Quaternary Vegetation Change and Dune Formation on Bermuda: A Discussion

Stanley R. Herwitz

Global Ecology and Biogeography Letters, Vol. 2, No. 3. (May, 1992), pp. 65-70.

Stable URL:
http://links.jstor.org/sici?sici=0960-7447%28199205%292%3A3%3C65%3AQVCADF%3E2.0.CO%3B2-3

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 14:11:01 2006

Global Ecology and Biogeography Letters (1992) **2**, 65–70

RESEARCH LETTER

Quaternary vegetation change and dune formation on Bermuda: a discussion

STANLEY R. HERWITZ *Graduate School of Geography, Clark University, Worcester, Massachusetts 01610, U.S.A.*

Abstract. The Bermuda oceanic islands are comprised mainly of lithified dunes (i.e. calcareous eolianites) which formed during Quaternary sea-level regressions. This short communication considers the vegetation history of Bermuda in relation to these dune-building episodes.

At 32°N, Bermuda is the northernmost limit of most frost-intolerant subtropical vascular plant species in the northern hemisphere. The global cooling that caused the Quaternary glacial periods and also the lowering of sea level, may have led to the local extinction of Bermuda's subtropical interglacial floras. Located >900 km from the nearest continental source area, the filling of the vacated niches on Bermuda by long-distance dispersal may have involved low frequency events requiring more than 6000 years. The result would have been a very sparse vegetative cover during the dune-building episodes which would explain why the Bermuda eolianites reach elevations greater than 60 m above the present-day sea level. This hypothesis is supported by: (1) the absence of reliable fossil evidence for vegetation interfering with, or interbedded within, the eolian deposits; and (2) preliminary palynological analyses of the clay-rich fossil soils intercalated between the eolianite formations which have revealed pollen that does not appear to correspond to the existing native flora of Bermuda.

Key words. Bermuda, subtropical vegetation, latitudinal limits, Quaternary climate change, dune formation.

INTRODUCTION

Past studies of the biogeographic history of isolated oceanic islands have focused mainly on research questions pertaining to long-distance dispersal, survivorship, species composition, species turnover, and evolutionary biology (Darwin, 1859; Gulick, 1932; Axelrod, 1952; Holdgate, 1960; Sauer, 1969; Carlquist, 1974; Bramwell, 1979). Among the more frequently cited studies are those that examined the Galápagos (Darwin, 1859; Kroeber, 1916; Hamilton & Rubinoff, 1963; Johnson & Raven, 1973; Simpson, 1974; Amerson, 1975; Connor & Simberloff, 1978) and the Hawaiian islands (Fosberg, 1948; Gressitt, 1963; Carlquist, 1966; Juvik & Austring, 1979). The Bermuda oceanic island system, located in the western North Atlantic >900 km from the nearest continent, is of particular interest (Crowell, 1962) because it is more geographically isolated than the Galápagos islands and because at 32°N latitude it represents the northernmost limit of most subtropical vascular plant species in the northern hemisphere.

Bermuda's indigenous flora is predominantly subtropical, having strong affinities with south Florida and the West Indies (Britton, 1918; Rendle, 1936). Noting that Bermuda is the northernmost occurrence of mangroves, Woodroffe & Grindrod (1991) recently provided a useful discussion of the evidence for disruptions in the distribution of mangroves at their latitudinal limits during Quaternary climate and sea-level changes. The objective of this short communication is to consider the effect that Quaternary changes in the flora of Bermuda may have had on the dune-building episodes responsible for the formation of the Bermuda oceanic island system.

GEOLOGY OF BERMUDA

The oceanic island system of Bermuda currently exposed above sea level is essentially a lithified, non-migratory dunefield (i.e. calcareous eolianites) overlying a submerged volcanic seamount in the western North Atlantic. The eolianite formations of Bermuda are Quaternary in age, constitute >90% of the total rock volume above sea level, and are derived from windblown biogenic beach sediments (Sayles, 1931; Bretz, 1960; Mackenzie, 1964a; Land, Mackenzie & Gould, 1967; Land & Mackenzie, 1969; Harmon, Schwarcz & Ford, 1978; Harmon *et al.*, 1981; Vacher & Hearty, 1989; Rowe, 1990). The succession of onlapping and, in some cases, overlapping eolianites reflects a pattern of seaward accretion of progressively younger dune units (Vacher, 1973). Five eolianite formations have been distinguished on the basis of their stratigraphic position, their relative degree of lithification, uranium-series dating of speleothems and fossil coral samples, and amino-acid racemization dating of eolianite, fossil land snail, and fossil marine mollusk samples (Harmon *et al.*, 1983; Vacher & Hearty, 1989; Vacher, Rowe & Garrett, 1989; Hearty, Vacher & Mitterer, 1992). Intercalated between the eolianites and some localized marine carbonates are clay-rich 'terra rossa' fossil soils (Ruhe, Cady & Gomez, 1961; Bricker & MacKenzie, 1970; Vacher & Harmon, 1987; Herwitz & Muhs, 1993).

