



Tropical salt marsh succession as sea-level indicator during Heinrich events

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ABSTRACT

Centennial–millennial dynamics of tropical salt marsh vegetation are documented in the pollen record from marine core MD03–2622, Cariaco Basin, Venezuela, which spans the glacial period between 63 and 29 ka. Five rapid and abrupt expansions of salt marsh vegetation are linked with North Atlantic Heinrich events (HEs). Within each event, a recurrent pattern – starting with species of Chenopodiaceae, followed by grasses, and subsequently by Cyperaceae species – suggests a successional process that is determined by the close relationship between sea-level and community dynamics. The salt tolerant Chenopodiaceae, at the base of each sequence, indicate hypersaline intertidal environments, which were most likely promoted by extremely dry atmospheric conditions. Rapid sea-level rise characterizes the onset of HE stadials, causing erosion of marsh sediments, and continued recruitment of pioneer species (Chenopodiaceae), which are the only ones capable of tolerating the rapid rate of disturbance. Once, as sea-level drops or as rise decelerates, marsh plants are able to trap and stabilize sediments, favouring the establishment of more competitive species (graminoids). The increment of marsh height as a result of autochthonous sediment accumulation reduces the extent of hypersaline environments, and allows the establishment of mesohaline species. These results add to the scarce knowledge on tropical salt marsh ecosystems, and provide independent paleoclimatic evidence on sea-level changes occurring simultaneously with Antarctica climate variations.

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1. Introduction

High-resolution paleorecords indicate that during the Last glacial period, abrupt massive discharges of icebergs occurred frequently within the North Atlantic Ocean, referred to as the so-called Heinrich events (HEs). HEs are typically documented in the North Atlantic as anomalous and wide-spread occurrences of ice-rafted debris that coincided with the coldest final phases of some consecutive cold stadials (i.e. every 7–10 kyr) and appear to have had global impacts (e.g. Voelker et al., 2002). It is believed that these events are linked to strong reductions of the Atlantic meridional overturning circulation and that their impact propagated to mid/low-latitudes by atmospheric and oceanic teleconnections (Broecker, 2003; Rahmstorf, 2002). Four cycles of sea-level change in the order of 15–30 m have been recorded during Marine Isotope Stage (MIS) 3, and modeling results emphasize their importance as plausible mechanism for transmitting and triggering HEs (Flückiger et al., 2006). However, the timing of available sea-level reconstructions is still under debate

and no definitive consensus has been reached on defining which climatic pattern is causing the sea-level changes during this interval, that is either Antarctic or North Hemisphere ice-sheet fluctuations, or a combination of both (see Arz et al., 2007; Rohling et al., 2004).

Understanding the response of tropical ecosystems to these rapid climate changes is crucial for a meaningful assessment of the mechanisms underlying current global climate change. In the same way, the estimation of ecological responses of terrestrial proxies to rapid climate changes is required to improve the ability of models to simulate realistic feedbacks between the climate and the biosphere, and to validate paleoclimate reconstructions.

Today, most evidence of vegetation response to rapid climate change derives from pollen records spanning the last deglaciation and Holocene periods, the majority of which coming from mid- and high-latitudes (see Peteet, 1995; Velichko et al., 1997). In addition, a more recent body of paleoclimatic evidence has arisen from tropical areas (Hughen et al., 2004; Ledru et al., 2002; Van der Hammen and Hooghiemstra, 1995). However, vegetation records spanning the late Pleistocene with sufficient resolution to resolve millennial-scale climate oscillations are sparse. Some of the most manifest examples of HEs imprints in vegetation records come from Europe (Allen et al., 1999; Sánchez Goñi et al., 2002) and North America (Grimm et al., 1993, 2006). In the Neotropics, correlations

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between marine and continental proxy data in ocean cores off northeastern Brazil (Behling et al., 2000) and the Cariaco Basin (González et al., 2008) have provided explicit evidence of terrestrial vegetation changes correlated with HE intervals. Both records show complementary responses indicating dry climatic conditions in northernmost South America simultaneous with very humid conditions in northeastern Brazil being the result of a southward shift of the Intertropical Convergence Zone (ITCZ). Nevertheless, high-resolution studies are still needed to provide insight into the role that alternative mechanisms, other than the ITCZ latitudinal migration, might have played in the propagation of HES to the tropics.

Of special interest is the role of sea-level as an active mechanism of rapid climate change. The ecological response of sensitive terrestrial ecosystems can be used to understand this role and provide independent information that complements the almost exclusively marine body of evidence. For this purpose, intertidal tropical ecosystems can be particularly useful, since they are known to be very sensitive to environmental gradients in the sea–continent interface, and thus might provide valuable information on sea-level variations in the past. Indeed, pollen cycles (palynocycles) of coastal plant communities have been associated with eustatic oscillations during the Eocene and Neogene of Asia, Africa and Venezuela (Poumot, 1989; Rull and Poumot, 1997). According to the palynocycles concept, phases of marine lowstand, transgression, highstand, and regression can be traced in pollen records biostratigraphically. Here, we present new palynological evidence of marine core MD03-2622 (10°42.69' N; 65°10.15' W; 877 m water depth) from the Cariaco Basin, Venezuela. We present detailed information on the development of intertidal plant communities along the basin during HES linking them to the well-constrained North Atlantic signal of millennial to sub-millennial variability.

2. Setting and background

The Cariaco Basin is located on the northern shelf of Venezuela (Fig. 1). Due to its northern equatorial position, it is particularly sensitive to the seasonal shifts of the ITCZ, which deeply influence present hydrological and oceanographic features of the basin.

When the ITCZ is at its southernmost position (January–March), strong easterly trade winds predominate along the coast of Venezuela, promoting strong coastal upwelling and dry conditions over the continent. The wet season starts in June–July with the northward shift of the ITCZ, which triggers high precipitation over the region increasing terrigenous runoff from local rivers. This seasonality is reflected in the Cariaco Basin sedimentary record as an annually laminated, unbioturbated and almost continuous sequence (Hughen et al., 1996; Peterson et al., 2000a) that extends back to 14 ka (1 ka = 1000 yr BP). At longer timescales, the Cariaco Basin sedimentary record displays an alternation between bioturbated (oxic) and laminated (anoxic) sediments related to glacial–interglacial variability (Peterson et al., 2000b). During MIS 3, the Cariaco Basin record displays a clear North Atlantic climatic variability, shifting from dry conditions during cold stadials to wet conditions and increased river runoff during warm interstadials (González et al., 2008; Peterson et al., 2000b; Peterson and Haug, 2006). This pattern is reflected by variations in terrestrial derived fractions from the adjacent South American continent, whereas the latitudinal migration of the ITCZ has been proposed as the most plausible mechanism responsible for this hydrological pattern (Haug et al., 2001; Martínez et al., 2007; Peterson et al., 2000a; Peterson and Haug, 2006; Yarincik et al., 2000).

