

Neotropical vegetation response to rapid climate changes during the last glacial period: Palynological evidence from the Cariaco Basin

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Abstract

We present new palynological information from the anoxic Cariaco Basin, off Venezuela, that provides insight into the response of northernmost South American vegetation to rapid climate changes between 68 and 28 ka, specifically during North Atlantic Heinrich events (HEs) and Dansgaard/Oeschger cycles. We defined three different vegetation modes: (1) an interstadial mode characterized by the highest pollen concentration and the maximum extension of semi-deciduous and evergreen forests; (2) a stadial mode characterized by increases of salt marshes, herbs, and montane forests; and (3) a Heinrich event mode characterized by the lowest pollen concentrations, abrupt increases of salt marshes, and decreased forest abundance. Similarly, indices of C4/C3 plants show increases during stadials with clear peaks during the onset of HEs, though grasslands did not become dominant during these periods. We alternatively propose that these expansions of C4 plants are associated with the expansion of coastal salt marshes. Our vegetation record suggests the prevalence of humid conditions during interstadials, dry and cold conditions during stadials, and dry and cold conditions together with changes in sea level during HEs. This new palynological evidence supports previous interpretations that main environmental changes in northernmost South America were driven by latitudinal displacements of the Intertropical Convergence Zone and sea-level changes.

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Introduction

During the last glacial period, the Earth has experienced a series of large and abrupt climate changes, shifting from cold to warm climates within a few decades. Two main types of abrupt climate changes are recorded in Greenland ice and in detailed paleoclimate records from the Northern Hemisphere: Dansgaard/Oeschger (D/O) cycles and Heinrich events (HEs) (Oeschger, 1984; Bond et al., 1993; Dansgaard et al., 1993). D/O cycles are the abrupt warming (interstadials) and cooling (stadials) events within glacial periods, and HEs are documented in the North Atlantic as anomalous occurrences of ice-rafted

detritus that coincide with the coldest final phases of some consecutive stadials. These events have left a broad spatial imprint (Voelker et al., 2002) and are believed to be linked to different states of the ocean's thermohaline circulation (THC) and to be propagated by atmospheric and oceanic means (Rahmstorf, 2002; Broecker, 2003). For several decades, climatologists and paleoecologists have focused their attention on the tropics due to their potential to alter the global oceanic heat and fresh water balance, their role as a source of water vapor to the atmosphere, and as a source or sink of atmospheric CO₂. There have been great efforts to elucidate the relative role that the tropics play in triggering and transmitting these abrupt climate changes, but models and paleoclimatic evidence are still ambiguous for the mid-low latitudes, as they suggest contrasting responses, mechanisms, and timings (Cane and Clement, 1999; Rühlemann et al., 1999; Vidal et al., 1999; Broecker, 2003; Hughen et al., 2004a; Jennerjahn et al., 2004; Prange et al., 2004).

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D/O cycles and HEs have both correlative and distinct expressions in wide-ranging climate records. Broad and consistent evidence from mid- and low-latitude paleorecords shows D/O variability to be synchronous with the northern Atlantic millennial-scale changes. Atmospheric linkages, such as the Intertropical Convergence Zone (ITCZ) and the monsoon system, have been proposed as plausible mechanisms in propagating the effects of D/O cooling between the northern latitudes and the tropics. Presumably, a more southerly position of the ITCZ occurred during stadial periods, being simultaneously recorded as dry conditions in the Cariaco Basin (Peterson et al., 2000a), and more humid conditions over the Bolivian Altiplano (Baker et al., 2001) and northeast Brazil (Wang et al., 2004). Data from other tropical regions have provided evidence of analogous paleohydrological changes, such as the stalagmite records from Hulu and Dongge caves in China (Wang et al., 2001; Yuan et al., 2004), the paleosalinity record of the western Tropical Pacific (Stott et al., 2002), and the records from Socotra Island in the Indian Ocean (Burns et al., 2003).

Heinrich events have also been widely correlated with clear climatic signals, but contrary to D/O cycles, their linkages with tropical areas are less understood. Apparently, a large reduction in the THC during HEs was transmitted to lower latitudes by both atmospheric mechanisms, as seen for D/O oscillations, and oceanic mechanisms (Alley et al., 1999). At low latitudes, HEs have been recorded off NW Africa as 2–4°C cooling phases (Zhao et al., 1995) and severe aridity intervals (Jullien et al., 2007), as periods of weakening of tropical easterly winds in the equatorial Atlantic (McIntyre and Molino, 1996), as pluvial periods in northeast Brazil (Arz et al., 1998; Behling et al., 2000; Wang et al., 2004), and as cool and wet periods in Lake Tulane in Florida (Grimm et al., 1993). In the Arabian Sea, HEs have been recorded as periods of decreased wind-induced upwelling, precipitation, and intensity of monsoonal activity (Leuschner and Sirocko, 2000; Burns et al., 2003). The only evidence of HEs in northern South America derives from the Tobago basin core M35003-4, which records abrupt shifts to oligotrophic sea surface conditions (Vink et al., 2001).

Due to the strong feedbacks that exist between vegetation and climate (e.g., albedo, hydrological cycle, carbon cycle), it is essential to understand the ecological responses of terrestrial ecosystems to abrupt climate changes at longer time scales. The neotropics have been subject of numerous vegetation reconstructions that mainly focus on the arid vs. wet or the cold vs. warm debate (e.g., Salgado-Labouriau, 1997; Hooghiemstra and Van der Hammen, 1998; Colinvaux et al., 2000), frequently facing dating uncertainties that do not allow the adequate comparison with other records. On the other hand, pollen analysis from marine sediments has shown to be a useful and sensitive tool that provides long and well-dated records of vegetation change on adjacent continents, which can be used to establish terrestrial–marine and local–regional correlations (Dupont, 1999; Hooghiemstra et al., 2006; and references therein).

Because the Cariaco Basin is one of the best marine locations to study Atlantic Ocean and tropical climate variability, it has been the focus of numerous studies of various scientific disciplines (e.g., Hughen et al., 1996; Clayton et al., 1999;

Herbert and Schuffert, 2000; Peterson et al., 2000a,b; Yarincik and Murray, 2000; Piper and Dean, 2002; Hughen et al., 2004a). Cariaco sediments are highly sensitive to changes in regional climate systems and are capable of recording responses to climate change of both marine and terrestrial systems. Hence, they constitute a useful tropical counterpart to high-latitude and ice core records for the study of past climate changes. In this study, we present palynological reconstructions for the period 68–28 ka in the Cariaco Basin, which provide insight into marine–continental linkages and the ecological development of the northernmost South American tropical vegetation during the abrupt stadial–interstadial shifts that characterized Marine Isotope Stage (MIS) 3.

