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ScienceDirect
Chemical Geology 249 (2008) 377–392
CHEMICAL GEOLOGY INCLUDING ISOTOPE GEOSCIENCE
www.elsevier.com/locate/chemgeo

Stable isotope ($\delta^{18}O$, $\delta^{13}C$, and δD) signatures of recent terrestrial communities from a low-latitude, oceanic setting: Endemic land snails, plants, rain, and carbonate sediments from the eastern Canary Islands

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Received 18 May 2007; received in revised form 24 November 2007; accepted 20 January 2008

Editor: S.L. Goldstein

Abstract

Stable isotopes of oxygen and carbon extracted from fossil land snail shells have been used increasingly to interpret past environments. To evaluate the utility of this approach for low-latitude oceanic islands, populations of the modern helicid land snail *Theba geminata* – a species also abundant in the Quaternary fossil record of the region – were sampled at ten low altitude (<300 m) sites from coastal areas of the eastern Canary Islands. The results include stable isotopes of (1) 17 aragonite shells of live-collected adult snails; (2) 17 body tissue samples from the same snail individuals; (3) 10 samples of carbonate sediments; (4) 69 plant tissue samples representing all 24 identified species; and (5) 7 rain water samples. The mean isotopic composition of the rain water is −5‰ (V-SMOW) for δD and −2‰ (V-SMOW) for $\delta^{18}O$, ranging from −11‰ to +2‰ (V-SMOW) and from −2.6‰ to −0.7‰ (V-SMOW), respectively. The local vegetation is heterogeneous, including C_3, C_4, and CAM plants. $\delta^{13}C$ values vary from −13.0‰ to −29.0‰ (V-PDB) across plant species. Of the 24 species, five are C_4, 15 are C_3, and four are CAM plants. The $\delta^{18}O$ values for shells represent a narrow range of values (from −0.3‰ to +2.5‰ [V-PDB]), which is consistent with the low climate seasonality typifying low-latitude oceanic settings. Hypothetical model of the expected $\delta^{18}O$ value for shell aragonite precipitated in equilibrium suggests that the most negative $\delta^{18}O_{shell}$ represent the closest estimate for $\delta^{18}O_{rain\ water}$. The $\delta^{13}C$ values of shells range from −9.4‰ to +1.7‰ (V-PDB). The most positive $\delta^{13}C$ values are attributed to a diet based on C_4 plants. The comparison of $\delta^{13}C$ values of soft tissues and shells suggests that snails ingested notable amounts (from ~20% up to ~40%) of foreign carbonates. Consequently, fossil shells with the most negative $\delta^{13}C$ values should be selected for radiocarbon dating in future geochronological studies of the region. The $\delta^{13}C$ values of body tissues vary from −12.0‰ to −27.2‰ (V-PDB), indicating that land snails consumed C_3 and C_4 plants indiscriminately. The mean carbon isotopic composition, averaged across multiple fossil specimens, may thus provide a useful tool for reconstructing paleoclimates and paleoenvironments throughout the Quaternary history of the Canary Islands and other comparable low-latitude oceanic settings.

Keywords: Stable isotopes; Terrestrial gastropods; C3/C4 plants; Eolian deposits; Quaternary; Canary Islands

1. Introduction

Stable isotope signatures extracted from shells of live-collected land snails have been widely used to characterize paleoenvironmental and paleoclimatic parameters such as

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doi:10.1016/j.chemgeo.2008.01.008

temperature and humidity (e.g., Bonadonna and Leone, 1995; Bonadonna et al., 1999; Goodfriend and Ellis, 2002; Stott, 2002; Metref et al., 2003; Balakrishnan et al., 2005a,b; Zanchetta et al., 2005; Baldini et al., 2007). Specifically, $\delta^{13}C$ values of shell carbonates may provide quantitative estimates of the proportion of C_3 and C_4-type plants in local habitats, and thus, offer a multitude of paleoclimatic, paleoenvironmental, and paleoecological insights (e.g., Stott, 2002; Metref et al., 2003; Balakrishnan and Yapp, 2004; Baldini et al., 2007). In addition, $\delta^{18}O$ values extracted from shells may relate to the isotopic composition of local meteoric waters (e.g., Yapp, 1979; Lécolle, 1985; Balakrishnan and Yapp, 2004; Balakrishnan et al., 2005a; Zanchetta et al., 2005). Numerous studies have shown the sensitivity of shell oxygen ratios to air–soil interface temperature and humidity (e.g., Goodfriend and Magaritz, 1987; Goodfriend et al., 1989; Metref et al., 2003) or evaluated the relationship between the oxygen isotopic ratios of the shell aragonite and the mean annual oxygen isotope composition of meteoric precipitation and the mean annual temperature (e.g., Lécolle, 1985).