During glacial periods, including MIS 3, sea-level was ca 80–120 m lower than at present (Lambeck and Chappell, 2001; Siddall et al., 2003). The sills surrounding the Cariaco Basin became shallower, the broad Unare platform became exposed, and the mouths of the local rivers that drain the northern coast of Venezuela (Manzanares, Neverí, Unare and Tuy Rivers) were closer (~50 km) to the edge of the basin. Results from X-ray fluorescence scanning (elemental ratios) and clay mineralogy of bulk sediments corroborate that the input of terrigenous sediments mainly records the discharge of local rivers during glacial periods (Clayton et al., 1999; Martínez et al., 2007; Yarincik et al., 2000). Consequently, the Cariaco Basin sediments during glacial periods are sensitive to local processes occurring in adjacent watersheds and, in particular, to those of the mouth of local rivers.

Today, the coastal region neighbouring the Cariaco Basin is characterized by a narrow littoral stripe covered by sandy beaches,

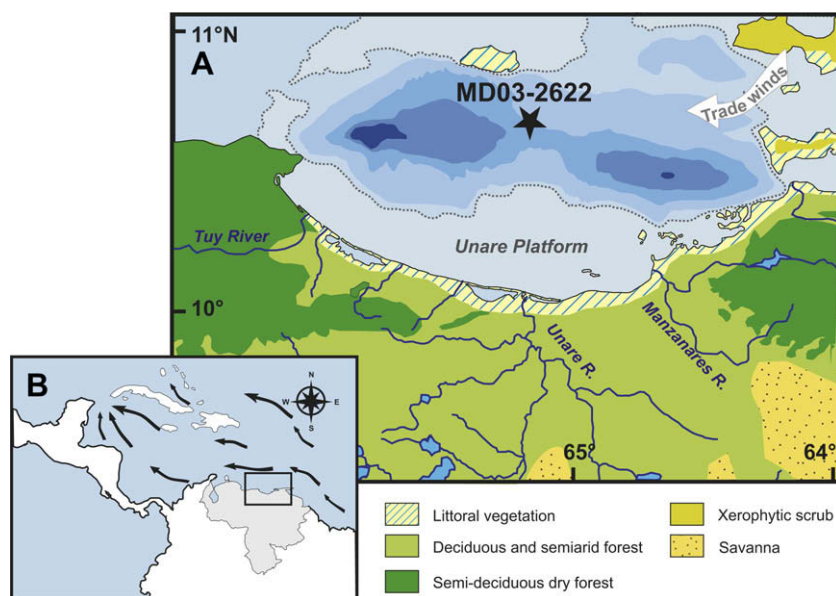


Fig. 1. Map of the study area. (A) The Cariaco Basin, bathymetry and location of core MD03-2622 (star) and main vegetation types on the adjacent continent (adapted from Huber and Alarcón, 1988). Note the wide and shallow Unare platform (<100 m water depth, dotted isobath) that became exposed during MIS 3. (B) Regional location of the Cariaco Basin in the South American continent. Arrows represent main surface currents in the Caribbean.

steep rocky slopes, and a large complex of lagoons. The Coastal Cordillera, with a maximum elevation of 2765 m, extends parallel to the coast, where the Unare depression (0–100 m) forms a natural division between the Central and the Western sections of the Cordillera (Fig. 1). The climate has a seasonal pattern of rainfall and annual average temperatures of 27 °C and is strongly influenced by the northeast trade winds. During severe dry seasons, local rivers dry out and hypersaline conditions develop in the coastal lagoons causing the formation of salt crusts over wide areas (Medina et al., 1989).

Vegetation of the coastal range is characterized by halophytic and psammophytic coastal herbs, and littoral xerophytic thorn scrubs (Huber and Alarcón, 1988). Coastal salt marshes are formed in intertidal areas, lagoons and depressions that are seasonally inundated by seawater and that have been filled with sand driven back by the trade winds (Lüttge, 2008). These coastal marshes are covered by herbaceous, species-poor communities that tolerate the marked seasonality in soil salinity, which can reach concentrations several times that of seawater (Medina et al., 1989). The distribution of vegetation is related soil salinity and topographic position, where non-saline patches can be found slightly elevated above the salt flat level. According to observations by Medina et al. (1989), these elevations respond to the process of aggregation of sediment by salt tolerant plants that further allow leaching of salts during the rainy season, thereby creating favourable conditions for the establishment of salt-intolerant plant species. Most common halophytic species include *Atriplex pentandra*, *Heterostachys ritteriana*, *Salicornia fruticosa*, *Batis maritima*, *Sporobolus virginicus*, *Portulaca rubricaulis* and *Sesuvium portulacastrum*. Areas where freshwater accumulates are occupied by almost pure stands of a few species of Cyperaceae (Medina et al., 1989). Sandy dunes are covered by psammophytic coastal herbs that form open to dense communities. These are mainly characterized by *Scaevola plumieri*, *Portulaca pilosa*, *Cakile lanceolata*, *Cyperus planifolius*, *S. virginicus*, *Ipomoea pes-capreae*, and *Euphorbia buxifolia* (Huber and Alarcón, 1988). Mangroves flourish in scattered spots close to river mouths and coastal lagoons. Typical mangrove species in the area are *Avicennia marina*, *Rhizophora mangle*, *Laguncularia racemosa*, and *Conocarpus erecta* and some epiphytes such as the fern *Acrostichum aureum*. At a more regional scale, semi-deciduous dry forests occupy the areas behind the littoral zone on the lower ranges of the Coastal Cordillera between 300 and 600 m, and are mostly covered by arboreal species such as *Anacardium excelsum*, *Ceiba pentandra*, *Bourreria coumanensis*, *Croton* sp., and legumes (Huber and Alarcón, 1988; Lüttge, 2008).

