Pleistocene–Holocene environmental change in the Canary Archipelago as inferred from the stable isotope composition of land snail shells

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A B S T R A C T

The isotopic composition of land snail shells was analyzed to investigate environmental changes in the eastern Canary Islands (28°–29°N) over the last ~50 ka. Shell δ13C values range from −8.9‰ to 3.8‰. At various times during the glacial interval (~15 to ~50 ka), moving average shell δ13C values were 3% higher than today, suggesting a larger proportion of C4 plants at those periods. Shell δ18O values range from −1.9‰ to 4.5‰, with moving average δ18O values exhibiting a noisy but long-term increase from 0.1‰ at ~50 ka to 1.6–1.8‰ during the LGM (~15–22 ka). Subsequently, the moving average δ18O values range from 0.0‰ at ~12 ka to 0.9‰ at present. Calculations using a published snail flux balance model for δ18O, constrained by regional temperatures and ocean δ18O values, suggest that relative humidity at the times of snail activity fluctuated but exhibited a long-term decline over the last ~50 ka, eventually resulting in the current semiarid conditions of the eastern Canary Islands (consistent with the aridification process in the nearby Sahara). Thus, low-latitude oceanic island land snail shells may be isotopic archives of glacial to interglacial and tropical/subtropical environmental change.

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Introduction

The Canary Archipelago (27°–29°N), ~100 km off the Moroccan Coast, is an excellent area to study subtropical climatic variations since it is affected by recurrent interactions between atmospheric (i.e., trade winds, Saharan winds, etc.) and oceanic (i.e., Canarian cool current, seasonal coastal upwelling, etc.) circulation systems, which are in turn, linked to the seasonal migration of the intertropical convergence zone (ITCZ) and monsoon wind shifts in West Africa (e.g., Moreno et al., 2001). The eastern Canary Islands contain eolian deposits with alternating sequences of dunes and paleosols (e.g., Petit-Maire et al., 1986; Rognon and Coudé-Gaussen, 1988, 1990a,b; Dammati et al., 1996; Ortiz et al., 2006), which contain abundant late Quaternary land snail shells (Yanes et al., 2007, 2008a; Huntley et al., 2008) that represent a rare, relatively continuous, terrestrial fossil record in the islands.

Land snails offer the prospect of a carbon and oxygen isotope record of environmental changes. Shell δ13C values are commonly used to document variations in the proportions of C3/C4 plants in paleovegetation (e.g., Goodfriend and Ellis, 2000, 2002; Stott, 2002; Metref et al., 2003; Balakrishnan et al., 2005a,b; Baldini et al., 2007; Colonese et al., 2007, 2010; ZongXiu et al., 2007; Yanes et al., 2008b, 2009). Shell δ18O is often empirically related to the local rainwater δ18O values (e.g., Lécolle, 1985; Goodfriend, 1991; Zanchetta et al., 2005), but snail body fluid (and corresponding shell) is enriched in 18O with respect to unmodified rainwater (Yapp, 1979). According to Balakrishnan and Yapp (2004), this is explained by a flux balance model in which shell is deposited at oxygen isotope equilibrium with body fluid that experiences 18O enrichment as a consequence of evaporation while snails are forming shell. The factors that most affect the oxygen isotopic composition of the shell are: (1) rain δ18O, (2) relative humidity (RH), (3) atmospheric water vapor δ18O, and (4) temperature (Balakrishnan and Yapp, 2004).

Here, we report the first isotope study of fossil land snail shells and bulk sediment carbonates from the late Quaternary eolian successions of the eastern Canary Islands. These data represent a source of information on lower latitude environmental changes recorded at the soil–air interface in the westernmost part of the Saharan Climatic Zone. Interpretations are derived from application of the aforementioned model to the land snail data. Environmental changes deduced
for the Canary Islands are discussed in the context of published results from mid and high-latitude climatic proxies.

**Background**

**Sample setting and eolian successions**

The study area includes the easternmost islands of the Canary Archipelago: Fuerteventura, Lanzarote, La Graciosa, Montaña Clara and Aleganza (Fig. 1; Table S1). These islands consist primarily of Miocene to Holocene subaerial volcanic rocks (e.g., Coello et al., 1992) and contain abundant late Quaternary eolian deposits with numerous fossil land snail shells of multiple native species suitable for paleoecological and paleoenvironmental studies (e.g., Huntley et al., 2008; Yanes et al., 2008a).

