there is not a clear distinction between zones 3 and 4. This is probably caused by recent bioturbation, there being dense populations of the burrowing crab *Goniopsis cruentata* in the landward basin of the swamp.

DISCUSSION

Although Hungry Bay is the largest mangrove area in Bermuda, it was only colonized by mangroves 2100 yr

BP. The second largest area at Mangrove Lake also is not a long-term refuge, pollen of *Rhizophora mangle* appearing only 3000 yr BP, and *Avicennia germinans* not at all (Watts & Hansen, 1986). There are no records of the common Caribbean mangrove *Laguncularia racemosa* (L.) Gaertn. f. ever being present in Bermuda, earlier records by Lefroy and Verrill being a misidentification (Britton, 1918). Older peat deposits have been found (Verrill, 1907; Ashmore & Leatherman, 1984), but these are marsh peats, not red fibrous mangrove peat. The indication is that mangroves recolonized Bermuda during the mid-Holocene and successfully established as sea-level stabilized and habitats became available.

It would take a substantial program to investigate all possibilities of longer term mangrove refuges in Bermuda. Stratigraphic evidence could have been eroded during Holocene sea-level rise, or destroyed during enlargement of St. David's Island for the U.S. Naval Base (Wingate, 1985). Other lines of evidence support the pollen evidence that mangroves may have a discontinuous presence in Bermuda.

First, results of the *Rhizophora mangle* propagule flotation experiment indicates that the majority can float for over 3 months. As shown by spread of the water-borne pathogen that caused the 1983 *Diadema antillarum* Philippi dieoff, passage from Florida to Bermuda on the Gulf Stream takes about three weeks (Lessios, Robertson & Cubit, 1984). Flotation results from Bermuda confer with those of Rabinowitz (1978) in Panama, who found that *Rhizophora* propagules initially sink, but if not finding a suitable substrate become buoyant for a minimum of 104 days, producing roots after 40 days. Rabinowitz found that *Avicennia germinans* had a similar dispersal capability, but that *Laguncularia racemosa* was unable to establish if floating for more than 8 days. This indicates that propagules of *Rhizophora* and *Avicennia* could reach Bermuda from the Caribbean at any time, and establish if finding suitable habitats, but *Laguncularia* could not.

Second, Keffer, Martinson & Corliss (1988) showed that during the last glacial period (18,000 years ago) the boundary between the N. Atlantic subpolar-sutropical gyres, and therefore the position of the Gulf Stream and the subpolar-subtropical front, was further south than at present. This would have caused winter temperatures in Bermuda to be less moderated, and the likely occurrence of frost. In general, mangroves are limited in their distribution to frost-free regions, with frost events causing heavy defoliation and mortality (Lugo & Patterson-Zucca, 1977). This suggests that mangroves in Bermuda would not survive glacial periods, but would recolonize during interglacials. Examination of pollen from Bermuda's Pleistocene eolianite paleosols by Herwitz (1992) suggests that sub-tropical plant species that inhabit the dunes were also lost during glacial periods. This is already known from the faunal record, Richards, Abbott and Skymer (1969) recording loss of five marine molluscs between the Stage 7 interglacial and Stage 6 glacial, and Gould (1970) showing oscillation in diversity of land snails with glacial periods.

Third, presence of endemic species restricted to mangrove swamps would suggest continuous presence of mangroves in Bermuda. Owing to the isolation of the islands endemicity is relatively high. There are fifteen endemic vascular plants (Britton, 1918) of which five occur in marsh habitats and ten in dry, rocky habitats. There are no endemic plants of mangrove swamp habitats. In the insects there are thirteen endemic Lepidoptera (Ferguson, Hilburn & Wright, 1991), three endemic Homoptera (Wilson & Hilburn, 1991) and four endemic Psocoptera (Mockford, 1989), none of which are restricted to mangroves. Information on Bermuda's marine endemics has not been compiled, but there seem to be none restricted to mangrove environments (W. Sterrer, pers. comm.). Collette (1962) listed thirteen endemic fish in Bermuda, of which the Killifish *Fundulus bermudae* Günther has a habitat in mangrove swamps as well as brackish water ponds (Sterrer, 1986). The species has been successfully introduced in a brackish pond constructed on Nonsuch Island, where the mangroves are as yet poorly established. Berrill (1932) described thirty-one sea squirts from Bermuda of which a minimum of three are endemic, but not restricted to mangroves. The lack of endemic species with a specific mangrove habitat in Bermuda lends support to a theory that the mangrove habitat has been discontinuous over Bermuda's history.