3. Materials and methods

The marine calypso core MD03-2622 was retrieved from the Cariaco Basin during the P.I.C.A.S.S.O cruise in 2003 (Fig. 1; Laj, 2004). It was drilled at nearly the same location as ODP Site 1002D (Peterson et al., 2000a). Pollen samples were taken every 15 cm for the interval comprising MIS 3 and 4 (30–75 ka) resulting in an average temporal resolution of ~600 years, and every 2 cm for the interval corresponding to Interstadial 8 (38.4–36.4 ka) resulting in an average temporal resolution of ~80 years. Samples for palynological analysis were prepared using standard laboratory methods, which include decalcification with HCl (~10%) and posterior removal of silicates with HF (~40%). Two *Lycopodium clavatum* tablets were added during the decalcification process. After neutralization with KOH and washing, the samples were sieved with ultrasound over a 8 µm nylon mesh during ~60 s to remove particles <10 µm. Permanent slides were mounted in a gelatin–glycerin medium for microscopic examination. Up to 300 terrestrial

palynomorphs were counted, including herb pollen, fern spores, and indeterminates. Fern spores were included in the pollen sum since they are important constituents of the terrestrial flora and provide information on specific plant communities. On the other hand, deteriorated (and unidentified) pollen grains should be included in the pollen sum in order to avoid overrepresentation of known pollen types. Other microfossils like algae and some fungal spores were also counted but not included in the sum on which the percentage calculation is based. In this study we present the pollen percentages of most relevant taxa belonging to coastal plant communities. For comparison, we also include the relative abundances of the semi-deciduous forests, which were already described and explained in detail in González et al. (2008). For more information on all identified species and pollen groups please refer to González et al. (2008). For identification of Chenopodiaceae/Amaranthaceae and Poaceae, morphometric measurements of 40 pollen grains were performed with the imaging facilities at the Department of Palynology and Climate Dynamics, University of Göttingen (digital camera Leica DFC 320 adapted to a Leica DM600B light microscope).

The chronology used in this study (28–75 ka BP) was established by linking similar features of sediment reflectance profile of Cariaco site MD03-2622 (Fig. 2) with that of the nearby ODP Site 1002D (Hughen et al., 2006), which has an extremely high-resolution age model for the past 60 ka based on more than 350 AMS ¹⁴C data on planktic foraminifera (Hughen et al., 2004, 2006). However, the chronology has its limitations, especially prior to 40 ka, when some of the stadials recorded in the Cariaco Basin appear to be shifted relative to the Greenland GISP2 record. This occurs because the chronology of ODP Site 1002D is tied to that of the ²³⁰Th-dated Hulu Cave stalagmites (Hughen et al., 2006; Wang et al., 2001), which differs from NGRIP and GISP2 chronologies.

Calculation of surface areas and linear distances to the coast bordering the Cariaco Basin were calculated using the General Bathymetric Chart of the Oceans (GEBCO) 1-min grid (www.ngdc.noaa.gov/mgg/gebco/gebco.html), after converting the latitude and longitude data to the Universal Transverse Mercator (UTM) coordinate system.

4. Results

Five high-amplitude vegetation shifts are displayed in the pollen record during MIS 3 (60–25 ka), indicating rapid oscillations of environmental conditions in northernmost South America. Recurrent halophytic vegetation expansions correlate with HES 3–6, which are characterized in the Cariaco Basin as intervals with light-coloured sediments (Fig. 2). Within single HE intervals, a recurrent and directional alternation of pollen taxa is observed in the following order: abrupt Chenopodiaceae increments up to 20–60% are followed by Poaceae (6–12%) increments, which are in turn replaced by Cyperaceae peaks (20–50%). Only during HES 3 and 5a Chenopodiaceae and Poaceae increments occur simultaneously. Once interstadial conditions resume, as indicated by lower values in the colour reflectance curve, salt marsh pollen percentages decline and are replaced by those of mangroves and other tree species.

4.1. Chenopodiaceae phase

In all five intervals coinciding with HES, a phase dominated by Chenopodiaceae pollen denotes the first centuries of stadial conditions. During HES 4 and 6, Chenopodiaceae percentages increase rapidly up to 60% within ca 600 years and subsequently