The eolian successions are comprised of bioclastic dunes which were transported inland during glacial times, when sea level was lower (e.g., Rognon and Coudé-Gaussen, 1988, 1996a,b). These eolian dunes are capped by ~20- to 60-cm-thick paleosols (Fig. S1) which have a carbonate-dominated matrix, and they are not well-developed (entsisol and/or luvic calcisol paleosols: Williamson et al., 2004; Alonso-Zarza et al., 2008). Eolianites contain a mixture of marine and...
continental carbonates (calcite, magnesium calcite, and aragonite) with total proportions of 50–90% by weight (Dammati et al., 1996). In addition, there are minor amounts of clay minerals such as authigenic smectite and African-derived illite–kaolinite (Dammati et al., 1996). Quartz grains from the Sahara and basaltic clasts (augite, olivine, chlorite, titanomagnetite, pylogorskite: Williamson et al., 2004) from erosion and weathering of local rocks are also common. A large proportion (> 65% by weight) of the dust (~ 20–40 μm) originates from the Sahara (Rognon and Coudé-Gaussen, 1988, 1996a,b; Dammati et al., 1996; Williamson et al., 2004).

A total of 59 shell beds from 24 eolian deposits were sampled from the five eastern islands (Fig. 1, Fig. S1, Table S1). The shells were dated by amino acid racemization (AAR) calibrated against radiocarbon (Ortiz et al., 2006). The sections display variable thickness and horizons with a sub-desertic climate. Their low altitude and the environmental setting

Environmental setting

The eastern Canary Islands are situated in a warm and dry climatic zone, with a sub-desertic climate. Their low altitude and the orientation parallel to the prevailing winds contribute to the dryness of the climate (Dorta, 2005). The average annual precipitation is ~210 mm/yr, with long intervals of dryness (Reyes-Betancort et al., 2001). Rainwater in the study area (Madeira and Canary Islands) has an annual, weighted average δ18O value of ~−3.5‰ (IAEA: http://www.iaea.org). The average RH is ~70% (Dorta, 2005). Monthly average temperatures range between 16°C and 24°C, and the annual average is ~20°C. Average temperature of the rainy months (from October to April) is ~19°C (Reyes-Betancort et al., 2001; Dorta, 2005).

The vegetation of the study area contains over 800 species (e.g., Reyes-Betancort et al., 2001; Scholz, 2005) characterized by herbaceous-shrub xerophytes, halophytes and psamophytes. Around 67% by weight (Damnati et al., 1996). In the eastern islands nowadays.

Subaerial Quaternary deposits are commonly geographically scattered (e.g., Fig. 1) and can pose correlation problems. Temporal relationships among Quaternary land snails in such deposits can be addressed with AAR dating calibrated against radiocarbon (Cook et al., 1993; Goodfriend et al., 1996; Hearty, 1997, 2003; Brooke et al., 2003a,b; Hearty et al., 2004; Hearty and Kaufman, 2009). Ortiz et al. (2006) showed that the eastern Canary Islands exhibited a generally good correspondence among AAR, radiocarbon ages and field-stratigraphy. The AAR ages of snail shells ranged from 4.6 (±0.7) ka to 55.7 (±5.5) ka (Table 4 in Ortiz et al., 2006). Uncertainty in AAR (Table 1) is represented by the standard deviation of the ages of multiple shells from the same horizon (Ortiz et al., 2006). Although the AAR method commonly has a large age uncertainty, the AAR data of Ortiz et al. (2006) are the most complete chronology presently available for this material. Such aminochronology is consistent with previous local studies (e.g., Petit-Maire et al., 1986; Rognon and Coudé-Gaussen, 1988, 1996a,b; Hillaire-Marcel et al., 1995; Dammati et al., 1996). Yanes et al. (2007) suggested that the multimillennial-age mixing of various shell beds, as expected for shell-rich assemblages (see review in Kowalewski and Bambach, 2003), was a consequence of the progressive accumulation of successive

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n: Number of entire-shells analyzed of equivalent age; ^a: age data taken from Ortiz et al. (2006); ^b: modern isotopic data taken from Yanes et al. (2008b); ±: indicates standard deviation of the observed range of the measured values.
generations of shells during the sedimentation process (paleosol genesis), which takes from hundreds to thousands of years. Since dunes are somewhat sealed by paleosols, shell reworking from older into younger beds was improbable (Yanes et al., 2007). The AAR dates of Ortiz et al. (2006) were adopted as credible indicators of the comparative ages of shells.

Methods

Sampling strategy, species and shell preservation

Fossil shells (n = 329) were collected from 30 to 50 cm into the exposed surface to avoid possible contamination or reworked material. Bulk paleosol and dune samples were collected directly from 40 stratigraphic horizons.

Ten species were included in this study. The assemblages were dominated by *Theba geminata* (Mousson, 1857) and *T. arinagae* Gittenberger & Ripken, 1987 (Yanes, 2003; Yanes, 2005; Huntley et al., 2008; Yanes et al., 2008a), which were continuous and abundant throughout space and time. Modern *Theba* specimens display an herbivorous and epifaunal strategy with an annual/bi-annual life cycle (Cowie, 1984). The majority of shells belong to the *Theba* genus (n = 278). The remaining eight species (n = 51), which were discontinuous in the record and less abundant, included *Ruminia decollata* (Linnaeus, 1758) (n = 15), *Pomatias laranzatensis* (Wollaston, 1878) (n = 10), *Monilearia monilifera* (Webb & Berthelot, 1833) (n = 9), *M. granostriata* (Mousson, 1857) (n = 2), *Hemicycly sarcostoma* (Webb & Berthelot, 1833) (n = 9), *Ferussacia folliculus* (Gmelin, 1791) (n = 1), *Canaliculina lenticularis* (Michaud, 1831) (n = 1), *Candidula ultima* (Mousson, 1872) (n = 1) and *Canariella plutonia* (Lowe, 1861) (n = 2).