In the early literature on the geology of Bermuda, the prevailing view was that the paleosols formed during interglacial periods under conditions comparable to the present-day interglacial, and that the dunes, which lithified to become eolianite, formed during glacial low sea stands when the Bermuda platform was more exposed (Verrill, 1907; Sayles, 1931; Livingston, 1944; Officer, Ewing & Wuenschel, 1952). Bretz (1960) reversed this interpretation, and argued that the dunes developed during interglacial high sea stands and the clay-rich soils formed during glacial periods. More recently, Vacher & Hearty (1989) refined this interpretation, providing strong stratigraphic evidence that the large dune ridges characterizing the Bermuda eolianites formed mainly during periods of Quaternary sea-level lowering.

ELEVATIONS OF BERMUDA EOLIANITES

A striking characteristic of the Bermuda eolianites is their height above sea level. The youngest eolianite formation, the Southampton Formation with an estimated age of 85,000 years, reaches a height of 73 m above sea level on Gibb's Hill. The highest elevation on Bermuda, however, does not occur on the Southampton Formation, but rather on the much older Town Hill Formation (Table 1). The highest dune ridge is 79 m above sea level and is locally referred to as 'The Peak'. Fig. 1 shows the location of the highest point on each of the five eolianite formations.

The elevations of the eolianite formations are not attributable to tectonic instability because it is generally agreed that Bermuda has been tectonically stable throughout the Quaternary (Gees, 1969; Harmon *et al.*, 1978; Harmon *et al.*, 1981), representing a reliable 'tide gauge' for the assessment of Quaternary changes in sea level (Land *et al.*, 1967). For this reason, the elevations of the Bermuda eolianites are attributable entirely to local wind deposition. If the dunes accumulated during a lowering of sea level, then they may have been subaerially exposed depositional features with elevations >100 m above the lower sea level at the time of their formation. The occurrence of submerged eolianite ranging from 18 to 75 m below the present-day sea level has been reported by Pirsson (1914) and Stanley & Swift (1967).

Table 1. Highest elevations of Bermuda eolianites above present-day sea level.

Eolianite formation	Estimated age (10^3 years)*	Elevation sea level (m)	Location
Southampton	85	73	Gibb's Hill (Gibb's Lighthouse)
Rocky Bay	125	67	White Hill
Belmont	204	76	North of Mount Hope
Town Hill	>325	79	The Peak (Folly's Tower)
Walsingham	>880	29	North of Ship Hill

*Based on Harmon *et al.* (1983), Vacher *et al.* (1989), and Hearty *et al.* (1992).