Environmental setting

The Cariaco Basin is located on the northern shelf of Venezuela (Fig. 1). Today, anoxia occurs below ~300 m as a result of the high seasonal productivity and the shallow sills that restrict the horizontal water exchange with the rest of the Caribbean and the large river plumes from the Orinoco and Amazon (Muller-Karger et al., 2004). Due to its northern equatorial position, the Cariaco Basin is particularly sensitive to the seasonal shifts of the ITCZ. When the ITCZ is at its southernmost position (January and March), strong easterly trade winds predominate along the coast of Venezuela, resulting in strong coastal upwelling, high marine productivity 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. This annual migration of the ITCZ has a deep influence on the present hydrological and oceanographical features of the basin that, together with the very high sedimentation rates (30–100 cm/ka), produce an annually laminated, unbioturbated and almost continuous record, ideal for paleoclimatic reconstructions (Hughen et al., 1996; Peterson et al., 2000a). Throughout the late Quaternary, the Cariaco Basin has followed an alternation between periods of oxic and anoxic conditions, related to glacial–interglacial cycles, that are clearly reflected in the sequence as fluctuations between bioturbated (oxic) and laminated (anoxic) sediments (Peterson et al., 2000b). At these larger scales, the ITCZ has been proposed as the most probable linkage between northern high latitude and tropical climate patterns (Peterson and Haug, 2006).

Pollen transport agents

Terrigenous material is deposited into the Cariaco Basin by fluvial and aeolian mechanisms. Sea level has played an active role in modulating the sediment supply of major and minor local rivers and their relative contribution of sediments during interglacial high stands vs. glacial lowstands.

During glacial periods such as MIS 3, the 150-m water depth sills surrounding the basin became shallower, and the isolation of the basin reduced the potential contribution of the Amazon and Orinoco Rivers, while the local rivers (Cumaná, Neverí, Unare, and Tuy) that drain the northern coastline of Venezuela flowed directly into the basin and became volumetrically more

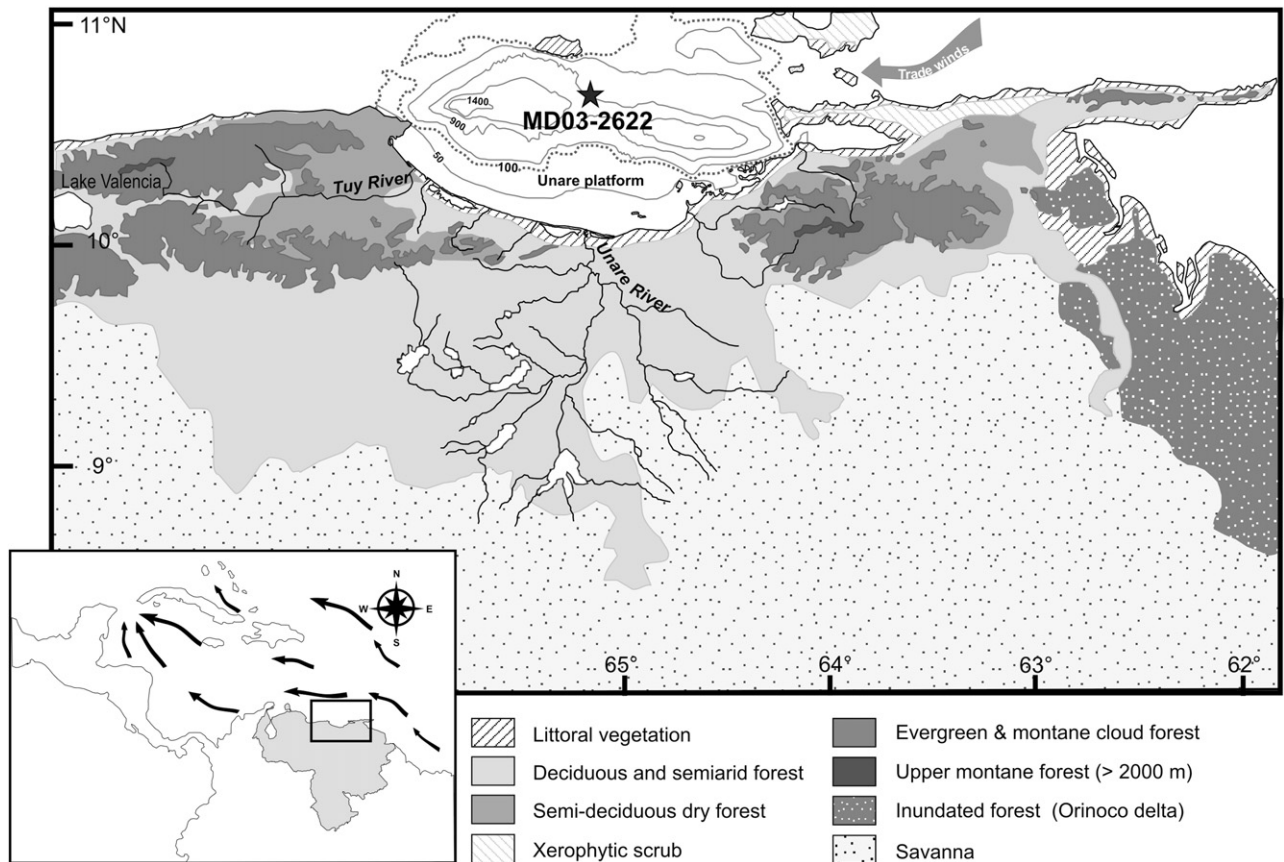


Figure 1. Map showing the location of core MD03-2622 in the Cariaco Basin and main vegetation types on the adjacent continent (adapted from Huber and Alarcón, 1988). Black arrows in the lower panel represent main oceanic currents. Note the wide and shallow Unare platform (<100 m water depth, dotted isobath).

important. Studies on Al/Ti and K/Ti ratios in bulk sediment (Yarincik and Murray, 2000) and clay mineralogy (Clayton et al., 1999) from the Cariaco Basin confirm this, showing that the imprint from the Amazon and Orinoco differ greatly from the ones from Cariaco, and that during glacial periods the input of terrigenous sediments mainly records the input from local rivers.

Aeolian sediment, specifically dust from the Sahara and Sahel regions, has been traced over the tropical Atlantic all the way to the Caribbean (Prospero and Lamb, 2003). It has been shown that during glacial periods, maximum dust input coming from Africa reached the western equatorial Atlantic (Yarincik and Murray, 2000). However, some evidence indicates that the pollen record from the Cariaco Basin was not contaminated with long-distance elements. Firstly, low altitude trade winds mainly carry very fine particles (<6–8 μm) to the pelagic environment and do not transport pollen over the Atlantic Ocean (Calleja and Van Campo, 1990). Some long-term studies on the biological constituents of modern African dust have found no pollen grains in dust traps from the Caribbean (E. Blades, personal communication, 2007). Secondly, terrestrial biomarkers from the Cariaco Basin (Hughen et al., 2004a) have a signature different from modern samples of Saharan dust.

Therefore, we feel confident that within the time frame of our study, the potential sources of pollen are restricted to the catchment areas of local rivers, and thus pollen variations can be

interpreted as vegetation changes rather than changes in source areas.

Modern vegetation and pollen source areas

The coastal region of Venezuela adjacent to the Cariaco Basin is characterized by a narrow littoral strip covered by sandy beaches and steep rocky slopes (Fig. 1). The Coastal Cordillera, with a maximum height of 2765 m, extends parallel to the littoral, where the Unare depression (0–100 m) forms a natural separation between the Central and the Western sections of the Cordillera. The climate is strongly influenced by the north-eastern trade winds, which originate in a seasonal pattern of rainfall and annual average temperatures of 27°C. During severe dry seasons, local rivers dry out and hypersaline conditions develop in the coastal lagoons, even causing the formation of salt crusts over wide areas (Medina et al., 1989). The presence of mountains also determines an altitudinal gradient of temperatures and precipitation, the latter ranging from 600–1000 mm along the coast to 1500–2000 mm in the highlands.

