Earth and Planetary Science Letters 479 (2017) 50–59

Contents lists available at ScienceDirect

Earth and Planetary Science Letters

www.elsevier.com/locate/epsl

Response of the Amazon rainforest to late Pleistocene climate variability

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ARTICLE INFO

Article history:
Received 28 April 2017
Received in revised form 29 July 2017
Accepted 2 September 2017
Available online xxxx
Editor: H. Stoll

Keywords:
Amazon
rainforest
paleoclimate
late Pleistocene
biodiversity
long-chain *n*-alkanes

ABSTRACT

Variations in Amazonian hydrology and forest cover have major consequences for the global carbon and hydrological cycles as well as for biodiversity. Yet, the climate and vegetation history of the lowland Amazon basin and its effect on biogeography remain debated due to the scarcity of suitable high-resolution paleoclimate records. Here, we use the isotopic composition (δD and δ^{13}C) of plant-waxes from a high-resolution marine sediment core collected offshore the Amazon River to reconstruct the climate and vegetation history of the integrated lowland Amazon basin for the period from 50,000 to 12,800 yr before present. Our results show that δD values from the Last Glacial Maximum were more enriched than those from Marine Isotope Stage (MIS) 3 and the present-day. We interpret this trend to reflect long-term changes in precipitation and atmospheric circulation, with overall drier conditions during the Last Glacial Maximum. Our results thus suggest a dominant glacial forcing of the climate in lowland Amazonia. In addition to previously suggested thermodynamic mechanisms of precipitation change, which are directly related to temperature, we conclude that changes in atmospheric circulation are crucial to explain the temporal evolution of Amazonian rainfall variations, as demonstrated in climate model experiments. Our vegetation reconstruction based on δ^{13}C values shows that the Amazon rainforest was affected by intrusions of savannah or more open vegetation types in its northern sector during Heinrich Stadials, while it was resilient to glacial drying. This suggests that biogeographic patterns in tropical South America were affected by Heinrich Stadials in addition to glacial–interglacial climate variability.

1. Introduction

Lowland Amazonia is covered by the largest and most biodiverse rainforest on Earth and is one of the major centers of tropical deep convection (Fig. 1) (Olson et al., 2001; Werth and Avissar, 2002). Hence, environmental changes in lowland Amazonia have major implications for the global carbon and hydrologic cycles (Brienen et al., 2015; Werth and Avissar, 2002). To predict the potential response of Amazonian vegetation and precipitation to future global climate shifts, a firm comprehension of past variability is critical. Especially the responses of Amazonian environmental conditions to Pleistocene glaciations, characterized by large changes in atmospheric greenhouse gas concentrations, and to abrupt shifts in the North Atlantic and global climate, are of great interest (Cheng et al., 2013; Kanner et al., 2012; Wang et al., 2017). While glacial–interglacial variability can be used to study the impact of large global temperature and sea level variations, millennial-scale variability such as Heinrich Stadials (HS) can be used to determine the impacts of variations in ocean circulation and shifts in the meridional position of the tropical rain belt.

Due to the scarcity of high-resolution climate records, there are conflicting scenarios regarding the late Pleistocene vegetation and climate history of lowland Amazonia (Cheng et al., 2013; Colinvaux et al., 1996; D'Apolito et al., 2013; Haffer, 1969; Kanner et al., 2012; Mosblech et al., 2012; Wang et al., 2017). Early studies based on biogeographic observations proposed that savannah expansion during glacial periods led to the formation of isolated forest refugia, where speciation took place ("refugia hypothesis") (Haffer, 1969). This scenario was initially supported by lacustrine pollen records from the fringes of the Amazon basin (Absy, 1991). However, first records from the interior of the Amazon basin (Hill of Six Lakes, Fig. 1) and marine sediment cores from the Amazon fan indicated that the Amazon rainforest persisted through colder and potentially drier conditions during

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http://dx.doi.org/10.1016/j.epsl.2017.09.013
0012-821X/