Prior to stable isotope analysis, XRD results of 94 specimens indicate that shells preserved their aragonite composition (Yanes et al., 2007, 2008a). Thus, substantial diagenetic alterations were unlikely. Scanning Electron Microscope (SEM) micrographs of modern (Fig. S2A–B) and fossil (Fig. S2C–D) shell fragments of *Theba geminata* showed no evidence of recrystallization.

Stable isotope analyses

Entire shells and bulk sediment samples were analyzed in the Huffington Department of Earth Sciences (SMU, USA), the Savannah River Ecology Laboratory (UGA, USA) and the Instituto Andaluz de Ciencias de la Tierra (CSIC, Spain). Samples were analyzed using a Finnigan DeltaS+XL continuous flow isotope ratio mass spectrometer and a dual inlet Finnigan MAT 252 isotope ratio mass spectrometer. All carbonate isotopic results are reported in δ notation relative to the international standard PDB. The δ values are defined as:

\[
\delta X = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 (\text{‰})
\]

where \(X = ^{13}C, ^{18}O\) or \(X = ^{18}O, ^{16}O\) for \(R = ^{13}C/^{12}C\) or \(R = ^{18}O/^{16}O\). Analytical uncertainty was ±0.1‰ for both δ^{13}C and δ^{18}O. For δ^{18}O values of water, the standard is SMOW (IAEA: http://www.iaea.org/).

Shells were cleaned ultrasonically in deionized water and pulverized with an agate mortar and pestle. Organic matter was removed by placing the sample in a reagent-grade 3% NaOCl solution for 48 h at room temperature (~22°C). Samples were thereafter rinsed with deionized water and dried in an oven at 40°C. The NaOCl method was tested at SMU on a powdered shell of *Cepaea hortensis* (Müller, 1774). Within analytical uncertainty, the treatment with reagent-grade 3% NaOCl (~0.0002% Ca impurity) had no significant effect on the shell isotopic values. This is consistent with Wierzbowski (2007), who found that 5% NaOCl treatment had no substantial effect on aragonite shell δ^{18}O (±0.1‰) or δ^{13}C (±0.2‰) values. Consequently, the variations in shell isotopic values of this study are not biased by NaOCl treatment. All shells were treated at room temperature with 3% NaOCl as a precaution to minimize possible organic matter interferences.

Intra-shell aliquots were collected from seven pre-cleaned (as described above) shells using an electronic dremel along ontogeny. Shell carbonate (~150 μg) was placed in a 6 ml extainer™ vial and flushed with helium. The carbonate was converted to CO₂ gas by adding 0.5 ml of 100% H₃PO₄ at 25°C. The CO₂ was analyzed after 24 h using the GasBench II and the CF-IRMS. Results were calibrated against the international standards NBS-18 and NBS-19 and in-house standards. The precision of the analyses was ±0.1‰ (1σ standard deviation) for δ^{18}O and δ^{13}C based on the repeated measurement (n = 30) of standards. Replicate analyses of shells had a precision of ±0.2‰ for both isotopes.

Sediment samples were homogenized by grinding under methanol in a mortar and pestle and treated with 3% H₂O₂ overnight to eliminate organic contaminants. Samples were rinsed with deionized water and dried at room temperature. The carbonate (~10–20 mg) was reacted overnight in vacuum with 100% H₃PO₄ at 25°C. The CO₂ was analyzed on a Finnigan MAT 252 mass spectrometer. Analytical uncertainty was ±0.1‰ for both isotopes.

Results

Carbon and oxygen isotopic composition of fossil land snail shells

Fossil shell δ^{13}C values are plotted against age in Figure 2A and scatter over a range from −8.9‰ to +3.8‰ (Table 1; Appendices S1). Shells of similar age but from different locales showed comparable values (Appendices S1). Average δ^{13}C values of age-equivalent shells are shown in Figure 2B along with the uncertainties (error bars) of AAR ages.

The substantial scatter and the large overlap of shell δ^{13}C values among beds suggest the simultaneous presence of C₃/C₄ plants on the islands over the last ~50 ka (Fig. 2A). Although not all time intervals are equally well represented by numbers of analyzed shells, there is general accord of the average isotopic compositions of age-equivalent shells. Thus, this unevenness of temporal distribution of numbers of samples and the effects of possible overlap associated with the uncertainties of AAR ages may be mitigated by the 3-point moving average (Fig. 2C) of the mean values (Fig. 2B). Notwithstanding the rather large uncertainties in the AAR ages, if the emphasis is on overall, longer-term temporal variations, moving averages should have some credibility. This approach suggests that recent snails ingested higher proportions of C₃ plants than the snails at ~20–24 ka.