A wide diversity of vegetation types coexists in the region, showing an altitudinal gradation from the coast to the inland that ranges from scrub vegetation in the coastal areas to very humid cloud forests in the upper mountains (Fig. 1).

Here we describe a typical zonal vegetation sequence in the Venezuelan Coastal Cordillera. General characterization and

distribution of the flora were based on previous works by Huber and Alarcón (1988) and Huber et al. (1998). Detailed information on specific biomes, individual taxa and local florules, were provided by Matteucci (1987), Medina et al. (1989), Conde and Alarcón (1993), Gentry (1993), Meier (1998), Marchant et al. (2002), Fajardo et al. (2005), Veneklaas et al. (2005), and Rull (2007). Local variations due to edaphic, climatic and topographic particular conditions are not considered. Emphasis is on taxa that are palynologically recognizable in the fossil record.

The littoral vegetation in the region is characterized by drought and salt-resistant herbaceous plants and scattered mangrove stands of *Rhizophora*, *Avicennia*, *Laguncularia*, and *Conocarpus* that mostly fringe coastal lagoons. Herbaceous halophytic vegetation (e.g., *Batis maritima*, *Sesuvium portulacastrum*, Chenopodiaceae, Amaranthaceae, Poaceae, and Cyperaceae) covers the understory of mangroves and the salt marshes that form during dry seasons.

Savannas and related herbaceous formations occur on lower slopes of the Cordillera, mainly toward the interior valleys and plains surrounding the base of the montane forests. Savannas with shrubs and trees are more common than grass savannas, where the herbaceous stratum is mainly dominated by Poaceae. Common tree and shrub species are *Curatella americana* (Dilleniaceae), *Byrsonima crassifolia* (Malpighiaceae), *Casearia sylvestris* (Flacourtiaceae), and *Bodwichia virgilioides* (Fabaceae).

Xerophytic thorn scrubs form dense stands covering the lowermost slopes (0–200 m) of the Coastal Cordillera that are mostly dominated by cacti (Cactaceae), spiny and sclerophyllous shrubs (e.g., Mimosaceae, Capparidaceae), and herbs belonging to Malvaceae, Euphorbiaceae, and Erythroxylaceae.

Semi-deciduous dry forests occupy the slopes between 300 and 600 m and are covered by trees such as *Anacardium excelsum* (Anacardiaceae), *Ceiba pentandra* (Bombacaceae), *Bourreria coumanensis* (Boraginaceae), and legumes. Lianas and dense understories are frequent.

Evergreen forests are dominated by Moraceae, Meliaceae, Burseraceae, Rutaceae, Flacourtiaceae (e.g., *Banara nitida*), and the endemic emergent *Gyranthera gigantea* (Bombacaceae). The understory is dominated by shrubs of the families Acanthaceae, Rubiaceae, Heliconiaceae, Araceae, and Marantaceae. Gallery forests develop in dense narrow strips along rivers and creeks, resembling floristically and physiologically the evergreen forests, although they are mostly inserted in large savanna areas. Species from the families Leguminosae (e.g., *Copaifera* sp., *Lonchocarpus* sp., *Machaerium* sp.), Anacardiaceae (*Tapirira* sp.), Myrtaceae, and Meliaceae (*Trichilia* sp., *Guarea* sp.) are common, whereas the palm *Mauritia flexuosa* dominates in more inundated sites.

Montane cloud forests occur in the 1000- to 2200-m belt and are characterized by orographic dense mists and low clouds. The plant communities are rich and complex with canopies characterized by large trees including *Sloanea* spp., *Neea* spp., *Eschweilera*, *Ocotea*, *Podocarpus*, *Juglans*, and *Myrsine*. A dense shrub understory is mainly composed by *Hedyosmum* and species of Rubiaceae and Araceae. Solitary

and clumped palms are very common, as well as epiphytes and tree ferns. The highest peaks of the mountains are covered by subparamo forests dominated by *Clusiaceae*, *Weinmannia* (Cunoniaceae), *Podocarpus* (Podocarpaceae), and several species of Asteraceae.

Materials and methods

Marine piston core MD03-2622 (10°42.69'N, 65°10.15'W; Fig. 1) was recovered during the P.I.C.A.S.S.O cruise in 2003 on board the R.V. Marion Dufresne from a water depth of 877 m (Cruise Report, 2003) and has remarkable well-preserved sediments and high sedimentation rates (ca. 40 cm/ka). Sediments of MIS 3 were sampled with a spacing of 15 cm (ca. 350 yr). Samples (3–4 cm³) were prepared for pollen analysis using standard laboratory methods, which include decalcification with HCl (~10%) and removal of silicates with HF (~40%). Two *Lycopodium* tablets were added during the decalcification process. After neutralization and washing, the samples were sieved with ultrasound over an 8- μ m mesh to remove particles <10 μ m. Permanent slides were mounted in a gelatin-glycerin medium for microscopic examination. In total, 74 samples were counted up to 300 palynomorphs (including herbs, spores, indeterminates, grains filled with pyrite and broken grains), other microfossils like algae and some fungal spores were also counted but not included in the sum. Most types were identified based on published morphological descriptions (Palacios Chávez et al., 1991; Roubik and Moreno, 1991; Herrera and Urrego, 1996; Colinvaux et al., 1999; Bush and Weng, 2007) and the pollen reference collection held at the Department of Palynology and Climate Dynamics (University of Göttingen). The chronology used was developed by tuning the reflectance curve of core MD03-2622 with the reflectance of the well-dated core ODP 1002D (Hughen et al., 2004b) (Fig. 2).

Tropical forests are generally represented in the pollen records by a large number of taxa, the majority represented by single grains. Hence, it is necessary to establish groups that aggregate pollen coming from one vegetation type. Grouping has to be done with care since many genera can be represented in several vegetation types and the species cannot always be distinguished by their pollen grains. Since the potential sources of pollen are restricted to the local catchments areas, we grouped our taxa according to their occurrence in the immediate catchments around the Cariaco Basin today. We defined seven pollen groups based on published studies, trying to be consistent with the present-day vegetation types: (1) littoral vegetation (including mangroves), (2) xerophytic scrub, (3) savanna, (4) semi-deciduous dry forest, (5) evergreen forest (including gallery forest), (6) montane cloud forest, and (7) salt marsh vegetation (see Supplementary data).