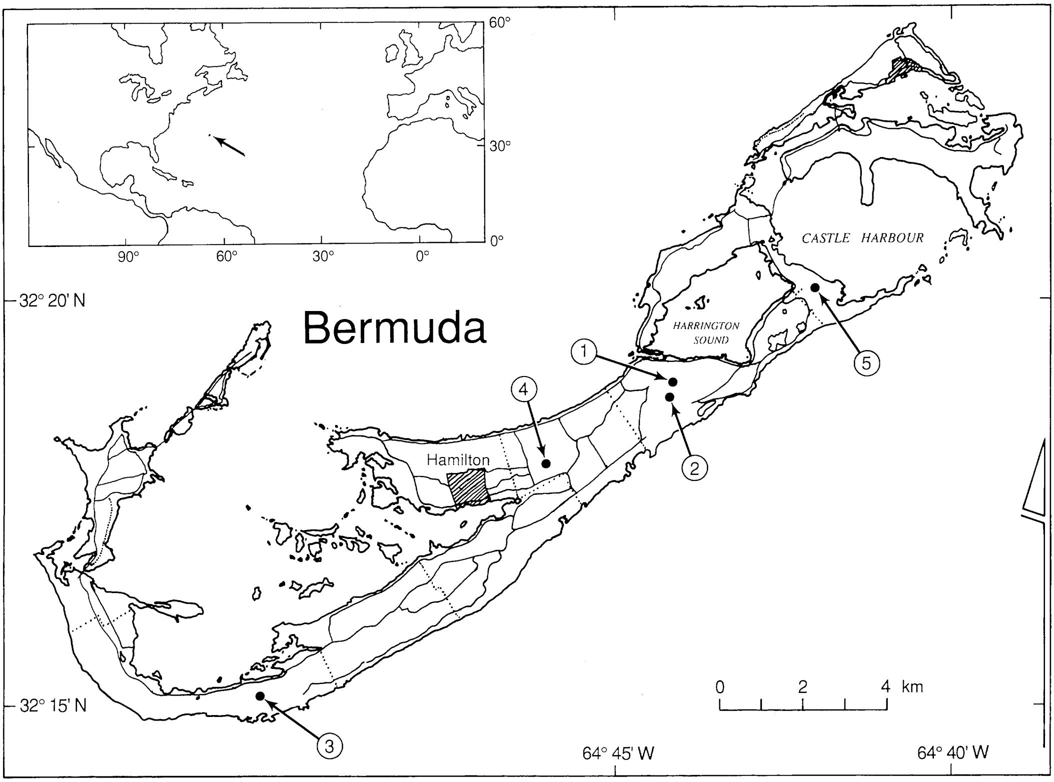

Fig. 1. Location of the highest elevations of the Bermuda eolianites: (1) Town Hill Formation; (2) Belmont Formation; (3) Southampton Formation; (4) Rocky Bay Formation; (5) Walsingham Formation.

VEGETATION INFLUENCES ON DUNE FORMATION

It is well known that vegetation can inhibit or, at least, limit dune growth by obstructing the near-ground eolian transport of sediments (Chepil, 1945; Mabbutt, 1977; Pye & Tsoar, 1990). According to Gardner (1983), individual dunes rarely reach 100 m in thickness. Although superimposition of sands of different ages may give rise to greater thicknesses, eolian deposits generally become unstable above 100 m. Dunes reach their highest elevations in arid environments where the vegetative cover is limited or absent (Greeley & Iversen, 1985). There is, however, no evidence that Bermuda experienced arid or semiarid conditions during the Quaternary.

Under the moist subtropical conditions that currently exist on Bermuda (Macky, 1957), it is not clear how such elevated dune systems could have formed unless there was a significant change in the vegetative cover. Most of the protected natural coastlines of Bermuda are characterized by indigenous subtropical shrubs such as *Scaevola plumieri*, *Coccoloba uvifera*, *Suriana maritima*, *Mallotonia gnaphalodes, Borrichia arborescens, Chiococca bermudiana, Randia aculeata,* and *Dodonaea jamaicensis.* The early inhabitants of Bermuda recognized the stabilizing effect of this vegetation in their accounts of active dune building only where the coastal brush had been cleared (Rowe, 1990). The only active dune system under present-day conditions is at Tucker's Town Beach east of Harrington Sound (Fig. 1), where land development has reduced the vegetative cover. Even at this location, the elevation and areal extent of the dune system is very limited.

QUATERNARY CLIMATE AND VEGETATION CHANGE

Although Bermuda is subject to moderating maritime influences, climatic conditions in the western North

Atlantic at 32°N latitude may have been significantly different during glacial maxima. In an analysis of the Gulf Stream–North Atlantic Current system, Keffer, Martinson & Corliss (1988) concluded that changes in sea surface temperatures in the North Atlantic during Quaternary glaciations caused a significant southward shift in the position of the subtropical–subpolar frontal system. Such a change would be expected to result in colder temperatures on Bermuda, with a high likelihood of winter frosts (i.e. night temperatures <5°C).

Freezing temperatures are known to produce serious injury and mortality in frost-sensitive plants (Burke *et al.*, 1976). Winter frosts during the change from interglacial to glacial conditions would result in the local extinction of most of Bermuda's indigenous subtropical flora. This flora consists not only of frost-sensitive coastal shrubs, but also the mangroves *Rhizophora mangle*, *Avicennia germinans* and *Conocarpus erectus*, and the endemic Bermuda palmetto *Sabal bermudiana*.