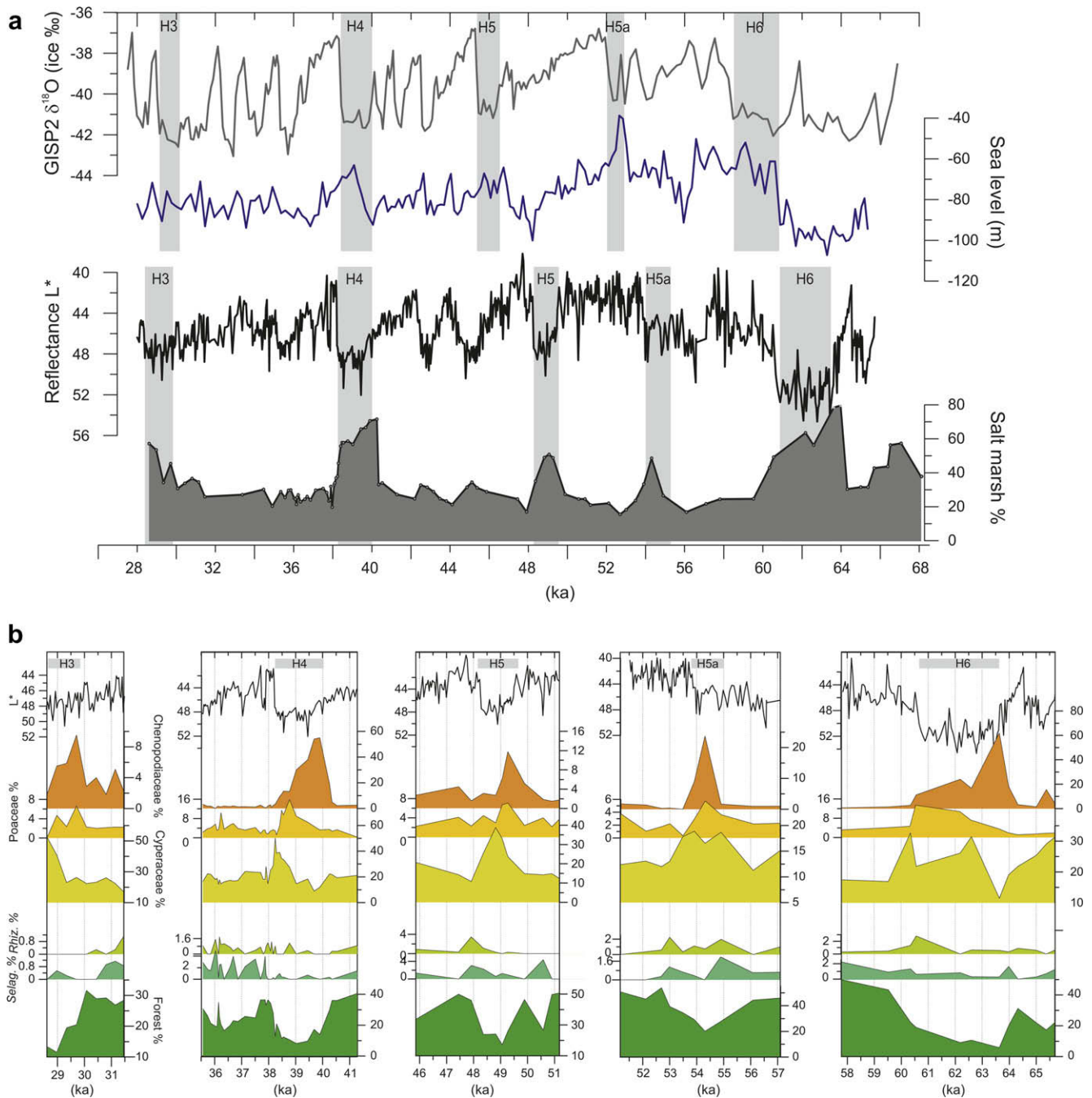


Fig. 2. (a) From top to bottom: GISP2 $\delta^{18}O_{ice}$ (Rasmussen et al., 2006; Stuiver and Grootes, 2000), sea-level reconstruction from the central Red Sea (Siddall et al., 2003), colour reflectance (L^*) of core MD03-2622 (Cariaco Basin, Laj, 2004), and relative abundance of salt marsh pollen from core MD03-2622. Correlation of Heinrich events (HEs) between Greenland and Cariaco Basin is shown with gray bars according to Hemming (2004). The Cariaco Basin chronology is coupled to the age model of Hulu Cave, which differs somewhat from the GISP2 chronology. (b) Detailed pollen profiles representing salt marsh species (Chenopodiaceae, Poaceae, Cyperaceae), *Rhizophora*, *Selaginella*, and semi-deciduous forest relative abundances for five HEs during Marine Isotope Stage 3.

decline gradually. During HEs 3, 5, and 5a, Chenopodiaceae increments are not as high, reaching 10–20% within ca 400–600 years.

4.2. Poaceae phase

Poaceae ($24.82 \pm 2.82 \mu m$, see Supplementary material) pollen abundance starts to increase simultaneously with that of Chenopodiaceae but rises more gradually. Maximum percentages of Poaceae coincide with maximum percentages of Chenopodiaceae in HEs 3 and 5a. During HEs 4, 5, and 6, however, maximum

abundances of Poaceae pollen lag Chenopodiaceae peaks by ca 1000–1500 years. In all cases the decline to low Poaceae values occurs rapidly within ca 200–500 years.

4.3. Cyperaceae phase

Percentage maxima of Cyperaceae pollen characterize the latest phase of vegetation development during intervals coinciding with HEs. Increments of Cyperaceae up to 20–50% lag maximum values of Poaceae by ca 200–500 years. The decline of Cyperaceae

percentages is simultaneous with the return of interstadial conditions. Values for *Rhizophora* (mangrove tree) and *Selaginella* (moss fern) increase during the transition between stadials and interstadials. They occur simultaneously or slightly after the Cyperaceae maximum intervals.

5. Tropical salt marsh response to Heinrich events

The five recurrent intervals of abrupt vegetation change observed in Cariaco Basin sediments during MIS 3 are related to North Atlantic HEs 3 through 6. During glacial periods, when sea-level was ca 80–120 m below present height, the broad, shallow Unare platform became exposed, which is similar to what happens today during prolonged dry seasons (Medina et al., 1989). Therefore, periods of extremely dry atmospheric conditions in the past might have resulted in hypersaline coastal environments. Extreme conditions generated by reduced freshwater input from the continent, as indicated by low Ti and reflectance values (Haug et al., 2001; Peterson et al., 2000a), and the permanent influence of tides, could have been tolerated only by a limited number of plant species, succulents and grasses being the most likely (Adam, 1990).

Chenopodiaceae, Poaceae and Cyperaceae are the three plant families that contain the most common representatives of halophytic plants in tropical and subtropical wetlands (Adam, 1990). Although it is difficult to identify their pollen grains at subfamily levels (Bush, 2002; Flores Olvera et al., 2006), four lines of evidence support the idea that MD03-2622 pollen record of HE intervals represents plant communities expanding in hypersaline coastal environments: (a) modern representatives of these three families growing in the immediacy of the Cariaco Basin belong to genera that are tolerant to high soil salinities (e.g. *Atriplex*, *Salicornia*, *Sporobolus*, *Spartina*, *Cyperus*), which typically occupy intertidal habitats and sand dunes along shores (Huber and Alarcón, 1988); (b) morphological features of pollen grains from our record, such as grain diameter and number of pores (Supplementary material), permit the partial exclusion of most genera typical from other environments (e.g. savannas, dry forest); (c) comparing the pollen record and the stable carbon isotopic composition ($\delta^{13}\text{C}$) of plant waxes from the nearby core ODP 1002D (Drenzek, 2007) suggests that peaks of enriched $\delta^{13}\text{C}$ (indicating more C_4 plants) are most likely caused by coastal Chenopodiaceae expansions and not by C_4 -Poaceae (savanna) expansions; and (d) the consistent and directional sequence in relative abundance of taxa during all HE intervals – initial pollen percentage maxima of Chenopodiaceae subsequently followed by those of Poaceae, Cyperaceae, and *Rhizophora* – strongly suggests a gradational pattern indicative of marked environmental changes typical of intertidal habitats.

In tidal salt marsh plant communities, species composition varies with elevation, usually in a banded pattern parallel to the shore. This variation is often thought to reflect environmental gradients that result from the interaction between tidal regime, local topography, freshwater input, and biota. It has been proposed that zonation is a spatial expression of successional changes over time, although until now there was insufficient long-term evidence to support this idea (Adam, 1990). The palynological record from the Cariaco Basin corroborates the model of successional change by providing evidence of tropical salt marsh development over hundreds of years as a response to recurrent environmental alternations during HEs (Fig. 3).