Correspondence analysis (CA) was carried out with MVSP v3.1 software (Kovach, 1998) for both species and groups. Input data for the CA were the cumulative pollen percentages of vegetation groups (7 variables \times 74 cases) and the percentages of the individual taxa >1% (112 variables \times 74 cases). Samples

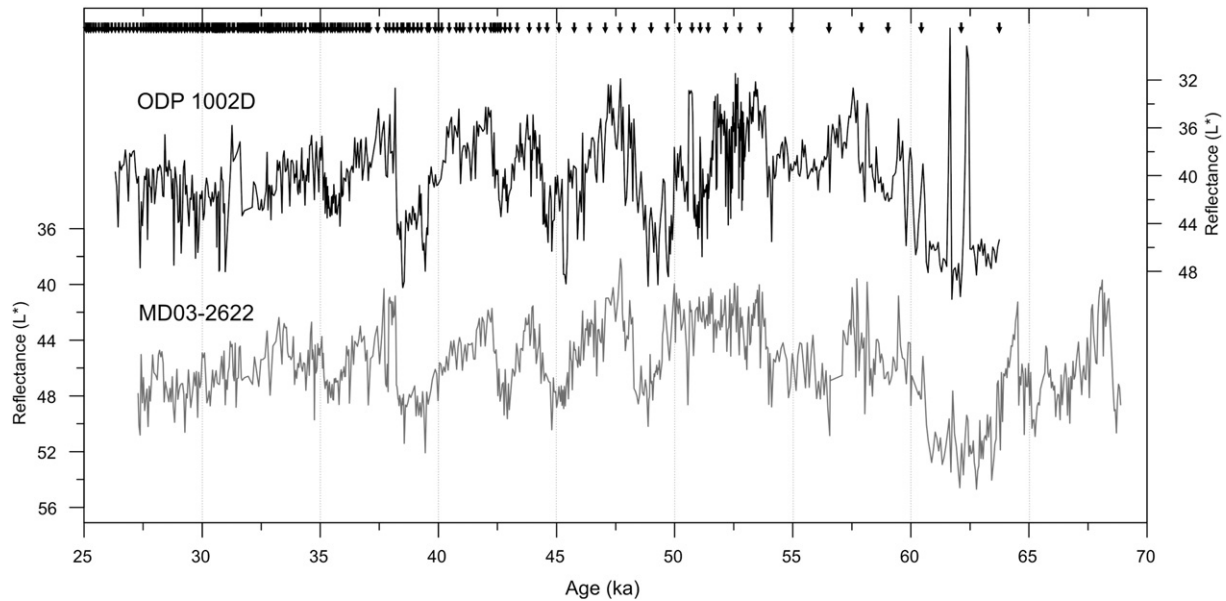


Figure 2. Age model for core MD03-2622 was constructed by tuning to the reflectance curve of core ODP 1002D. Age control of nearby core ODP 1002D is based on AMS ^{14}C dates (arrows) of the planktonic foraminifera *Globigerina bulloides* and *Globigerinoides ruber* (Hughen et al., 2004b).

and groups/taxa were scaled symmetrically using the Hill algorithm; rare species were downweighted.

Results and discussion

Pollen concentration fluctuates between 900 and 10,000 grains/ cm^3 and shows a good match with the color reflectance curve (Cruise Report, 2003). Higher pollen concentration is concurrent with darker clay-rich sediment (i.e., low reflectance) and lower concentration with lighter, organic-poor sediment, respectively (Fig. 3). One exception to this general pattern is the dark laminated interval corresponding to the youngest part of interstadial 8 (37–36 ka), which reveals low pollen concentration similar to those of lighter intervals. Although some degree of discrepancy is expected when comparing signals of different resolutions, these atypical values of interstadial 8 seem to be related to marine productivity changes, and ultimately to low-latitude insolation (González et al., in preparation). The color reflectance curve (L^*) of the Cariaco Basin sediments correlates with changes in Ti and Fe contents (Haug et al., 2001). Ti and Fe contents have been utilized as proxies for the total terrigenous fraction and therefore have been taken as indices of past regional hydrological change. Higher values, corresponding to darker sediments, are interpreted to reveal increased rainfall and river discharge (Haug et al., 2001). Furthermore, these shifts in the hydrologic cycle of the tropical Atlantic, as well as the organic matter content (Aycard, 2004), have been shown to closely mimic shifts between interstadial and stadial conditions in Greenland. Warm interstadials in the northern latitudes are in-phase with high rainfall, increased runoff, and high organic matter contents over northern South America, and conversely to cold stadial periods that coincide with reduced riverine discharge in the Cariaco region (Peterson et al., 2000a; Haug et al., 2001).

It is important to take into account that deposited organic matter, including palynomorphs, is susceptible of degradation under oxic conditions. The rapid and repeated shifts between oxic and anoxic conditions during MIS 3 in the Cariaco Basin could have caused differential oxidation of pollen grains, leading to an over-representation of resistant pollen taxa and a misleading picture of the paleovegetation. Periods of lower pollen concentration coincide with oxic periods (Fig. 3). Nevertheless, during these oxic phases, high percentages of fragile pollen such as Cyperaceae and *Typha* (Sangster and Dale, 1964) occur (see discussion below), suggesting that differential oxidation of organic matter was not the primary factor driving changes of the paleosignal.

Another process, which is governed by oxic-anoxic shifts and is linked to the preservation of organic matter in marine sediments, is pyrite formation. Pyrite, or iron sulfide (FeS_2), usually forms in iron-rich environments under reducing conditions, for example in marine sediments, in acid sulfate soils associated with mangroves, salt marshes, and coastal flats. Pyrite formation is also highly dependent on the availability of organic matter. In the pollen samples from the Cariaco Basin, grains filled with framboidal pyrite exclusively occur during stadial periods, which are characterized by oxic bottom and low organic content conditions. Two processes could explain this apparently contradictory pyrite pattern: first, the occurrence of a downward sulphidisation front and consequent diagenetic pyrite formation below organic-rich sediments, analogous to what was previously described for oxic-anoxic transition around 14.5 ka in the adjacent ODP 1002 core (Lyons et al., 2003) and similar to what was found in sapropels of the Mediterranean Sea (Passier et al., 1996). A second possibility could be the formation of pyrite on a dried-out continental shelf covered by marshes, rather than in a marine basin, and its posterior transport to the deep sea. In the latter case, pyrite could be considered as a good indicator of anoxic terrestrial environments. Nevertheless, due to the