Ellison & Stoddart (1991) reviewed evidence for development of expansive mangrove systems being subject to relatively stable sea-level positions. Discontinuous and low levels of mangrove pollen occur earlier than 3000 yr BP, in both the Mangrove Lake diagram (Watts & Hansen, 1986) and the Hungry Bay diagrams (Figs 5 and 6). This indicates regular arrival of propagules and occasional growth to flower of a few trees, but before 3000 yr BP sea-level was rising at 26 cm/100 years so keeping mangroves in refuge mode. After 3000 yr BP the pollen records show establishment of larger areas of mangroves, when the rate of sea-level rise had slowed to 7 cm/100 years. This concurs

with the record from Florida, where expansive mangroves did not establish until after 3500 yr BP (Scholl, 1964).

Discontinous presence of mangroves on remote islands has also been shown from Mangaia in the Cook Islands, where Ellison (1994) found *Rhizophora* pollen for periods during the Holocene, reaching maximum concentrations of 2691 grains/cm^3 at around 7250, 5000 and 2000 years BP. *Rhizophora* was not previously believed to be indigenous east of Samoa, and did not persist in Mangaia due to decreasing salinity in conditions of sea-level fall. It seems that mangrove ranges in the Pacific and Caribbean are more controlled by availability of habitats and less by dispersal capability than was previously thought (Mepham, 1983).

CONCLUSION

Bermuda is both the most northerly and most isolated location for indigenous mangroves in the world. The ecological communities described at Hungry Bay indicate that although mangroves may be low in arboreal diversity especially at their limits of distribution, they have a considerable diversity of invertebrates, fish and birds. The dryland forest described around Hungry Bay exemplifies the present domination by introduced species, and the pollen diagrams indicate the unique forest of endemics that has been replaced.

This study indicates that mangroves were not present in Bermuda during glacial periods of the Late Pleistocene, owing to inclement climate, as has been found for other tropical species. Significant mangrove areas did not, however, establish when the climate became warmer in the Early Holocene, but established since 3000 yr BP with slowing of the rate of sea-level rise.

Bermuda has high endemicity in flora and fauna, but as no species is restricted to mangrove there is support for only a discontinuous presence of mangrove habitats. Examination of the habitats of endemic species would indicate that dry rocky hillsides, marsh habitats and shallow nearshore environments are the long term habitats in Bermuda.

This study shows that mangrove ranges may be more plastic than was previously thought, subject to availability of habitats rather than dispersal capability.

ACKNOWLEDGMENTS

This research was funded by a National Science Foundation Dissertation Improvement Grant (SES-9104526), and by a Carl O. Sauer Memorial Fellowship from the University of California at Berkeley. I thank Bruce Rueger for loan of a pollen reference collection for Bermuda.

REFERENCES

Ashmore, S. & Leatherman, S.P. (1984) Holocene sedimentation in Port Royal Bay, Bermuda. *Mar. Geol.* **56**, 289–298.

Benninghoff, W.S. (1962) Calculation of pollen and spores density in sediments by addition of exotic pollen in known quantities. *Pollen et Spores* **4**, 332–333.

Berrill, N.J. (1932) Ascidians of the Bermudas. *Biol. Bull.* **62**, 77–88.

Britton, N.L. (1918) *Flora of Bermuda.* 586 pp. Charles Scriber's Sons, New York.

Challinor, D. & Wingate, D.B. (1971) The struggle for survival of the Bermuda cedar. *Biol. Conserv.* **3**, 220–222.

Collette, B.B. (1962) *Hemiramphus bermudensis*, a new Halfbeak from Bermuda, with a survey of endemism in Bermudian shore fishes. *Bull. Mar. Sci.* **12**, 432–449.

Ellison, J.C. (1993) Mangrove retreat with rising sea-level, Bermuda. *Est. Coa. Shelf Sci.* **37**, 75–87.

Ellison, J.C. (1994) Palaeo-lake and swamp stratigraphic records of Holocene vegetational and sea-level changes, Mangaia, Cook Islands. *Pacif. Sci.* **48**, 1–15.

Ellison, J.C. & Stoddart, D.R. (1991) Mangrove ecosystem collapse during predicted sea-level rise: Holocene analogues and implications. *J. Coast. Res.* **7**, 151–165.