In the studied sequence, salt marshes started to develop under extremely arid stadial conditions (González et al., 2008; Peterson and Haug, 2006) when intertidal habitats became hypersaline due to extended periods of evaporative water loss. The salt marshes were most likely restricted to narrow intertidal areas below the highest astronomical tide level because, under arid or strongly

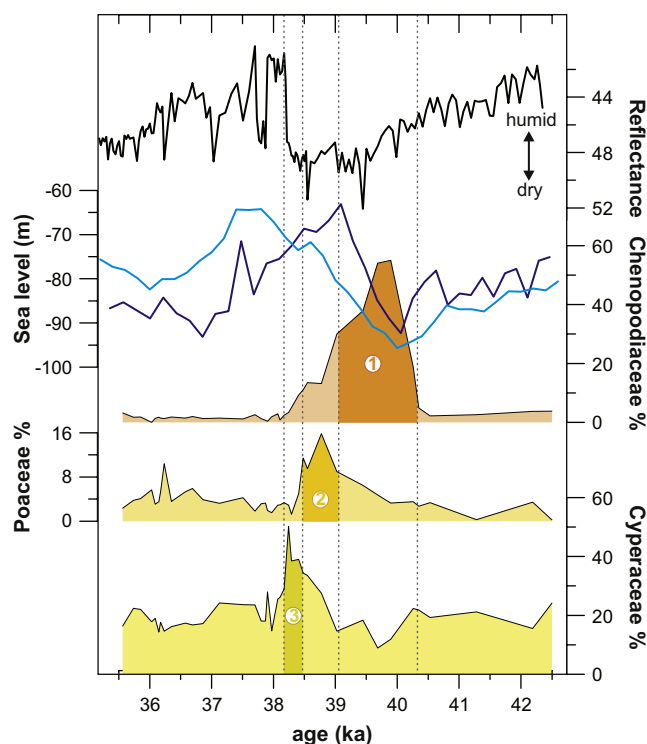


Fig. 3. Comparison of the high-resolution palynological record from core MD03-2622 (Cariaco Basin) and sea-level reconstructions from the Red Sea during HE 4. From top to bottom: reflectance data from core MD03-2622 (Laj, 2004). Sea-level data; the dark line denotes the sea-level curve from the central Red Sea (Siddall et al., 2003) and the light-coloured line denotes the one from the northern Red Sea (Arz et al., 2007). Pollen percentages of Chenopodiaceae, Poaceae, and Cyperaceae from core MD03-2622 indicating the directional alternation of salt marshes along the Cariaco Basin.

seasonal conditions, tropical salt marshes are usually fringed on their landward side by extensive hypersaline vegetation-bare flats (Fig. 4a and b; Adam, 2002). Pioneer species of salt marshes, e.g. annual *Atriplex* and *Salicornia* (Chenopodiaceae), first colonize bare zones of lower and middle marsh areas, which are characterized by a high incidence of wave brake and prolonged inundation regimes (Ranwell, 1972). Intervals of maximum representation of Chenopodiaceae in the pollen record are, therefore, interpreted as periods of direct tidal influence and consequent sediment relocation. Changes in sea-level would account for significant shifts in the tidal frame, having considerable repercussions for salt marshes. Frequent tidal flooding under accelerated sea-level rise would result in flooding of the marsh surface, transforming it into a new seafloor, with the subsequent landward accretion of new, low marsh sediments (Fig. 4b).

To test whether sea-level was a driving factor of the early succession stages in these tropical coastal areas during HEs, available sea-level reconstructions with well-constrained ages in the 40.5–38 ka interval (Arz et al., 2007; Siddall et al., 2003), were compared to high-resolution pollen data from the Cariaco Basin. The interval of dominating Chenopodiaceae pollen percentages corresponds with the interval of accelerated sea-level rise (~ 3 cm/yr; Fig. 3), confirming that only representatives of the pioneer Chenopodiaceae, which have high colonizing abilities, survived the stressful, high rates of change of the early succession stages. Moreover, the erosion of low marsh sediments would enhance the washout and subsequent transport of autochthonous pollen to the basin (Fig. 4b).

Using local bathymetry maps, we estimated an increment of ~ 2.3 km²/yr of intertidal marsh surface area that might have

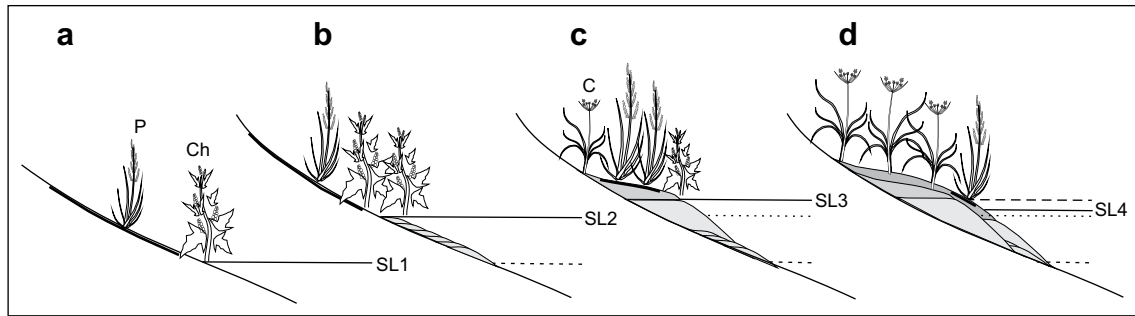


Fig. 4. Schematic representation of salt marsh community dynamics in a sea-level changing environment. P: Poaceae, Ch: Chenopodiaceae, and C: Cyperaceae. Areas of soil hypersalinity are indicated by thicker lines. (a) Establishment of salt marshes when arid conditions promote extensive hypersaline environments, (b) rapid sea-level rise causes erosion, only pioneer species survive, (c) sea-level rise decelerates, and accretion of sediments and autochthonous material takes place; more competitive species (graminoids) take advantage of less extreme conditions, and (d) sea-level drops, sediment accumulation constrains the tidal influence to the seaward edge.

resulted by the mere effect of rising sea-level from -90 to -60 m below sea-level at the mentioned rate of 3 cm/yr (Fig. 5).

As soon as sea-level rise decelerated, some vegetation was able to establish permanently, acting as a trap of sediments and auto-genic organic matter, which stabilizes sediments and increases tidal height. The build-up of middle- and high-marsh environments probably favoured the expansion of more competitive perennial graminoids replacing pioneer species (Bertness et al., 1992; Valiela and Rietsma, 1995). This process is indicated in our record by the subsequent maxima of Poaceae and Cyperaceae pollen percentages shown for each HE (Figs. 2 and 3). In contrast, the presence of Cyperaceae necessarily indicates less saline conditions, since sedges typically colonize mesohaline swamps and do not tolerate salinity excess (Crain et al., 2004). Alternatively, and given that there is no evidence of enhanced freshwater input during HEs, Cyperaceae pollen maxima might reflect broadening of higher marsh areas that are less frequently flooded (Fig. 4c and d).