Carbon and oxygen isotopic compositions of shells are not correlated. Fossil shell δ^{18}O values range from −1.9‰ to +4.5‰ (Fig. 3A; Table 1; Appendix S1). The isotopic scatter among shell beds probably reflects environmental variability at the microhabitat scale in which snails live (e.g., Balakrishnan et al., 2005a,b). Overlaps in δ^{18}O values suggest some similarities in the extremum values of microhabitats through time (Fig. 3A), since snails tend to be active under optimum conditions, and thus select for a restricted range of environmental variability. Notwithstanding the scatter (Fig. 3A), average δ^{18}O values of age-equivalent shells may be sources of information on larger scale, longer-term, climatic variations, because a large standard deviation does not automatically imply inaccuracy of the mean as an indicator of the average conditions in a locale. Moreover, a moving average of the means emphasizes longer-term trends. Average δ^{18}O values of age-equivalent shells are shown in Figure 3B together with the uncertainty of AAR ages (error bars in Fig. 3B). Generally, age-equivalent shells from different locales had analytically indistinguishable mean δ^{18}O values (Appendices S1). Three-point moving averages (Fig. 3C) of the mean values exhibit an overall increase in shell δ^{18}O values from ~0.1‰ at ~50 ka to ~1.6-
1.8‰ during the LGM (~15-22 ka). The moving averages also indicate that there was an abrupt decline in post-LGM \(\delta^{18}O\) followed by an irregular, but overall increase of shell \(\delta^{18}O\) values to modern values of ~0.9‰ (Fig. 3C). This coincides with the pattern of change found by Colonese et al. (2010) in shell \(\delta^{18}O\) values from the late Pleistocene to Holocene in southern Italy.

Carbon and oxygen isotopic composition of fossil land snail shells among taxa

Shells from all “rare” land snail species (those with low abundance and sporadic in the fossil record) displayed ranges of isotopic values that overlapped with those of the dominant *Theba* species (Appendices S1). The overall isotopic variations through time of the dominant species alone did not differ from those observed when all ten species were considered in combination. These results are consistent with studies of modern land snails from Tenerife Island, for which the stable isotope composition of multiple species did not substantially differ among taxa (Yanes et al., 2009). Consequently, the isotopic compositions of all species were used to infer the environmental conditions of the last ~50 ka in the eastern Canary Islands.

Intra-shell carbon and oxygen isotopic variability of modern and fossil shells

Intra-shell \(\delta^{13}C\) values of two modern *Theba geminata* individuals exhibited ranges (\(\Delta^{13}C\)) of 0.3‰ and 1.7‰, while corresponding \(\delta^{18}O\) values had ranges (\(\Delta^{18}O\)) of 0.3‰ and 0.5‰ (Table 2; Fig. S2A–B; Appendix S2). The magnitude of the modern intra-shell isotopic ranges was smaller than in fossil individuals. \(\Delta^{13}C\) values of five fossil shells ranged from 1.2‰ to 3.3‰ and \(\Delta^{18}O\) values from 1.2‰ to 2.8‰ (Table 2; Fig. S2C–G). The patterns of intra-shell isotopic variations differed among specimens through ontogeny (Fig. S2). Many studies have increasingly used the isotopic composition through the ontogeny of the organisms’ hard skeleton in an attempt to reconstruct high resolution (daily, monthly and/or seasonal) climatic conditions.
Figure 3. Stable oxygen isotopic composition of fossil land snail shells from the Canary Islands through time. (A) Individual entire-shell $\delta^{18}O$ values (gray circles) and average $\delta^{18}O$ values of age-equivalent samples (black diamonds). (B) Mean $\delta^{18}O$ values of age-equivalent shells (dashed line). Age uncertainty is indicated by gray error bars. (C) 3-point moving average of the mean $\delta^{18}O$ values through time.

Table 2
Carbon and oxygen stable isotope composition of modern and fossil snail shells sampled subsequently through ontogeny.