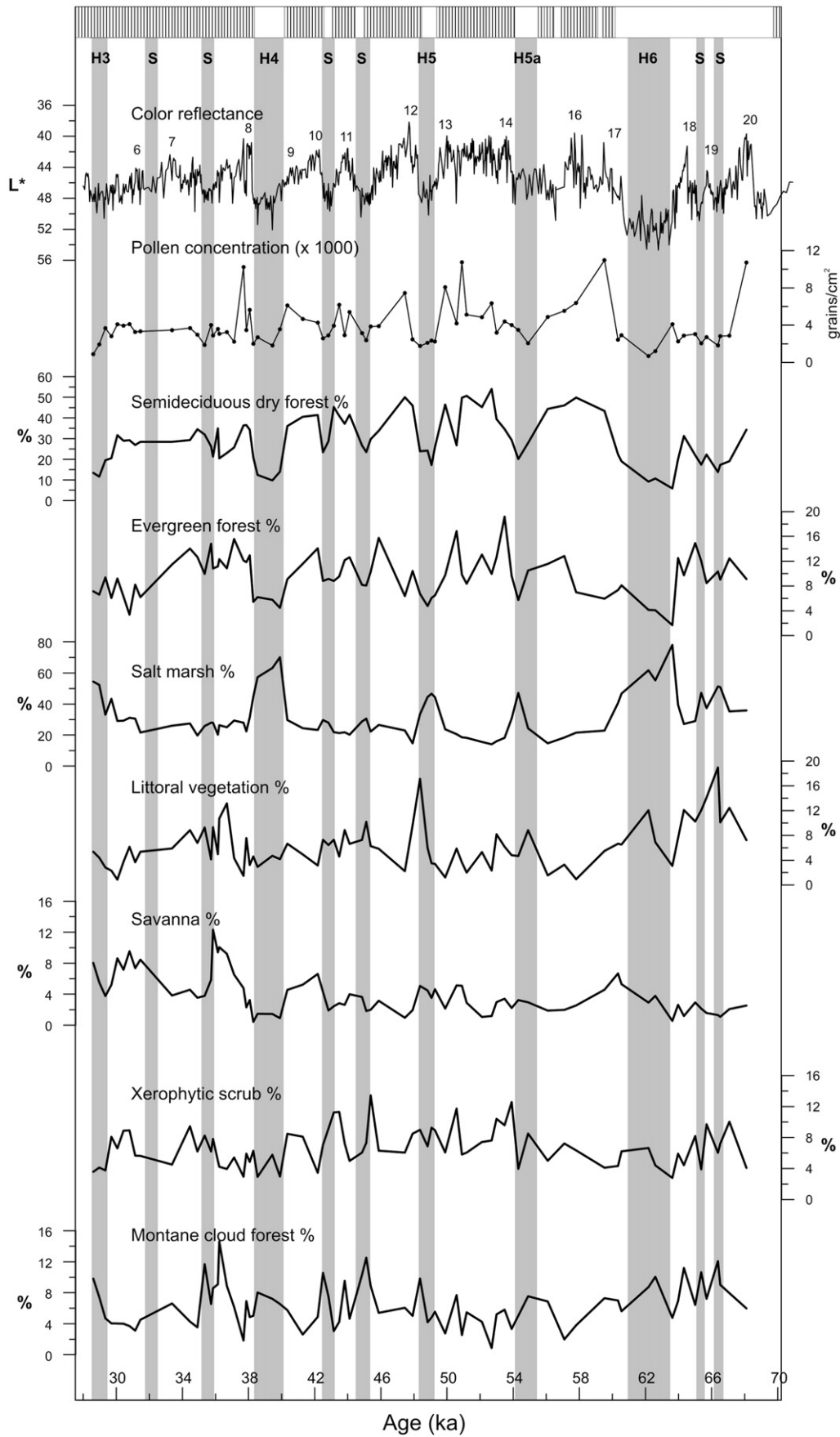


Table 1
Summary of the three vegetation modes described in the text

	Interstadial mode	Stadial mode	Heinrich event mode
Pollen concentration	++	–	–
Semi-deciduous and Evergreen forest	++	–	–
Savanna and Xerophytic scrub	– (+)	+ (–)	+ (–)
Montane forest	–	+	+
Salt marsh	–	+	++
Paleoecological interpretation	Expansion of forests; humid climate, enhanced fluvial input; northern position of the ITCZ	Dryer conditions; colder at higher altitudes; ITCZ displaced to the south; recurrent vegetation response	Combined effect of sea-level rise and dry atmospheric conditions; development of hypersaline environments; southernmost position of ITCZ

++: high increase; +: increase; +(-): mostly increase; -(+): mostly decrease; -: decrease.

presence of marine dinoflagellates filled with pyrite (González et al., in preparation), and to the fact that the pyrite signal closely follows the pattern of laminations rather than salt marsh patterns during MIS 4, we lean towards the first proposed mechanism or a combination of the two.

Vegetation modes

The composition of the pollen assemblage is also consistent with rapid humid/dry (stadials/interstadials) shifts, which characterize MIS 3. Three contrasting vegetation modes were distinguished in pollen from the Cariaco Basin: a stadial mode, an interstadial mode, and a Heinrich event mode (Fig. 3, Table 1).

Stadial mode

In the Cariaco Basin pollen record, a typical stadial mode is represented between interstadials 7–8, 10–11, 11–12, and 18–19 (S-shadings in Figure 3). Regular and nearly simultaneous increases occurred in the percentages of montane cloud forests pollen (10–13%), xerophytic scrub pollen (6–14%), and salt marsh pollen (30–45%). Simultaneously, semi-deciduous and evergreen forests pollen abundance declined. It is noteworthy that not only the timing of the changes, but also their magnitudes, were recurrent, showing the cyclical character of the plant community response.

Nearly all the individual taxa that are positively related to this mode are characteristic of open and dry areas, such as Cyperaceae, *Ambrosia*, Poaceae (>50 µm), and montane cloud forest-like *Podocarpus*, *Juglans*, *Ilex*, and fern spores (e.g., Cyatheaceae, Monolete spores) (Fig. 4). Montane cloud forests and dry forest elements have contrasting hydrological preferences. On one side, tropical montane cloud forests occur where mountains are immersed in tradewind-derived orographic clouds and mist and thus are favored by humid conditions. In contrast, tropical dry forests tolerate long dry seasons and therefore are favored under drier conditions. Intuitively one should expect opposite trends in the paleorecord of these two groups under the same hydrological regime. However, contrary

to the expected pattern, these groups show similar behavior, simultaneously expanding during most stadials and indicating a divergence between lowland and highland hydrological regimes.

In general, our pollen data support the view of drier climates during stadials, which favored the increase of open vegetation and the structural change of forested areas in the lowlands. The synchronous expansions of the saprophytic fungus *Tetraploa aristata*, usually indicative of decomposition of senescent grasses and sedges (Fig. 5), are in agreement with expanded herbaceous coverages. This predominance of drier conditions over the region has already been proposed by the hypothesis of a southward displacement of the mean latitudinal position of the ITCZ during cooler stadials (Peterson and Haug, 2006). Under this perspective, the expansion of montane cloud forest during stadials is not completely contradictory since the humid character of these forests is strongly dependent on orographic rainfall more than on ITCZ shifts. Moreover, the strengthening of the northeast trade winds during stadials implies an enhanced transport of moisture from the Atlantic Ocean into the continent, promoting heavier orographic rain over the high mountains of the Coastal Cordillera. Additionally, the prevalence of colder and drier conditions would have resulted in the formation of more abundant radiative fog and the lowering of the cloud base in the highlands. Consequently, more clouds would have been formed and the cloud forest would have expanded. Indeed, the pollen record is consistent with the above model. An analogous antiphasing of precipitation between coastal Venezuela and the Venezuelan Andes has been documented for the Little Ice Age (Polissar et al., 2006). Similarly, our findings suggest that two contrasting hydrological regimes coexisted during stadials, when colder and possibly more humid conditions dominated in the mountains whereas drier conditions dominated in the lowlands and coastal drainages.

The coincidence between pyrite occurrence and Cyperaceae, Chenopodiaceae–Amaranthaceae (Cheno–Ams; Fig. 5) pollen increments during stadials suggests that in this case pyrite is indeed a good indicator of anoxic terrestrial environments. In this way, our data confirm the development of coastal marshes and swamps during stadials as a result of partial desiccation of

Figure 3. Relative abundance of vegetation groups from core MD03-2622, Cariaco Basin. Gray bars denote stadials (S) and Heinrich events (H). Heinrich events (H3–H6) are denoted according to cited ages (Rashid et al., 2003; Hemming, 2004), and interstadials are numbered as in ice core GISP 2. Note the different vertical scales for different vegetation groups. Distribution of laminated sediments is indicated in the bar at the top. Sediments were not recovered for the interval 53.34–55.08 ka.