Once interstadial conditions resumed and the average position of the ITCZ shifted northwards (Peterson and Haug, 2006), the increased availability of freshwater might have alleviated salinity stress on soils, allowing a more complex plant community to develop on the shelf, pushing the upper borders of the salt marsh seawards. Simultaneous increments of mangrove (*Rhizophora*) pollen and *Selaginella* spores suggest that coastal environments became less saline and more suitable for the establishment of more developed forests during stadial–interstadial transitions (Cintrón et al., 1978). Additionally to freshening, decelerated sea-level rise (or sea-level fall) would be required to allow the establishment of mangroves, since mangroves do not survive if sea-level rise occurs too rapidly and exceeds natural accretion rates in the range of 0.8 – 6 mm/yr (Ellison, 1993; Woodroffe, 1999). Furthermore, in arid environments mangroves are very sensitive to freshwater input and fluvial sediment yield, given that they are strongly limited by the scarce input of allochthonous sediment (Woodroffe, 1992). Consequently, as enhanced precipitation would have had a direct effect on increasing sediment yield transported from the continent, it would have enhanced the survival ability of mangroves both by increased freshwater availability and increased sediment load.

6. Sea-level during HEs

Millennial sea-level changes during MIS 3 are difficult to assess since coral-based data are sparser and chronologies less precise; consequently, available knowledge relies greatly upon oxygen isotope records from deep-sea cores. The existing body of evidence consistently shows four cycles of similar amplitude of sea-level change in the order of 15 – 30 m during MIS 3 (Arz et al., 2007; Lambeck and Chappell, 2001; Siddall et al., 2003; Waelbroeck et al.,

2002; Yokoyama et al., 2001). However, there is no consensus on the exact timing of these changes or on the relative roles of the Southern and the Northern Hemisphere ice-sheets in global sea-level scenarios. The well resolved pollen record from the Cariaco Basin encompassing the 40.5 – 38 ka period indicates expansion of salt marsh pioneer species (Chenopodiaceae) and provides independent evidence of accelerated sea-level rise in the tropical Atlantic between 40 and 39 ka. The record suggests a similar relation between salt marsh expansion and sea-level rise during HEs 3, 5, 5a and 6, in spite of dating uncertainties and poorer resolution of the vegetation data. In all five cycles, maximum values of Chenopodiaceae pollen coincide with the onset of HE stadials in the North Atlantic, and with rising temperatures in Antarctica (Blunier and Brook, 2001; EPICA Community members, 2006) (Fig. 2).

According to our palynological evidence, sea-level started to rise before the ice-sheet collapse created Heinrich layers in the North Atlantic. This is in agreement with both central and northern Red Sea sea-level reconstructions during the HE 4 (Fig. 3; Arz et al., 2007; Siddall et al., 2003). On the other hand, our interpretation requires the subsequent decelerated rise or fall of sea-level to

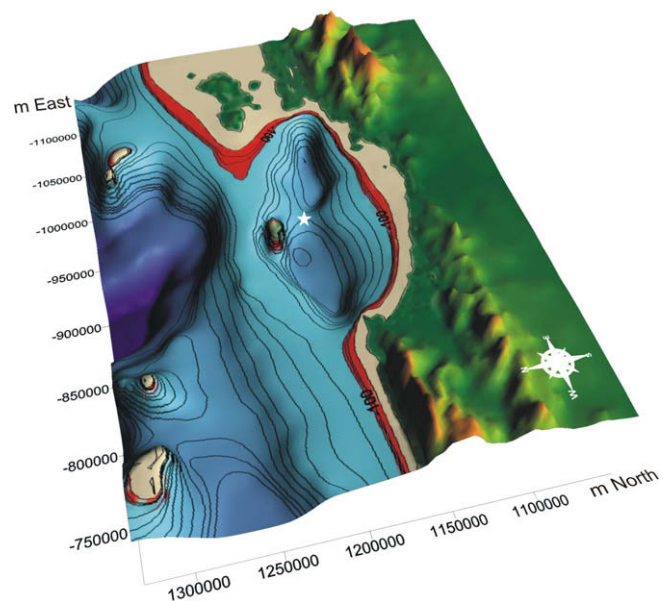


Fig. 5. Bathymetric map of Cariaco Basin and adjacent areas based on the GEBCO 1-min grid (<http://www.ngdc.noaa.gov/mgg/gebco/gebco.html>). Areas exposed by the glacial sea-level drop of 100 m are denoted in light gray. The shaded area above the 100 m isobath denotes the increment of marsh surface area by 30 m of sea-level rise (from -90 to -60 mbsl). White star indicates the position of core MD03-2622. Easting and northing (m) are in the UTM coordinate system.

coincide with the expansion of graminoids. If this is the case, our data support the timing of central Red Sea reconstruction (Rohling et al., 2008; Siddall et al., 2003) and models suggesting that warming in Antarctica might have accounted for a rise in sea-level of about 15 m within ca 500 years (Rohling et al., 2004; Weaver et al., 2003). The paleoecological evidence presented in this study strengthens the idea of sea-level changes triggering HEs as proposed by Flückiger et al. (2006) based on modeling simulations.

7. Conclusions

Through the palynological reconstruction of intertidal vegetation in core MD03-2622 we were able to identify specific responses of plant communities to oceanic (sea-level) and atmospheric (precipitation) alterations, and provide indirect evidence of rapid sea-level change during MIS 3. Our data elucidate the pattern and mechanisms driving tropical salt marsh succession at century millennial timescales. Five intervals of expanded salt marsh vegetation correspond to HEs of the northern high-latitudes and suggest periods of accelerated sea-level rise in the tropical Atlantic. The close relationship between sea-level rise and community dynamics is consistent with a resource-based mechanism of succession, where soil development and salinity gradients are the main factors determining the vegetation dynamics of coastal marshes. In this context, the Cariaco Basin palynological record has great ecological significance, as much as it deals with ecosystems that are poorly documented on longer timescales. It is especially informative on the timing of sea-level changes during MIS 3 and their connection with HEs, supporting the idea that sea-level fluctuations followed Antarctica climate variability.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.quascirev.2008.12.023](https://doi.org/10.1016/j.quascirev.2008.12.023).