<table>
<thead>
<tr>
<th>Shell ID</th>
<th>Nominal AAR age (ka)*</th>
<th>$n$</th>
<th>$\delta^{13}C$ (PDB)</th>
<th>Mean</th>
<th>Min</th>
<th>Max</th>
<th>$\Delta^{13}C$</th>
<th>$\delta^{18}O$ (PDB)</th>
<th>Mean</th>
<th>Min</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>TGL-1</td>
<td>Modern</td>
<td>9</td>
<td>−7.8 ±0.2</td>
<td>−8.0</td>
<td>−7.5</td>
<td>0.5</td>
<td>0.3 ±0.2</td>
<td>0.1 ±0.1</td>
<td>−0.1</td>
<td>0.2</td>
<td>0.5</td>
</tr>
<tr>
<td>TGF-1</td>
<td>Modern</td>
<td>8</td>
<td>−6.5 ±0.6</td>
<td>−7.1</td>
<td>−5.4</td>
<td>1.7</td>
<td>0.1 ±0.1</td>
<td>−0.1</td>
<td>0.2</td>
<td>0.3</td>
<td></td>
</tr>
<tr>
<td>FAG-6</td>
<td></td>
<td>23</td>
<td>−4.9 ±0.4</td>
<td>−5.6</td>
<td>−3.6</td>
<td>2.0</td>
<td>−0.1 ±0.4</td>
<td>−0.8</td>
<td>0.7</td>
<td>1.5</td>
<td></td>
</tr>
<tr>
<td>LTA-2</td>
<td></td>
<td>12</td>
<td>−5.7 ±0.3</td>
<td>−6.1</td>
<td>−4.5</td>
<td>1.6</td>
<td>0.9 ±0.3</td>
<td>0.3</td>
<td>1.6</td>
<td>1.3</td>
<td></td>
</tr>
<tr>
<td>FBP-1</td>
<td></td>
<td>7</td>
<td>−2.3 ±1.2</td>
<td>−4.6</td>
<td>−1.2</td>
<td>3.3</td>
<td>2.6 ±0.4</td>
<td>1.8</td>
<td>3.0</td>
<td>1.2</td>
<td></td>
</tr>
<tr>
<td>GLC-5</td>
<td></td>
<td>25</td>
<td>−5.9 ±0.5</td>
<td>−6.9</td>
<td>−5.2</td>
<td>1.7</td>
<td>2.1 ±0.7</td>
<td>0.0</td>
<td>2.9</td>
<td>2.8</td>
<td></td>
</tr>
<tr>
<td>FAG-1</td>
<td></td>
<td>55</td>
<td>−3.1 ±0.6</td>
<td>−4.7</td>
<td>−2.4</td>
<td>2.3</td>
<td>0.1 ±0.5</td>
<td>−1.3</td>
<td>0.8</td>
<td>2.0</td>
<td></td>
</tr>
</tbody>
</table>

*n*: Number of samples per shell; *Min*: minimum; *Max*: maximum; *Δ*: range of values; *a*: age data taken from Ortí et al. (2006); ± indicates standard deviation of the observed range of the measured values.
through the organisms’ life. This approach appears to be feasible for aquatic organisms because the environmental controls (temperature and water isotopic composition) affecting the shell biomineralization process are relatively well understood (Grossman and Ku, 1986). However, the interactions of environmental factors that control land snail shell isotopic values are significantly more complex than those for aquatic taxa. The relatively large values for intra-shell $\Delta^{13}C$ and $\Delta^{18}O$ (see also Leng et al., 1998; Goodfriend and Ellis, 2002; Baldini et al., 2007) emphasize the importance of analyzing entire shells that are carefully homogenized rather than portions of the shell (e.g., Balakrishnan et al., 2005a; Kehrwald et al., 2010).

Carbon and oxygen isotopic composition of bulk paleosol and dune carbonates

The $\delta^{13}C$ and $\delta^{18}O$ values of bulk paleosol and dune carbonates varied between $-5.2\%$ and $0.7\%$ (Fig. 4A–B) and between $-1.0\%$ and $1.3\%$, respectively (Fig. 4C–D; Table 3; Appendix S3). Paleosol and dune $\delta^{13}C$ and $\delta^{18}O$ values correlated positively ($r_s = 0.69; p < 0.001; n = 40$). The isotopic compositions of the sediment carbonates did not correlate with the aragonite/calcite ratio estimated from XRD analysis. Relatively low sediment $\delta^{13}C$ (from $-1.5\%$ to $-1.0\%$) and $\delta^{18}O$ ($-0.5\%$) values were observed before the LGM (~25–50 ka). More positive values (~$0.0$ for $\delta^{13}C$ and ~$0.9$ for $\delta^{18}O$) were common around the LGM (~15–22 ka). Early to mid-Holocene values (~5–10 ka) displayed a slight increase in $\delta^{13}C$ (to ~$-0.5\%$) and no significant change in $\delta^{18}O$ (0.8‰) (Fig. 4A–D; Table 3; Appendix S3).

Discussion

Paleosol and dune $\delta^{13}C$ and $\delta^{18}O$

Paleosols may contain pedogenic and non-pedogenic carbonates, which complicate paleoenvironmental interpretations. The $\delta^{13}C$ and $\delta^{18}O$ values of bulk sediment carbonates likely represent contributions from mixtures of marine-derived and continental-derived bioclasts together with some pedogenic carbonates and Saharan silt (e.g., Damnati et al., 1996). The difficulty of separating these fractions precluded measurement of their respective end member isotopic compositions.
Although the ages of these carbonate sources remain uncertain, a recent AAR study by Hearty and Kaufman (2009) of fossil land snail Cernion shells and bioclastic sediments from the Bahamas indicated that the marine sediments were rapidly transported inland and quickly colonized by snails. Such a quick sedimentation process (thousands to hundreds of years) and the rapid colonization by snails quickly colonized by snails. Such a quick sedimentation process that the marine sediments were rapidly transported inland and shells and bioclastic sediments from the Bahamas indicated stress during drier times and/or higher contributions of adventitious Environmental controls on modern shell δ18O