Faegri, K. & Iverson, J. (1975) *Textbook of pollen analysis*, 3rd edn. 295 pp. Hafner, New York,

Ferguson, D.C., Hilburn, D.J. & Wright, B. (1991) The Lepidoptera of Bermuda: Their main food plants, biogeography, and means of dispersal. *Mem. Ent. Soc. Can.* **158**, 3–105.

Gould, S.J. (1970) Coincidence of climatic and faunal fluctuations in Pleistocene Bermuda. *Science* **168**, 572–573.

Herwitz, S.R. (1992) Quaternary vegetation change and dune formation on Bermuda: a discussion. *Global Ecol. Biogeogr. Letts*, **2**, 65–70.

Keffer, T., Martinson, D.G. & Corliss, B.H. (1988) The position of the Gulf Stream during Quaternary glaciations. *Science* **241**, 440–442.

Land, L.S., Mackenzie, F.T. & Gould, S.J. (1967) Pleistocene History of Bermuda. *Bull. Geol. Soc. Am.* **78**, 993–1006.

Lessios, H.A., Robertson, D.R. & Cubit, J.D. (1984) Spread of *Diadema* mass mortality through the Caribbean. *Science* **226**, 335–337.

Lugo, A.E. & Patterson-Zucca, C. (1977) The impact

of low temperature stress on mangrove structure and growth. *Trop. Ecol* **18**, 149–161.

Mepham, R.H. (1983) Mangrove floras of the southern continents, Part I: The geographical origin of Indo-Pacific mangrove genera and the development and present status of the Australian mangroves. *S. Afr. J. Bot.* **2**, 1–8.

Mockford, E.L. (1989) Psocoptera (Insecta) from Bermuda. *J. Nat. Hist.* **23**, 1177–1193.

Morris, B., Barnes, J., Brown, F. & Markham, J. (1977) The Bermuda marine environment. *Bermuda Biological Station Special Publication* **15**, 120pp.

Neumann, A.C. (1971) Quaternary sea level data from Bermuda. *Quaternaria* **14**, 41–43.

Rabinowitz, D. (1978) Dispersal properties of mangrove propagules. *Biotropica* 10, 47–57.

Redfield, A. C. (1967) Postglacial change in sea-level in the western North Atlantic Ocean. *Science* **157**, 687–692.

Richards, H.G., Abbott, R.T. & Skymer, T. (1969) The marine Pleistocene mollusks of Bermuda. *Notulae Naturae of the Academy of Natural Sciences of Philadelphia* **425**, 10pp.

Rowe, M.P. (1990) *An explanation of the geology of Bermuda*, 28 pp. Bermuda Government Ministry of Works and Engineering.

Scholl, D.W. (1964) Recent sedimentary record in mangrove swamps and rise in sea-level over the southwestern coast of Florida. *Mar. Geol.* **2**, 343–364.

Sterrer, W. (ed.), 1986. *Marine Fauna and Flora of Bermuda*, 742 pp. Wiley-Interscience, New York.

Thomas, M.L.H. (1993) Mangrove swamps in Bermuda. *Atoll Res. Bull.* **386**, 17pp.

Tomlinson, P.B., 1986. *The botany of Mangroves*. 413 pp. Cambridge University Press, Cambridge.

Verrill, A.E. (1907) The Bermuda Islands, Part IV: Geology and paleontology. *Trans. Conn. Acad. Arts Sci.* **12**, 45–348.

Wanless, H.R. (1982) Sea level is rising – So what? *J. Sedim. Petrol.* **52**, 1051–1054.

Watts, W.A. & Hansen, B.C.S. (1986) Holocene climate and vegetation of Bermuda. *Pollen et Spores* **28**, 355–364.

Wilson, M.R. & Hilburn, D.J. (1991) Annotated list of the Auchenorrhynchous Homoptera (Insecta) of Bermuda. *Ann. Entomol. Soc. Am.* **84**, 412–419.

Wingate, D.B. (1985) The restoration of Nonsuch Island as a living museum of Bermuda's pre-colonial terrestrial biome. *Tech. Publ. Int. Council for Bird Preserv.* **3**, 225–238.

Woodroffe, C.D. & Grindrod, J. (1991) Mangrove biogeography: the role of Quaternary environmental and sea-level change. *J. Biogeogr.* **18**, 479–492.