References

- Adam, P., 1990. Saltmarsh Ecology. Cambridge University Press, Cambridge, 461 p.
- Adam, P., 2002. Saltmarshes in a time of change. *Environmental Conservation* 29, 39–61.
- Allen, J.R.M., Brandt, U., Brauer, A., Hubberten, H.-W., Huntley, B., Kellerk, J., Kraml, M., Mackensen, A., Mingram, J., Negendank, J.F.W., Nowaczyk, N.R., Oberhänsli, H., Watts, W.A., Wulf, S., Zolitschka, B., 1999. Rapid environmental changes in southern Europe during the last glacial period. *Nature* 400, 740–743.
- Arz, H.W., Lamy, F., Ganopolski, A., Nowaczyk, N., Pätzold, J., 2007. Dominant Northern Hemisphere climate control over millennial-scale glacial sea-level variability. *Quaternary Science Reviews* 26, 312–321.
- Behling, H., Arz, H.W., Pätzold, J., Wefer, G., 2000. Late Quaternary vegetational and climate dynamics in northeastern Brazil, inferences from marine core GeoB 3104-1. *Quaternary Science Reviews* 19, 981–994.
- Bertness, M.D., Gough, L., Shumway, S.W., 1992. Salt tolerances and the distribution of fugitive salt marsh plants. *Ecology* 73, 1842–1851.
- Blunier, T., Brook, E.J., 2001. Timing of millennial-scale climate change in Antarctica and Greenland during the last glacial period. *Science* 291, 109–112.
- Broecker, W.S., 2003. Does the trigger for abrupt climate change reside in the ocean or in the atmosphere? *Science* 300, 1519–1522.
- Bush, M.B., 2002. On the interpretation of fossil Poaceae pollen in the lowland humid neotropics. *Palaeogeography, Palaeoclimatology, Palaeoecology* 177, 5–7.
- Cintrón, G., Lugo, A.E., Pool, D.J., Morris, G., 1978. Mangroves of arid environments in Puerto Rico and adjacent islands. *Biotropica* 10, 110–121.
- Clayton, T., Pearce, R.B., Peterson, L.C., 1999. Indirect climatic control of the clay mineral composition of Quaternary sediments from the Cariaco Basin, northern Venezuela (ODP Site 1002). *Marine Geology* 161, 191–207.
- Crain, C.M., Silliman, B.R., Bertness, S.L., Bertness, M.D., 2004. Physical and biotic drivers of plant distribution across estuarine salinity gradients. *Ecology* 85, 2539–2549.
- Drenzek, N.J., 2007. The Temporal Dynamics of Terrestrial Organic Matter Transfer to the Oceans: Initial Assessment and Application. PhD. Thesis, Massachusetts Institute of Technology/Woods Hole Oceanographic Institution, 223 p.
- Ellison, J.C., 1993. Mangrove retreat with rising sea-level, Bermuda. *Estuarine, Coastal and Shelf Science* 37, 75–87.
- EPICA Community members, 2006. One-to-one coupling of glacial climate variability in Greenland and Antarctica. *Nature* 444, 195–198.
- Flores Olvera, H., Fuentes-Soriano, S., Martínez Hernández, E., 2006. Pollen morphology and systematics of Atriplicaceae (Chenopodiaceae). *Grana* 45, 175–194.
- Flückiger, J., Knutti, R., Watts, J.W.C., 2006. Oceanic processes as potential trigger and amplifying mechanisms for Heinrich events. *Paleoceanography* 21, PA2014, doi:10.1029/2005PA001204.
- González, C., Dupont, L.M., Behling, H., Wefer, G., 2008. Neotropical vegetation response to rapid climate changes during the last glacial: palynological evidence from the Cariaco Basin. *Quaternary Research* 69, 217–230.
- Grimm, E.C., Jacobson Jr., G.L., Watts, W.A., Hansen, B.C.S., Maasch, K.A., 1993. A 50,000-year record of climate oscillations from Florida and its temporal correlation with the Heinrich events. *Science* 261, 198–200.
- Grimm, E.C., Watts, W.A., Jacobson Jr., G.L., Hansen, B.C.S., Almquist, H.R., Dieffenbacher-Krall, A.C., 2006. Evidence for warm wet Heinrich events in Florida. *Quaternary Science Reviews* 25, 2197–2211.
- Haug, G.H., Hughen, K.A., Sigman, D.M., Peterson, L.C., Röhl, U., 2001. Southward migration of the intertropical convergence zone through the Holocene. *Science* 293, 1304–1308.
- Hemming, S., 2004. Heinrich events: massive late Pleistocene detritus layers of the North Atlantic and their global climate imprint. *Review of Geophysics* 42, 1–43.
- Huber, O., Alarcón, C., 1988. Mapa de vegetación de Venezuela. República de Venezuela, Ministerio del Ambiente y de los Recursos Naturales Renovables, Caracas, Venezuela.
- Hughen, K.A., Overpeck, J.T., Peterson, L.C., Trumbore, S., 1996. Rapid climate changes in the tropical Atlantic region during the last deglaciation. *Nature* 380, 51–54.
- Hughen, K., Lehman, S., Southon, J., Overpeck, J., Marchal, O., Herring, C., Turnbull, J., 2004. ¹⁴C activity and global carbon cycle changes over the past 50,000 years. *Science* 303, 202–207.
- Hughen, K., Southon, J., Lehman, S., Bertrand, C., Turnbull, J., 2006. Marine-derived ¹⁴C calibration and activity record for the past 50,000 years updated from the Cariaco Basin. *Quaternary Science Reviews* 25, 3216–3227.
- Lambeck, K., Chappell, J., 2001. Sea level change through the last glacial cycle. *Science* 292, 679–686.
- Laj, C., 2004. Cruise Report: MD 132 – P.I.C.A.S.S.O. Images XI, Fortaleza–Baltimore–Brest, Mai Juin 2003. Institut Polaire Français Paul Emile Victor, 53 p.
- Ledru, M.-P., Mourguiart, P., Ceccantini, G., Turcq, B., Sifeddine, A., 2002. Tropical climates in the game of two hemispheres revealed by abrupt climatic change. *Geology* 30, 275–278.
- Lüttge, U., 2008. *Physiological Ecology of Tropical Plants*, second ed. Springer, Berlin.
- Martínez, N.C., Murray, R.W., Thunell, R.C., Peterson, L.C., Müller-Karger, Frank, Astor, Y., Varela, R., 2007. Modern climate forcing of terrigenous deposition in the tropics (Cariaco Basin, Venezuela). *Earth and Planetary Science Letters* 264, 438–451.
- Medina, E., Cram, W.J., Lee, H.S., Lüttge, U., Popp, M., Smith, J.A., Diaz, M., 1989. Ecophysiology of xerophytic and halophytic vegetation of a coastal alluvial plain in northern Venezuela, I: site description and plant communities. *New Phytologist* 111, 233–243.
- Peteet, D., 1995. Global Younger Dryas? *Quaternary International* 28, 93–104.
- Peterson, L.C., Haug, G.H., Hughen, K.A., Röhl, U., 2000a. Rapid changes in the hydrologic cycle of the tropical Atlantic during the last glacial. *Science* 290, 1947–1951.
- Peterson, L.C., Haug, G.H., Murray, R.W., Yarinicik, K.M., King, J.W., Bralower, T.J., Kameo, K., Rutherford, S.D., Pearce, R.B., 2000b. Late Quaternary stratigraphy and sedimentation at ODP Site 1002, Cariaco Basin (Venezuela). In: Leckie, R.M., Sigurdsson, H., Acton, G.D., Draper, G. (Eds.), *Proceedings of the Ocean Drilling Program Scientific Results*, vol. 165, pp. 85–99.
- Peterson, L., Haug, G., 2006. Variability in the mean latitude of the Atlantic inter-tropical convergence zone as recorded by riverine input of sediments to the Cariaco Basin (Venezuela). *Palaeogeography, Palaeoclimatology, Palaeoecology* 234, 97–113.
- Poumot, C., 1989. Palynological evidence for eustatic events in the tropical Neogene. *Bulletin des Centres de Recherches Exploration–Production Elf Aquitaine* 13, 437–453.