The evaporative steady-state flux balance model of Balakrishnan and Yapp (2004) was applied to modern snails from the Canary Islands. To predict the shell δ18O values, the model develops a quantitative relationship between the amount and isotopic composition of liquid water ingested by the snails, the amount and isotopic composition of liquid water evolved from the snail body fluid, and the temperature-dependent oxygen isotope fractionation between the snail body fluid and crystallizing aragonite shell. Thus, the model predicts that (1) ambient temperature, (2) the δ18O value of ingested water, (3) RH, (4) ambient water vapor δ18O values, and (5) the ratio (θ) of the flux of liquid water output from the body fluid (Jw) relative to the flux of liquid water ingested by the snail (Jin) during shell formation are important controls on the body fluid/shell δ18O values (Balakrishnan and Yapp, 2004).

Balakrishnan and Yapp (2004) showed that it is useful to assume that water vapor is in isotopic equilibrium with the liquid water ingested by the snail. Also, for θ ≤ 0.40, an assumption that snail body fluid is lost only by evaporation (i.e., θ = 0) is a good approximation, and a value of θ = 0 is adopted here (Balakrishnan and Yapp, 2004).

Two cases were examined to compare model predictions of RH with the modern conditions on the Canary Islands. Case 1: water vapor in isotopic equilibrium with rain (Fig. 5A) (see Balakrishnan and Yapp, 2004 for further details). Case 2: water vapor with a constant value of ~11‰ (marine vapor: Craig and Gordon, 1965). For both cases, the input parameters were T = 19°C (average temperature during the rainy season in the islands) and amount-weighted average δ18O values of rain of ~3.5‰ (SMOW), based on regional IAEA data. Using amount-weighted rain δ18O values emphasizes the importance of the wetter intervals when snails form shell material (Balakrishnan and Yapp, 2004).

For Case 1, measured δ18O values (~0.3‰ to 2.5‰: Yanes et al., 2008b) of modern shells are predicted by the model for RH between 0.86 and 0.94. In contrast, for Case 2, the more negative modern δ18O values are not predicted for any physically reasonable RH values (i.e., RH ≤ 1.00). Consequently, only the assumptions of Case 1 are used.

The relatively high values of modern RH (from 0.86 to 0.94) predicted by the model (for Case 1) are consistent with modern snail activity primarily at night and/or during or immediately after a rain event—times when snails are active (e.g., Cook, 2001). Much of the scatter in shell δ18O values among individuals may be attributable to variations of ambient environmental parameters among different microenvironments inhabited by those individuals (Balakrishnan et al., 2005b; Yanes et al., 2009). This emphasizes the need to analyze comparatively large numbers of shells per site to obtain a mean value that is reasonably representative of the average environmental conditions at that locale. The observed average δ18O value (0.9‰) of live-collected snails (Fig. 5A) and the model of Balakrishnan and Yapp (2004) suggest that, on average, for a combination of T ≈ 19°C and rain δ18O ≈ ~3.5‰ (SMOW), the average value of RH was ~0.91 during shell deposition. This RH is consistent with the high humidity that characterizes the times of recent snail activity in the Canary Islands and suggests that meaningful values of RH may be inferred from ancient shells.

Paleoclimatic inferences

Fossil shell δ18O values exhibit substantial scatter through time (Fig. 3A), and the magnitude of the scatter is comparable for different ages. However, variations in the mean shell δ18O values suggest that climatic conditions were not constant through time. The model of Balakrishnan and Yapp (2004) and independent, proxy-constrained estimates of temperature and rainfall δ18O values are used to extract changes in paleohumidity from changes in the fossil shell δ18O.
Published ancient sea-surface temperatures (SST) and ocean δ¹⁸O values were used to estimate paleotemperatures and δ¹⁸O values of ancient rain for model calculations (Fig. 6). Alkenone ratios in marine sediments (e.g., Zhao et al., 1995; Bard, 2002), indicate that SST in the ancient rain for model calculations (Fig. 6). Alkenone ratios in marine sediments (e.g., Zhao et al., 1995; Bard, 2002), indicate that SST in the eastern Atlantic Ocean at 37° and 20°N latitude only vary by 3°C or 4°C between glacial and interglacial intervals (Fig. 6B). These locations bracket the Canary Islands, implying a similar magnitude of glacial–interglacial temperature variation (modern interglacial T≈19°C; glacial T≈15°C). The SST data (Fig. 6B) suggest that there was no sustained, long-term temperature change in the Canary Islands between ~50 and 12 ka.