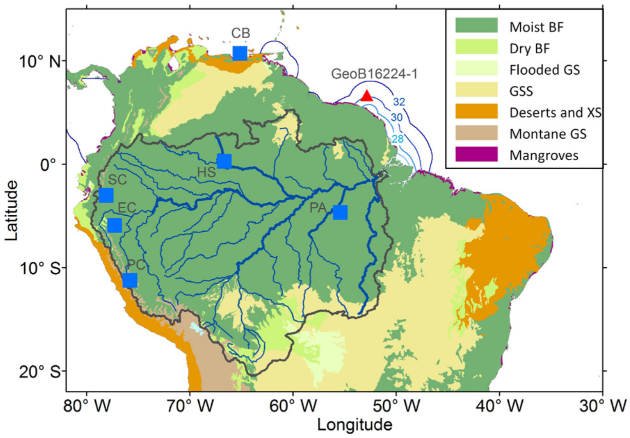

Fig. 1. Map of the Amazon basin and the adjacent Atlantic Ocean. Color shading represents the major modern-day biomes in tropical South America (Olson et al., 2001) (BF: Broad leaf forest; GS: Grassland and savannah; GSS: Grassland savannah and shrub land; XS: Xeric shrub land). The Amazon basin is outlined by a black line. Blue contour lines in the Atlantic Ocean represent sea surface salinity indicating the northward flow of Amazonian freshwater (Sbrocco and Barber, 2013). The location of core GeoB16224-1 is marked with a red triangle. The location of the other paleoclimate records from the Cariaco basin (CB) (Deplazes et al., 2013), the Santiago (SC) (Mosblech et al., 2012), El Condor (EC) (Cheng et al., 2013), Pacupahuain (PC) (Kanner et al., 2012) and Paraíso (PA) (Wang et al., 2017) caves, and the Hill of Six Lakes (HS) (Colinvaux et al., 1996) discussed in this study are marked with blue squares. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the late Pleistocene (Boot et al., 2006; Colinvaux et al., 1996; Haberle and Maslin, 1999). These records are, however, controversial due to their low temporal resolution, the presence of hiatuses and the potential overprint by gallery forests (Behling et al., 2009; D'Apolito et al., 2013). Meanwhile, phylogenetic studies have found no evidence for increased speciation during the Pleistocene that would have supported the refugia hypothesis (Hoorn et al., 2010; Smith et al., 2014). In western Amazonia, where biodiversity is highest, various climate records showed humid conditions through Pleistocene glaciations, indicating that species richness was rather the consequence of long-term stability than of repeated vegetation shifts (Baker and Fritz, 2015; Cheng et al., 2013; Mosblech et al., 2012; Smith et al., 2014). Nevertheless, the close relation of species inhabiting savannah regions to the north and south of the lowland basin suggests the presence of temporary dry corridors through lowland Amazonia (Behling et al., 2009; Quijada-Mascareñas et al., 2007). Recently, a speleothem record from Paraíso Cave in the eastern part of the lowland basin again indicated drier glacial conditions leading to the conclusion that changes in temperature, associated with variations in atmospheric CO_2 were the dominant forcing mechanism controlling lowland Amazonian hydrology (Wang et al., 2017). The millennial-scale hydrologic variability in this record has also led to speculation on the potential impact of abrupt climate shifts on the former connection of biomes north and south of the basin (Bush, 2017). However, high-resolution vegetation records to confirm this link are lacking. Moreover, it is unclear what forcing mechanisms are dominant on a lowland basin-wide scale. This highlights the need for proxy records reflecting the integrated lowland Amazonian vegetation and climate evolution.

Here we provide high-resolution plant-wax isotope records from a marine sediment core collected offshore the Amazon River (Fig. 1) to reconstruct the catchment-integrated vegetation and climate conditions in the lowland Amazon basin for the late Pleistocene (50,000–12,800 yr before present). Plant-wax biomarkers in the Amazon River predominantly originate from the lowland basin and broadly reflect catchment-integrated signals (Häggi et al., 2016; Ponton et al., 2014). The stable hydrogen isotope composition of plant-waxes has been employed to reconstruct the isotopic composition of precipitation and thereby past precipitation amounts in tropical areas (e.g. Schefuß et al., 2005; Tierney and deMenocal, 2013; Tierney et al., 2008). The stable carbon isotope composition of plant-waxes allows to differentiate between biomes with dominant C3 or C4 vegetation and thus to study potential savannah expansions in the past (Castañeda and Schouten, 2011). Therefore, the isotopic plant-wax based approach allows us to perform climate and vegetation reconstructions that integrate changes from spatially extensive areas in the lowland basin and circumvents the spatial limitations of previous records. Moreover, our approach allows to independently assess changes in vegetation and precipitation on the same compounds. Finally, we compare our paleoclimate reconstructions to results from a fully coupled general circulation model, which provide insight into processes controlling regional hydroclimatic changes.

2. Materials and methods

2.1. Present-day climate conditions in the Amazon basin

In the lowland Amazon basin, mean annual precipitation varies between 1500 and 3000 mm/yr and mean annual temperatures reach values between 24 and 28 °C, while drier and cooler conditions are found in the Andean sector of the basin (Hijmans et al., 2005). With exception of some north-western parts of the Amazon basin, which experience year-round precipitation, most of the Amazon basin is subject to substantial seasonal precipitation variations. The highest precipitation amounts in the southern and central Amazon basin are registered during the maximum of the South American Monsoon, which peaks during austral summer in January and leads to humid conditions over most of the basin (Garreaud et al., 2009). During peak monsoonal conditions, large amounts of humid air are transported by the South American Low-Level Jet along the eastern slopes of the Andes to the south (Marengo et al., 2004). Convection over the Amazon basin also connects to the South Atlantic Convergence Zone over south-eastern Brazil, leading to intense local precipitation (Carvalho et al., 2004). During boreal spring, convection moves northwards following the seasonal insolation maximum until it reaches its northernmost position during boreal summer. In July, precipitation takes mostly place in the northern sector of the basin, where it is aligned with the position of the Intertropical Convection Zone. During October, convection again shifts southward and precipitation over the central Amazon basin and in the South Atlantic Convergence Zone re-intensifies (Garreaud et al., 2009).

2.2. Study area and sample material

Paleoenvironmental reconstructions for the Amazon basin presented in this study are based on sediment core GeoB16224-1 (6°39.38′N, 52°04.99′W; 760 cm core length; 2510 m water depth) retrieved from the continental margin off French Guiana during *RV MS Merian* cruise MSM20/3 in February 2012 (Mulitza et al., 2013). While in the present-day sedimentological setting most of the Amazonian freshwater and sediment is transported along the continental shelf (Geyer et al., 1996), sedimentation during glacial sea-level low stands took place on the continental margin (Damuth and Flood, 1983). During glacial times, well-stratified sediment deposits formed on the continental margin off French Guyana and represent high-resolution archives for paleoclimate reconstructions (Loncke et al., 2009; Mulitza et al., 2013). A previous study on GeoB16224-1 showed that the core site received continuous fine-grained sedimentary input from the Amazon Plume from 50 kiloyears (ka) before present (BP) until the end of the Bølling–Allerød (12.8 ka BP) when rising sea levels shifted the main depositional