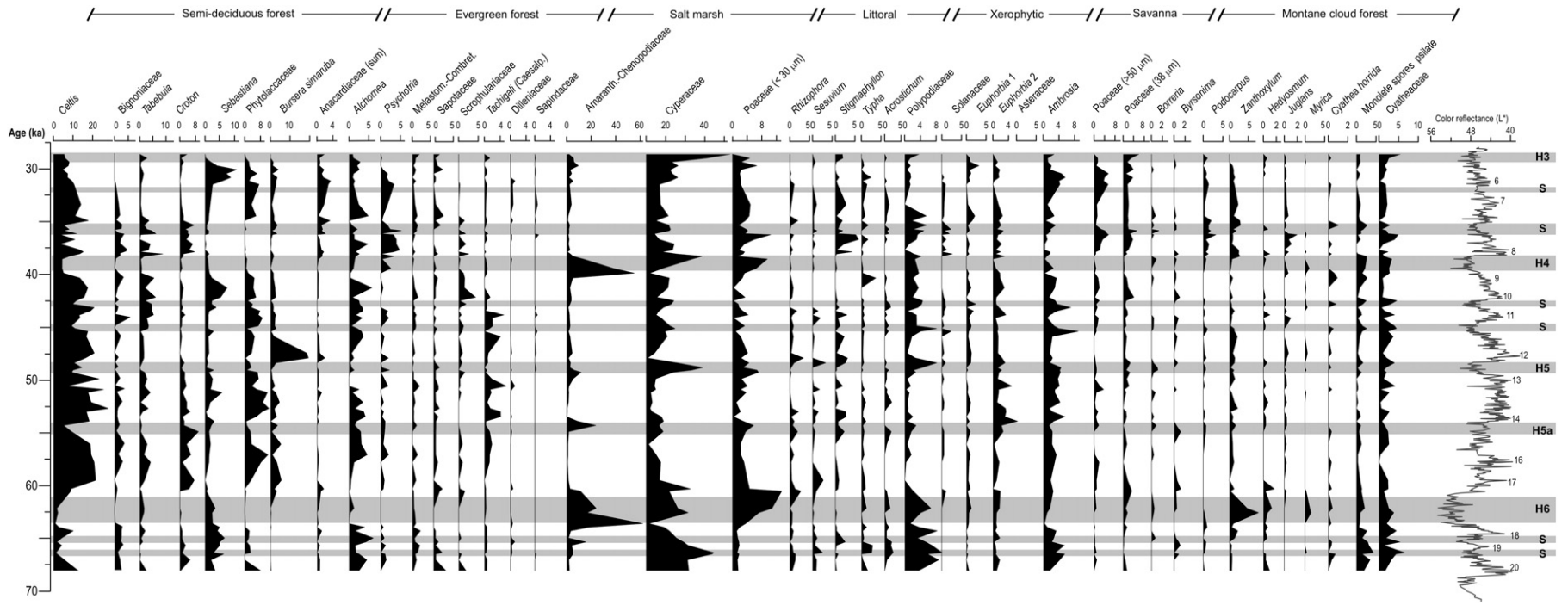


Figure 4. Percentage pollen diagram of selected taxa from core MD03-2622, Cariaco Basin. Note scale changes on x-axis.

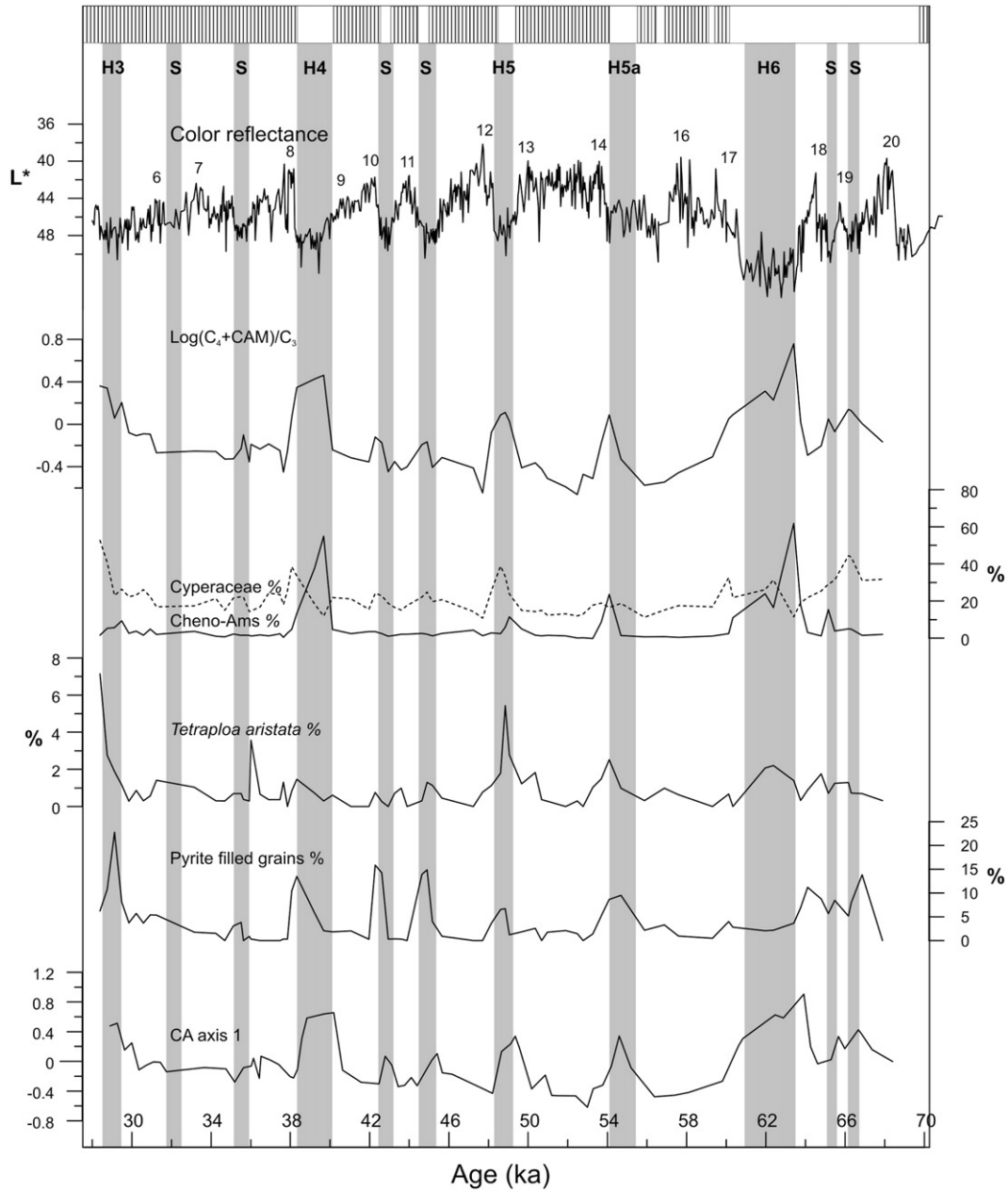


Figure 5. Downcore trends of vegetation change in the Cariaco Basin, comparing the color reflectance curve with the variations of C₄/C₃ ratios (log scaled), the relative abundance of the fungus *Tetraploa aristata*, the percentages of grains filled with pyrite, and the scores of the first CA ordination axis performed with the vegetation groups.

freshwater streams and the expansion of the exposed Unare Platform due to glacially lowered sea level.