Globally, δ¹⁸O values of the oceans were ~1‰ higher during the LGM than today (e.g., Zachos et al., 2001; Schrag et al., 2002), because of extensive Northern Hemisphere continental glaciation. Higher oceanic δ¹⁸O values might be expected to correspond to higher average δ¹⁸O values of Canary Islands rainfall (i.e., ~2.5‰). For the interglacial interval from ~12 ka to modern, the data of Zachos et al. (2001) suggest that global ocean δ¹⁸O values did not vary monotonically (Fig. 6D). We adopt the working hypothesis that longer-term average δ¹⁸O values of rain in the Canaries did not experience a monotonic shift over this interval and had values around ~3.5‰.

The snail flux balance model (Balakrishnan and Yapp, 2004), combined with the aragonite–water oxygen isotope fractionation equation of Grossman and Ku (1988), was applied to the interpretation of the fossil shell δ¹⁸O values (Fig. 6A). For Case 1 (see above), three boundary condition scenarios were examined.

However, uncertainties in AAR ages favored the use of moving average snail δ¹⁸O values and interpretations of only longer-term climatic change.

Scenario 1. Glacial age temperatures of ~15°C and rain δ¹⁸O values of ~2.5‰ were assumed. For these conditions, shell δ¹⁸O values of 0.1‰ indicate that ~50 ka ago, values of RH were ~0.97 (Fig. 5B). For the LGM (~15 to 22 ka) with shell δ¹⁸O values of 1.6‰ to 1.8‰, RH would have been ~0.92 (Fig. 5B). At ~12 ka, shell δ¹⁸O values of 0‰ suggest an RH of ~0.95 for rain δ¹⁸O≈3.5‰ (Fig. 5B). Finally, there is the change in the Holocene toward the modern values of 19°C, rain δ¹⁸O≈3.5‰, and RH≈0.91 (Fig. 5B). Thus, over the last ~50 ka there has been an overall decrease in RH to the modern, semiarid conditions of the eastern Canary Islands.

Scenario 2. Glacial–interglacial temperatures on the Canary Islands were again assumed to change from ~15°C to ~19°C. As an extreme case it was assumed that there was no change in the average δ¹⁸O values (~3.5‰) of rain over the past ~50 ka (i.e., glacial–interglacial changes in ocean δ¹⁸O values did not affect rain δ¹⁸O values). The model calculations suggest that shells at ~50 ka grew at average RH of ~0.95, while at ~15–22 ka (LGM) RH would have been ~0.90 (Fig. 5C). At ~12 ka, RH was ~0.95 before switching toward the modern value of ~0.91 (Fig. 5C).

Scenario 3. Again, the average Canary Islands temperatures are assumed to have changed from ~15°C during the glacial interval to ~19°C during interglacial times. However, closer examination of the benthic foraminifera data (Fig. 6D) suggests that global ocean water δ¹⁸O values increased by ~0.5‰ between ~50 ka and ~15–22 ka (LGM). Assuming that average local rainwater mimicked these ocean changes, long-term average rain δ¹⁸O values would have been ~3.0‰ at ~50 ka (Fig. 5D), ~2.5‰ at ~15 to 22 ka, and ~3.5‰ from ~12 ka to present. Under these conditions, RH at ~50 ka is calculated to have been ~0.96, while during the LGM (~15 to 22 ka) RH was ~1.95.}

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**Figure 5.** Calculated shell δ¹⁸O values as a function of relative humidity using the evaporative steady-state flux balance model by Balakrishnan and Yapp (2004). (A) Gray area represents the measured range of shell δ¹⁸O values of live-collected land snails from the eastern Canary Islands (Yanes et al., 2008b). Filled dot represents the average shell δ¹⁸O value (0.9‰) for modern shells. (B) Paleoclimatic scenario 1 for the last 50 ka in the Canary Archipelago as inferred from the land snail isotopic record (see text). Calculations were performed using interglacial (~19°C) and glacial (~15°C) temperatures estimated from SST proxies (Zhao et al., 1995; Bard, 2002) and initial interglacial (~19°C) δ¹⁸O values estimated from IAEA data and global ocean δ¹⁸O values, respectively (Zachos et al., 2001; Schrag et al., 2002). (C) Paleoclimatic scenario 2 assuming constant rainwater δ¹⁸O values. (D) Paleoclimatic scenario 3 using interglacial (~19°C) and glacial (~15°C) temperatures and interglacial (~3.5‰) and glacial (~2.5‰ and ~3.0‰) rain δ¹⁸O values. It is worth noting that the plausible paleoclimatic scenarios require a decline in RH to explain the land snail data (see text).
At ~12 ka, RH would have been ~0.95 with a subsequent decline to the modern RH of ~0.91 (Fig. 5D).

Regardless of which scenario is considered, the model-based interpretations of the shell δ¹⁸O data for the Canary Islands indicate an overall decrease in RH during the times of snail activity. However, the boundary conditions of Scenario 3 are the best supported by independent proxy data (Fig. 6).