If the interglacial floras of Bermuda did not persist through the glacial periods, then the question arises as to the rapidity with which the vacated niches were filled. Morphologic changes in Pleistocene fossils of the endemic, but now extinct, Bermuda pulmonate land snail *Poecilozonites* were interpreted by Gould (1970) as reflecting adaptive responses to changes in climatic conditions; it also was noted that the adaptive radiation of this genus was related to the 'extreme rarity of competitors and predators' (Land *et al.*, 1967), evidently reflecting the relative infrequency of successful long-distance dispersal events.

In the case of Bermuda's limited endemic floristic diversity, there is little evidence for adaptive radiation. For this reason, long-distance dispersal was probably the primary mechanism for the filling of the vacated niches. It should be recognized, however, that successful colonization of Bermuda by vascular plant species adapted to winter frosts in distant locations (>900 km from Bermuda) would have been a low frequency event. A lag in the filling of the vacated niches means that Bermuda's vegetative cover may have been quite limited during the period of sea-level lowering when the most significant dune-building episodes are believed to have occurred.

DUNE FORMATION

A sparse vegetative cover on those parts of the Bermuda platform exposed by the lowering of sea level has geological significance. With less interference from a vegetative cover, the calcareous biogenic sediments subaerially exposed by sea-level lowering may have been more available for local wind transport and dune formation. If, on the other hand, the subtropical vegetation of Bermuda withstood past climatic changes (e.g. decreased temperatures) and persisted throughout the Quaternary, then the primary seres created by the lowering of sea level would have been available for local plant colonization. The resulting vegetative cover, thus, could have limited the height and areal extent of dune formation. This is not to suggest that dune formation would not have occurred during the transitions from interglacial to glacial conditions in the presence of vegetation; however, without a significant number of species extinctions or without rapid in-filling of the vacated niches by long-distance dispersal, the dunes may not have reached elevations >60 m above the present-day sea level.

DISCUSSION

Fossil evidence for the presence of coastal vegetation interfering with, or influencing the formation of, the Bermuda dune units is questionable. It is generally agreed that the dunes cemented rapidly into eolianite (Bretz, 1960; Mackenzie, 1964b; Land *et al.*, 1967); however, solutional rillenkarren (Jennings, 1985), which formed subaerially after the dune-building episodes, have been mistakenly identified as fossil imprints of leaf fronds of the subtropical palmetto *Sabal bermudiana* (Bretz, 1960; Vacher, 1973; Vacher & Harmon, 1987; Rowe, 1990). In addition, what several past workers have considered buried fossil casts of 'palmetto stumps' (Livingston, 1944; Land *et al.*, 1967; Land & MacKenzie, 1969; Harmon *et al.*, 1981; Vacher & Harmon, 1987; Rowe, 1990) are stemflow-generated solution pipes that developed long after dune formation when the clay-rich 'terra rossa' soils accumulated from atmospheric dust while supporting stemflow-generating trees (Herwitz, 1993).

Preliminary palynological analyses of Bermuda paleosols intercalated between the eolianite formations suggest that subtropical plant species, currently located at their latitudinal limits, did not persist throughout the glacial periods of the Quaternary (Herwitz & Morrill, in preparation). The pollen content does not conform to Bermuda's existing indigenous subtropical flora, and suggests marked changes in species composition. Contrary to Knox's (1940) view that temperatures were not appreciably lowered during glacial maxima and that the floristic species composition of Bermuda remained the same throughout the Quaternary, the preliminary palynological results suggest local extinction of Bermuda's interglacial floras.

CONCLUSION

The dune-building episodes responsible for the occurrence of the Bermuda oceanic islands on a submerged volcanic seamount are generally attributed only to the sea-level changes associated with the interglacial-glacial cycles of the Quaternary. I hypothesize: (1) that the global climatic cooling, responsible for the Quaternary glacial periods and low sea-level stands, also may have led to the local extinction of Bermuda's interglacial subtropical floras; and (2) that the resulting reduction in the vegetative cover influenced the elevation and areal extent of the dunes that lithified to form the Bermuda eolianites. The vegetation history of Bermuda, thus, may be a previously unrecognized factor that could have influenced the present-day geological form of the Bermuda oceanic island system.