Interstadial mode

In the pollen record from core MD03-2622, interstadials are characterized by the highest pollen concentrations and the highest abundance of semi-deciduous pollen (30–55%) and evergreen forest pollen (7–20%) (areas without shadings in Figure 3). Concurrently, these periods are characterized by minimum percentages of pollen derived from salt marshes (15–22%). A wider variety in pollen types of trees such as *Celtis*, *Alchornea*, *Bursera simaruba*, *Tabebuia*, Bignoniaceae, *Croton*, *Sapium*,

and *Sebastiania* are common during interstadials, suggesting the development of structurally more diverse and complex forests (Fig. 4). The high percentages of semi-deciduous and evergreen forests and the high pollen concentrations during the “warm” North Atlantic interstadials are in agreement with depleted plant waxes $\delta^{13}\text{C}$ values from core PL07-58PC (Cariaco Basin) that reflected extended C₃ forest vegetation (Hughen et al., 2004a). Wetter conditions during interstadials can thus be inferred from enhanced fluvial inputs, reflected by high pollen concentration and high Ti and Fe concentrations (Haug et al., 2001), and by the dominance of tree species in the pollen record that suggest an expansion of tropical forests during these periods. A northward shift of the ITCZ has been proposed as the main mechanism to

promote wetter conditions over northern South America during these periods (Peterson et al., 2000a; Haug et al., 2001).

Heinrich event mode

During HEs 3 through 6, pollen of salt marsh vegetation, especially Chenopodiaceae, increased abruptly reaching values up to 40–70% with maximum amplitudes of change during H4 and H6 (Figs. 3 and 4). Pollen percentages of montane cloud forest, some herbaceous taxa, and the relative abundance of grains filled with pyrite showed increments, but changes were not larger than those during the stadial mode. Except for the abrupt increments of Chenopodiaceae pollen percentages, the HE mode resembles closely the stadial mode, suggesting that HEs are expressed as extreme cases of “normal” stadial conditions.

The processes that drive the shift from one state to the other are yet to be understood. Main climatic differences between normal stadial conditions and HEs reside in the latter showing more intense cooling in the northern Atlantic, a complete shutdown of North Atlantic Deep Water formation, and higher sea levels (10 to 35 m) (Chappell, 2002; Siddall et al., 2003). We interpret the marsh expansions during Heinrich events as the combined effect of rapid sea-level rise and extreme dry atmospheric conditions. Both these environmental factors favored the development of hypersaline environments over today’s submerged Unare Platform (Fig. 1), which at the time was only suitable for salt-tolerant species. In this case, the plant communities closer to river mouths (more local) comprise the difference between the stadial and Heinrich event modes, and the surrounding regional vegetation provides the common background pollen rain for all stadials. It is not surprising that the signal of local vegetation is intensified during HEs and stadials because during relative low sea-level phases, river mouths shifted closer to the edge of the basin, amplifying its sensibility to river discharge fluctuations. Additionally, dry conditions over the continent led to a weakened riverine transport, consequently favoring the transport from closer pollen sources (i.e., local vegetation).

Savanna or salt marshes: the C4/C3 dilemma

During photosynthesis, plants use two main pathways for carbon fixation, the C3 and the C4 cycles. The C3 pathway is used by most trees, shrubs, and herbs. The C4 pathway is particularly common among tropical grass species and plants in warm and arid environments due to its greater efficiency in water use and its high energetic requirements. Expansion of C4 plants in the past has been attributed to the decrease in atmospheric $p\text{CO}_2$; however, there is evidence that other environmental factors such as precipitation, seasonality, and temperature also influence the relative abundance of C4 versus C3 plants (Huang et al., 2001).

The specific isotopic signature of stable carbon in C3 and C4 plants has been utilized in the neotropics to track past expansion of high altitude grasslands and savannas (e.g., Boom et al., 2002; De Freitas et al., 2001; Kastner and Goñi, 2003). In the Cariaco Basin region, isotopic shifts in fatty acids of leaf waxes were

interpreted as rapid changes from wet forest to arid grasslands during the onset of the Younger Dryas (Hughen et al., 2004a). Our pollen data also support the repeated expansions of C4 plants during cold stadials and HEs (Figs. 4 and 5). However, based on the identification of individual pollen taxa, we alternatively propose that proliferation of salt marsh communities during these periods, and not a broad expansion of arid grasslands, was responsible for this trend. Representatives of the Chenopodiaceae and Amaranthaceae families prefer habitats in which C4 plants are favored and often dominant, namely, sand dunes, salt marshes, saline grasslands, semi-deserts, and deserts. Chenopodiaceae typically account for >60% of the pollen sum on desiccated lake muds in shorelines and salt marshes. In the Cariaco Basin pollen record, Chenopodiaceae pollen percentages rapidly increase from 0 to >50% at the onset of HEs 4 and 6, and exceed 10% during HEs 3, 5 and 5a, whereas savanna elements, mainly grasses, only represent 4–7% of the pollen sum. If we translate this into a C4/C3 ratio, C4 plants indeed predominate, without the necessity of a grassland expansion. We believe that the expansion of C4 plants was caused by the development of coastal marshes along the exposed Unare platform as the successional response to sea-level changes under drier and lower atmospheric $p\text{CO}_2$ conditions.

This alternative interpretation gives new insight to understanding tropical paleoenvironments of northern South America. First, in coastal areas the straightforward inference of tropical aridity reflected by C4 expansions during stadials and HEs must be handled with care. Mechanisms other than meridional displacement of the ITCZ, such as sea-level rise, can have a direct superimposed effect on the vegetation response to high-latitude climate changes. Secondly, our evidence shows that even in vulnerable water-stressed environments, such as the seasonal dry forest of northern Venezuela, savanna did not replace the forest in the region, confirming the high resilience of these ecosystems. Understanding what may have caused the weakening of the forest signal in the Cariaco Basin pollen record during cold stadials is a key aspect. Increments in the amount of herbs (e.g., Solanaceae, *Euphorbia*, *Ambrosia*), lianas (e.g., *Stigmaphyllon*), and vines (e.g., Dilleniaceae) imply less dense and structurally less complex forests, instead of a complete replacement of forest by grasslands. These structural changes might also be accompanied by slight increments in the C4/C3 ratio and weakening of the levels of specialization and diversity (Fig. 5).

Correspondence analysis

Correspondence analysis (CA) of the 74 pollen samples was performed to explore the consistency of the three proposed vegetation modes along MIS 3. The configuration of samples in the ordination space using individual taxa and group percentages resulted in a similar pattern (Fig. 6). In both cases, a relative environmental gradient could be assigned and distinct groups emerged.