Hadley circulation was weaker and precipitation decreased as a consequence of the southward shift of the Intertropical Convergence Zone (ITCZ) during the LGM (see recent review in Gasse et al., 2008). This may have resulted in the “aridification” of the Sahara zone into the LGM (e.g., Gasse et al., 2008). If so, this might account for the inferred overall decrease in RH in the neighboring Canary Islands during that interval.

Northern Africa experienced a further progressive increase in aridity during the late Holocene (with some brief returns to wetter periods) resulting in the ultimate desiccation of the Sahara (e.g., Gasse et al., 1990; DeMenocal et al., 2000; Swezey, 2001; Jung et al., 2004). The lowest values of RH calculated from the Canary Island land snail data are for the modern samples, which is consistent with the Holocene desiccation of the Sahara. However, the non-uniqueness of our data-constrained, but model-based, climatic interpretation suggests a need for more work to sort out the complexities of climate change in these low latitude islands.

Yanes (2003) and Huntley et al. (2008) observed that Theba species from the northeastern islets of the Canary Islands have experienced an overall decline in shell size through time. Multiple environmental and ecological factors control shell size, but humidity appears to be one of the most important. Thus, snail size is often larger under wetter conditions, but smaller at drier times (Goodfriend, 1986). The fact that shells have decreased in size over time in the region supports the proposed progressive decline in RH. Additionally, Yanes (2003, 2005) concluded that shell abundance and snail diversity were higher in glacial paleosols than in Holocene beds from the Canary Archipelago. Among other factors, wetter conditions normally favor snail proliferation and diversification (Cook, 2001). Thus, the proposed decline in RH is also supported by the decrease in shell abundances and diversity.

The relatively high average shell δ¹⁸O values for the Canary LGM contrast with the minimum in LGM δ¹⁸O values from Greenland ice cores (Fig. 6C: Dansgaard et al., 1993). However, the higher LGM shell δ¹⁸O values are consistent with higher δD or δ¹⁸O values for LGM proxies (groundwater, tree cellulose, paleosol carbonate and authigenic kaolinite) from ice-free North America (Yapp and Epstein, 1977; Plummer, 1993; Amundson et al., 1996), South America (Mora and Pratt, 2001), and southwestern Africa (e.g., Gasse, 2000; Gasse et al., 2008). Possible explanations include: (1) specificity in the ice-free records such as an increase in the proportion of summer precipitation, which has a higher δ¹⁸O value (Yapp and Epstein, 1977; Plummer, 1993; Amundson et al., 1996); (2) differing responses to environmental variables other than temperature and meteoric water isotope ratios in the ice-free records such as RH, water vapor δ¹⁸O values, and ocean δ¹⁸O values or the amount of precipitation, (e.g., Yapp and Epstein, 1977; Mora and Pratt, 2001); and/or (3) differences in LGM to Holocene climatic transitions between low/mid-latitudes (ice-free) and high latitudes (glaciated). Based on the current work, changes in RH and precipitation δ¹⁸O values seem to have been the most important influences on Canary Islands land snail shell δ¹⁸O values.

**Conclusion**

δ¹³C values of fossil land snail shells from the eastern Canary Archipelago suggest that C₃ and C₄ plants were simultaneously present in the islands over the last ~50 ka. However, C₃ plants were likely more abundant at various times during the last glacial cycle, especially around the last glacial maximum (LGM), probably as a response to drier conditions and/or lower atmospheric CO₂ concentrations.

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**Figure 6.** (A) 3-point moving average of mean δ¹⁸O values of fossil land snail shells from the Canary Islands. (B) Sea surface temperature at Iberian margin (gray line) estimated from alkenone method from deep see cores SU8118 and MD952042 (Bard, 2002); and at North West Africa from alkenone method from core ODP658C (Zhao et al., 1995). (C) Oxygen isotope composition from Greenland Ice Core (Dansgaard et al., 1989, 1993; GRIP members, 1993; Crootes et al., 1993; Johnsen et al., 1997). (D) Global compilation of benthic foraminifera oxygen isotopic data (Zachos et al., 2001).
δ18O variations of ancient land snail shells from the eastern Canary Islands appear to record oscillations in the relative humidity (RH) over the past ~50 ka, but with an overall decrease to the present. Information on changes in RH was extracted from the isotopic data by application of a published flux balance model constrained by proxy data on regional sea surface temperatures and δ18O changes of the global ocean between glacial and interglacial times. The patterns of RH variation were similar among different postulated paleoenvironmental scenarios. The inferred overall changes in RH are generally consistent with published evidence for increasing dryness in nearby northern Africa.

The results from the land snails endorse the use of average δ18O values of numerous time-equivalent entire shells to deduce patterns of climate change. Moreover, this successful use of long-term isotopic records of land snails from low-latitude islands in the eastern Atlantic suggests that studies of shells from other low-latitude islands could help to identify patterns of glacial to interglacial variations in the atmosphere over the tropical oceans.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://www.iaea.org/.

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