REFERENCES

Amerson, A.B., Jr (1975) Species richness on the non-disturbed northwestern Hawaiian islands. *Ecology*, **56**, 435–444.

Axelrod, D. (1952) Variables affecting the probabilities of dispersal in geologic time. *Bull. Am. Mus. nat. Hist.* **99**, 177–188.

Bramwell, D. (1979) *Plants and islands.* Academic Press, London.

Bretz, H. (1960) Bermuda: a partially drowned, late mature, Pleistocene karst. *Bull. geol. Soc. Am.* **71**, 1729–1754.

Bricker, O. & Mackenzie, F.T. (1970) Limestones and red soils of Bermuda: discussion. *Bull. geol. Soc. Am.* **81**, 2523–2524.

Britton, N.L. (1918) *Flora of Bermuda.* Charles Scribner, New York.

Burke, M.J., Gusta, L.V., Quamme, H.A., Weiser, C.J. & Li,P.H. (1976) Freezing and injury in plants. *Ann. Rev. Plant Physiol.* **27**, 507–528.

Carlquist, S. (1966) The biota of long-distance dispersal. I. Principles of dispersal and evolution. *Q. Rev. Biol.* **41**, 247–270.

Carlquist, S. (1974) *Island biology.* Columbia University Press, New York.

Chepil, W.S. (1945) Dynamics of wind erosion: II. Initiation of soil movement. *Soil Sci.* **60**, 397–411.

Connor, E.F. & Simberloff, D. (1978) Species number and compositional similarity of the Galapagos flora and avifauna. *Ecol. Mongr.* **48**, 219–248.

Crowell, K.L. (1962) Reduced interspecific competition among the birds of Bermuda. *Ecology*, **43**, 75–88.

Darwin, C. (1859) *On the origin of species by means of natural selection.* Murray, London.

Fosberg, F.R. (1948) Derivation of the flora of the Hawaiian Islands. *Insects of Hawaii, Volume I* (ed. by E.C. Zimmerman), pp. 107–119. University of Hawaii Press.

Gardner, R.A.M. (1983) Aeolianite. *Chemical sediments and geomorphology: precipitates and residua in the near-surface environment* (ed. by A.S. Goudie & K. Pye), pp. 265–300. Academic Press, London.

Gees, R.A. (1969) The age of the Bermuda seamount. *Marit. Sediments*, **5**, 56–57.

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

Greeley, R. & Iversen, J.D. (1985) *Wind as a geological process.* Cambridge University Press, Cambridge.

Gressitt, J.L. (1963) *Pacific basin biogeography.* Bishop Museum Press, Honolulu.

Gulick, A. (1932) Biological peculiarities of oceanic islands. *Q. Rev. Biol.* **7**, 405–427.

Hamilton, T. & Rubinoff, I. (1963) Isolation, endemism and multiplication of species in the Darwin finches. *Evolution*, **176**, 388–403.

Harmon, R.S., Land, L.S., Mitterer, R.M., Garrett, P., Schwarcz, H.P. & Larson, G.J. (1981) Bermuda sea level during the last interglacial. *Nature*, **289**, 481–483.

Harmon, R.S., Mitterer, R.M., Kriausakul, N., Land, L.S., Schwarcz, H.P., Garrett, P., Larson, G.J., Vacher, H.L. & Rowe, M. (!983) Uranium-series and amino-acid racemization geochronology of Bermuda: implications for eustatic sea-level fluctuations over the past 250,000 years. *Palaeogeogr. Palaeoclim. Palaeoecol.* **44**, 41–70.

Harmon, R.S., Schwarcz, H.P. & Ford, D.C. (1978) Late Pleistocene sea level history of Bermuda. *Quat. Res.* **9**, 205–218.

Hearty, P.J., Vacher, H.L. & Mitterer, R.M. (1992) Aminostratigraphy and ages of Pleistocene limestones of Bermuda. *Bull. geol. Soc. Am.* **104**, 471–480.

Herwitz, S.R. (1993) Stemflow influences on the formation of solution pipes in Bermuda eolianite. *Geomorphology* (in press).

Herwitz, S.R. & Morrill, J.B.M. (in preparation). Scanning electron micrographs of fossil pollen in the paleosols of Bermuda and their biogeographic significance (to be submitted to *J. Biogeogr.*).