Ordination by groups showed a stronger correlation between variables scores and cases scores (60.08% and 17.12% for axes 1 and 2, respectively) compared to the ordination by individual

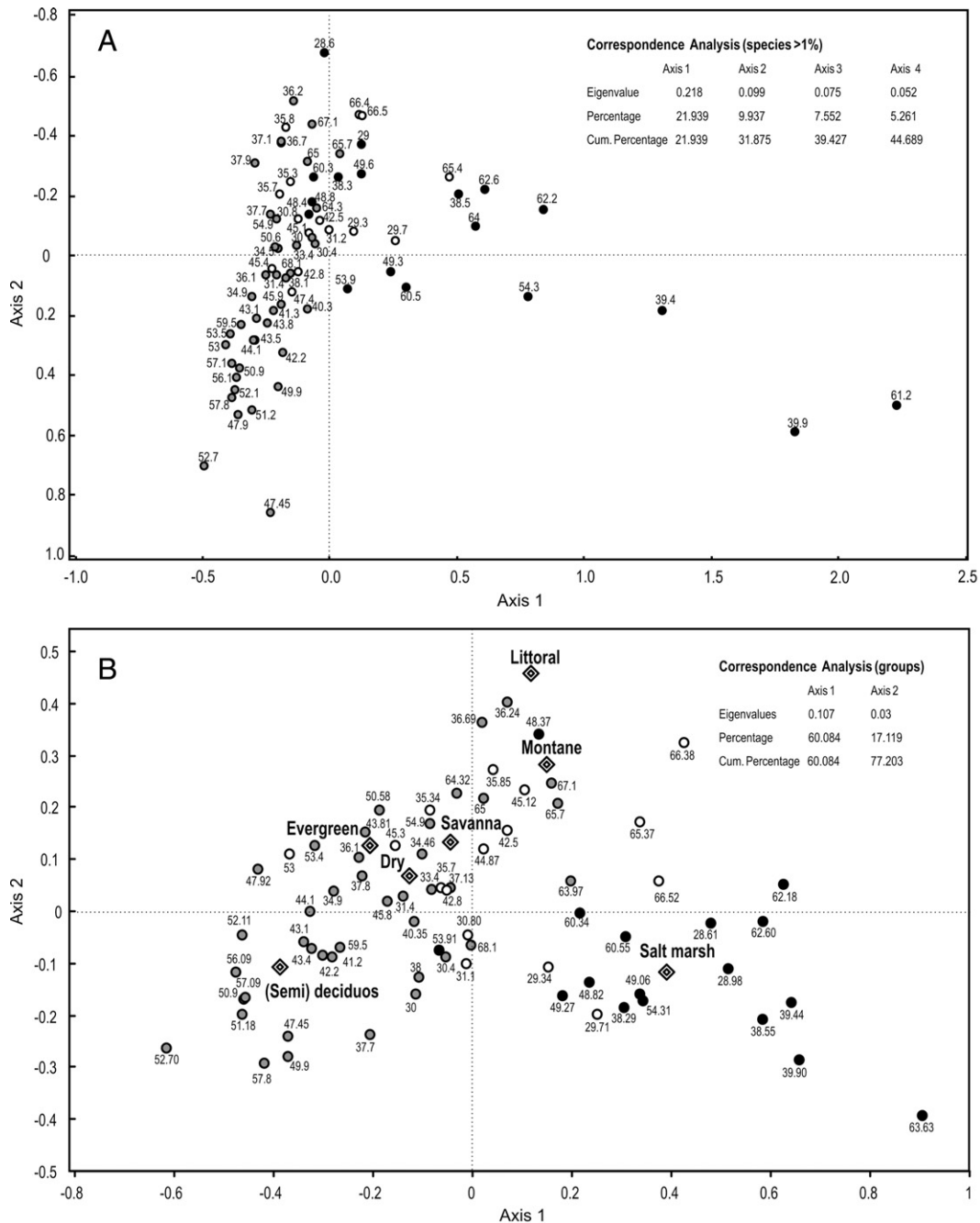


Figure 6. (A) CA ordination plot of individual species (>1%) and samples (ages in ka). (B) CA joint plot of vegetation groups and samples (ages in ka). Gray circles stand for interstadial mode samples; open circles for stadial samples, and black circles for Heinrich event samples.

species (21.9% and 9.93% for axes 1 and 2, respectively). This stronger correlation results from the reduction on the number of variables and the consequent heterogeneity reduction of the data throughout the grouping process. However, the distribution of the scores in the low-dimensional space defined by axes 1 and 2 confirmed that a clear and similar structure was preserved by both the pollen groups and the pollen species, revealing a regional–local gradient towards the more positive values of the first axis. We therefore have confidence in the ability of the groups to synthesize and reproduce the pattern showed by individual species.

The HE mode and the interstadial mode set the two opposite extremes among the ecological response gradient. The stadial mode, which is not as clearly defined as the other two, appears to be the intermediate stage giving way to two possible modes. This regional–local gradient is confirmed by the ordination of vegetation groups in the CA joint plot (Fig. 6b) The semi-deciduous forest scores on the left (mainly represented by *Celtis*, *Bursera*, and *Phytolaccaceae*), as the most regional vegetation type, go with enhanced precipitation and river transport. Evergreen forest scores, just right of the semi-deciduous forest,

corroborate the similar behavior of the two groups, their floristic affinity, and the difficulty to distinguish them based on pollen types. During the determination of ecological groups, we included gallery forest elements within the evergreen forest group due to their floristic and structural similarities. These similarities are conferred by constant water availability, although gallery forests are mostly surrounded by savannas. This overlapping among groups is reflected by the intermediate position of the evergreen forest scores between the semi-deciduous forests and the savanna scores. Moreover, both evergreen forests and savannas are less common vegetation types in the region (Huber and Alarcón, 1988) compared with semi-deciduous forests, which augments the relative importance of the latter in terms of pollen percentages and the CA ordination. On the most positive extreme of axis 1, salt marshes (Cheno–Ams, Cyperaceae, *Gomphrena*, *Polygonum*) characterize local plant communities that are associated with hypersaline conditions.

Axis 2 is more difficult to interpret, though it seems to reflect the sensitivity of biomes to local hydrological changes during colder periods. More positive values on the second CA axis characterize vegetation types that react positively to changes in local hydrographic conditions during stadials, as is the case for mangroves, xerophytic scrubs, and montane cloud forest.

Conclusions

Palynological analysis from marine core MD03-2622 drilled into the Cariaco Basin provides insight into how terrestrial ecosystems of northern South America responded to abrupt climate changes during MIS 3. Our pollen record shows that vegetation is sensitive to rapid climate changes associated with both the northern Atlantic D/O cycles and the HEs. Pronounced changes in the extension and composition of plant assemblages are thought to primarily reflect north-south displacements of the ITCZ, causing humid/dry conditions over the continent that are locally amplified by the sensitivity of the local river discharge. Additionally, sea-level changes during HEs have played an important role in modulating the local plant responses in coastal areas of northern South America by favoring the expansion or reduction of suitable areas for local colonization of salt marshes. The specific vegetation response to climate shifts in the Cariaco Basin on millennial time scales can be classified into three different modes: (1) an interstadial mode characterized by maximum extension of evergreen and semi-deciduous forests, and by high pollen concentrations that reflect more humid conditions and enhanced riverine transport; (2) a stadial mode characterized by lower pollen concentrations and increase of marshes, herbs, ferns, and montane forests; and (3) a Heinrich event mode characterized by the lowest pollen concentrations and abrupt increases of salt marshes.

In spite of the local character of vegetation's response during HEs, our pollen results are significant because HEs had not been previously identified as clear extremes in the Cariaco Basin (Hemming, 2004). Our data show the importance of local vegetation as an additional source of paleoclimatic information. This signal seems to be more sensitive to rapid climate changes than other proxies (e.g., color reflectance, $\delta^{18}\text{O}$, Fe, Ti, and Ca

contents) (see Herbert and Schuffert, 2000; Peterson et al., 2000a). This new evidence strengthens the idea of a tightly coupled tropical/high-latitude climate system during the last glacial period, but higher resolution studies will be necessary to address more specific processes.

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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.yqres.2007.12.001](https://doi.org/10.1016/j.yqres.2007.12.001).

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