- Rahmstorf, S., 2002. Ocean circulation and climate during the past 120,000 years. *Nature* 419, 207–214.
- Ranwell, D.S., 1972. *Ecology of Salt Marshes and Sand Dunes*. Chapman and Hall, 258 p.
- Rasmussen, S.O., Seierstad, I.K., Andersen, K.K., Bigler, M., Dahl-Jensen, D., Johnsen, S.J., 2006. IGBP PAGES/World Data Center for Paleoclimatology Data Contribution Series # 2006-120. NOAA/NCDC Paleoclimatology Program, Boulder, CO, USA.
- Rohling, E.J., Marsh, R., Wells, N.C., Siddall, M., Edwards, N., 2004. Similar melt-water contributions to glacial sea-level variability from Antarctic and northern ice sheets. *Nature* 430, 1016–1021.
- Rohling, E.J., Grant, K., Hemleben, C., Kucera, M., Roberts, A.P., Schmeltzer, I., Schulz, H., Siccha, M., Siddall, M., Trommer, G., 2008. New constraints on the timing of sea level fluctuations during early to middle Marine Isotope Stage 3. *Paleoceanography* 23, doi:10.1029/2008PA001617.
- Rull, V., Poumot, C., 1997. Eocene to Miocene palynocycles from Western Venezuela, and correlations with global eustatic cycles. In: *Memorias VIII Congreso Geológico Venezolano*, vol. II, pp. 343–349.
- Sánchez Goñi, M.F., Cacho, I., Turon, J.-L., Guiot, J., Sierro, F.J., Peypouquet, J.-P., Grimalt, J.O., Shackleton, N.J., 2002. Synchronicity between marine and terrestrial responses to millennial scale climatic variability during the last glacial period in the Mediterranean region. *Climate Dynamics* 19, 95–105.
- Siddall, M., Rohling, E.J., Almogi-Labin, A., Hemleben, Ch., Melschner, D., Schmeltzer, I., Smeed, D.A., 2003. Sea-level fluctuations during the last glacial cycle. *Nature* 423, 853–858.
- Stuiver, M., Grootes, P.M., 2000. GISP2 oxygen isotope ratios. *Quaternary International* 53, 277–284.
- Valiela, I., Rietsma, C.S., 1995. Disturbance of salt marsh vegetation by wrack mats in Great Sippewissett Marsh. *Oecologia* 102, 106–112.
- Van der Hammen, T., Hooghiemstra, H., 1995. The el Abra stadial, a Younger Dryas equivalent in Colombia. *Quaternary Science Reviews* 14, 841–851.
- Voelker, A.H.L., workshop participants, 2002. Global distribution of centennial-scale records for Marine Isotope Stage (MIS) 3: a database. *Quaternary Science Reviews* 21, 1185–1212.
- Velichko, A.A., Andrev, A.A., Klimanov, V.A., 1997. Climate and vegetation dynamics in the tundra and forest zone during the Late-Glacial and Holocene. *Quaternary International* 41–42, 71–96.
- Waelbroeck, C., Labeyrie, L., Michel, E., Duplessy, J.C., McManus, J.F., Lambeck, K., Balbon, E., Labracherie, M., 2002. Sea-level and deep water temperature changes derived from benthic foraminifera isotopic records. *Quaternary Science Reviews* 21, 295–305.
- Wang, Y.J., Cheng, H., Edwards, R.L., An, Z.S., Wu, J.Y., Shen, C.-C., Dorale, J.A., 2001. A high-resolution absolute-dated late Pleistocene monsoon record from Hulu Cave, China. *Science* 294, 2345–2348.
- Weaver, A.J., Saenko, O.A., Clark, P.U., Mitrovica, J.X., 2003. Meltwater Pulse 1A from Antarctica as a trigger of the Bølling–Allerød warm interval. *Science* 299, 1709–1713.
- Woodroffe, C.D., 1992. Mangrove sediments and geomorphology. In: Robertson, A.I., Alongi, D.M. (Eds.), *Tropical Mangrove Ecosystems*. American Geophysical Union, pp. 7–41.
- Woodroffe, C.D., 1999. Response of mangrove shorelines to sea-level change. *Tropics* 8, 159–177.
- Yarincik, K.M., Murray, R.W., Peterson, L.C., 2000. Climatically sensitive eolian and hemipelagic deposition in the Cariaco Basin, Venezuela, over the past 578,000 years: results from Al/Ti and K/Al. *Paleoceanography* 15, 210–228.
- Yokoyama, Y., Esat, T.M., Lambeck, K., 2001. Coupled climate and sea-level changes deduced from Huon Peninsula coral terraces of the last ice age. *Earth and Planetary Science Letters* 193, 579–587.