Herwitz, S.R. & Muhs, D.R. (1993) Bermuda solution pipe soils: a geochemical evaluation of eolian parent materials. *Terrestrial and shallow marine geology of the Bahamas and Bermuda* (ed. by H.A. Curran and B. White). *Geological Society of America Special Paper* (in press).

Holdgate, M.W. (1960) The fauna of the mid-Atlantic islands. *Proc. R. Soc. Lond.* **B, 152**, 550–567.

Jennings, J.N. (1985) *Karst geomorphology*. Basil Blackwell, New York.

Johnson, M.P. & Raven, P.H. (1973) Species number and endemism: the Galapagos Archipelago revisited. *Science*, **179**, 893–895.

Juvik, J.O. & Austring, A.P. (1979) The Hawaiian avifauna: biogeographic theory in evolutionary time. *J. Biogeogr.* **6**, 205–223.

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

Knox, A.S. (1940) The peat deposits of Bermuda and evidences of postglacial changes in sea-level. *J. Geol.* **48**, 767–780.

Kroeber, A.L. (1916) Floral relations among the Galapagos Islands. *Univ. Calif. Publ. Bot.* **16**, 199–220.

Land, L.S. & Mackenzie, F.T. (1969) *Field guide to Bermuda geology*. Penrose Conference at Bermuda Biological Station.

Land, L.S., Mackenzie, F.T. & Gould, S.J. (!967) Pleistocene history of Bermuda. *Bull. geol. Soc. Am.* **78**, 993–1006.

Livingston, W. (1944) Observations on the structure of Bermuda. *Geogr. J.* **104**, 40–48.

Mabbutt, J.A. (1977) *Desert landforms*. The MIT Press, Cambridge, Massachusetts.

Mackenzie, F.T. (1964a) Bermuda Pleistocene eolianites and paleowinds. *Sedimentology*, **3**, 51–64.

Mackenzie, F.T. (1964b) Geometry of Bermuda calcareous dune cross-bedding. *Science*, **144**, 1449–1450.

Macky, W.A. (1957) The rainfall of Bermuda. *Bermuda Meteorological Office Technical Note*, 8, 58 p.

Officer, C.B., Ewing, M., & Wuenschel, P.C. (1952) Seismic refraction measurements in the Atlantic Ocean. Park IV: Bermuda, Bermuda Rise, and Nares Basin. *Bull. geol. Soc. Am.* **63**, 777–808.

Pirsson, L.V. (1914) Geology of Bermuda Island: the igneous platform. *Am. J. Sci.* **38**, 189–206, 331–344.

Pye, K. & Tsoar, H. (1990) *Aeolian sand and sand dunes*. Unwin Hyman, London.

Rendle, A.B. (1936) Notes on the flora of the Bermudas. *J. Bot.* **74**, 42–50, 65–71, 101–112.

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

Ruhe, R.V., Cady, J.G. & Gomez, R.S. (1961) Paleosols of Bermuda. *Bull. geol. Soc. Am.* **72**, 1121–1142.

Sauer, J.D. (!969) Oceanic islands and biogeographical theory: a review. *Geogr. Rev.* **59**, 582–593.

Sayles, R.W. (1931) Bermuda during the ice age. *Proc. Am. Acad. Arts Sci.* **66**, 381–467.

Simpson, B.B. (1974) Glacial migrations of plants: island biogeographical evidence. *Science*, **185**, 698–700.

Stanley, D.J. & Swift, D.J.P. (1967) Bermuda's southern aeolianite reef tract. *Science*, **157**, 677–681.

Vacher, H.L. (1973) Coastal dunes of younger Bermuda. *Coastal geomorphology* (ed. by D.R. Coates), pp. 355–391. Publications in Geomorphology, State University of New York.

Vacher, H.L. & Harmon, R.S. (1987) *Field guide to Bermuda geology*. Penrose Conference at Bermuda Biological Station.

Vacher, H.L. & Hearty, P. (1989) History of stage 5 sea level in Bermuda: review with new evidence of a brief rise to present sea level during substage 5A. *Quat. Sci. Rev.* **8**, 159–168.

Vacher, H.L., Rowe, M. & Garrett, P. (1989) *The geological map of Bermuda*. Public Works Department, Hamilton, Bermuda.

Verrill, A.E. (1907) The Bermuda Islands, Part. IV. Geology and paleontology, Part. V. An account of the coral reefs. *Trans. of Connect. Acad. Arts Sci.* **12**, 45–348.

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