However, reconstructions based on isotopic signatures of gastropod shells are not straightforward because of the underlying assumptions about the feeding behavior and physiology of snails (e.g., Goodfriend, 1992). For example, attempts to utilize snail $\delta^{13}C$ values to estimate the distribution patterns of C_3 and C_4 plants necessarily assume that snails consume plants indiscriminately and in proportion to the abundance of these plants in the natural environment (Goodfriend and Magaritz, 1987; Goodfriend, 1988, 1990). Ideally, thus, stable isotope estimates extracted from fossil snail shells should be interpreted in the context of comparable isotopic data extracted from shells of their nearest living relatives, live-collected from well-understood present-day habitats. A development of such modern isotopic reference baseline for terrestrial ecosystems of the eastern Canary Islands (Fig. 1) is the main goal of this study.

This project has both regional and general implications. First, the bulk of previous stable isotope studies of modern (live-collected) land snails in natural settings come from high latitudes (but see Baldini et al., 2007): North America (e.g., Goodfriend and Ellis, 2002; Balakrishnan et al., 2005a and references therein), Great Britain (e.g., Yates et al., 2002), France (e.g., Lécolle, 1985), Italy (e.g., Zanchetta et al., 2005), and Israel (e.g., Goodfriend, 1992). In contrast, this project provides snail and plant stable isotope data from low-latitude oceanic islands (27° 37′ and 29° 25′ N), a setting representing a notably warmer and much more equitable climate. Second, the eastern Canary Islands support abundant modern and fossil populations of land snails, as well as the whole archipelago, which has around 80% of endemic species (Alonso et al., 2006; Alonso and Ibáñez, 2007), providing a unique regional biota for comparative analyses. Third, coastal arid-to-semi-arid ecosystems (precipitation rate below 200 mm/m^2 year) occurring in the study area are characterized by xerophytic grasses and bushes with dense populations of the helicid gastropod *Theba geminata* (Mousson) (Fig. 2A–C). This distinct, low-latitude community is a particularly attractive study target because of its outstanding fossil record (Fig. 2D–F) that extends back in the region for at least the last 50,000 years (Yanes et al., 2004, 2007, in press; Ortiz et al., 2006). Finally, to our knowledge, neither modern nor fossil components of this ecosystem have ever been studied for stable isotope signatures.

Here, using targeted habitats from the eastern Canary Islands, we integrate data on (1) $\delta^{13}C$ and $\delta^{18}O$ of aragonite land snail shells, (2) $\delta^{13}C$ of land snail soft tissues, (3) $\delta^{13}C$ of plants, (4) $\delta^{13}C$ and $\delta^{18}O$ of local carbonate-rich sediments (i.e., bioclastic sands and carbonate soils), and (5) δD and $\delta^{18}O$ of rain water. The aim of this paper is to assess stable isotope signatures extracted from live-collected land snails in relation to known/measurable environmental variables characterizing their habitats. This, in turn, should allow us to enhance the interpretative value of stable isotope data retrievable from the fossil record of those snails. In more general terms, the project tests empirically the environmental and climatic utility of stable isotope signatures provided by land snail shells, both for modern settings as well as fossil assemblages.

2. Geographical, geological and environmental context

The eastern Canary Islands, which include the Fuerteventura Island, Lanzarote Island, and La Graciosa Islet (north of Lanzarote Island), are located in the eastern part of the Canary Archipelago (Fig. 1), about 100 km west off the coast of Africa. The islands are characterized by an arid-to-semi-arid climate and represent the westernmost part of the Saharan Zone. This Archipelago is located in a region of strong interaction between atmospheric and oceanic circulation systems. The trade winds, which drive seasonal coastal upwelling and the dust storms from the adjacent Sahara Desert, are the major source of terrigenous sediments (Rognon and Coude-Gaussen, 1987, 1996).

The eastern Canary Islands consist of volcanic rocks recording three main cycles (Coello et al., 1992; Carracedo and Rodríguez Badiola, 1993): (1) submarine units of Oligocene age; (2) sub-aerial units of Miocene age; and (3) sub-aerial units of Pleistocene–Holocene age. These volcanic units are covered in many areas by eolian deposits, which are dominated by marine-derived bioclastic sands and provide extensive fossil and sedimentary records of the Quaternary history of the islands. The soils in the study area are characterized by high contents of clay minerals, volcanic clasts, Quartz minerals from Sahara, and carbonates (Torres, 1995). The high proportion of carbonates includes both bioclasts as well as precipitated $CaCO_3$. Three following explanation can be offered for the origin of the precipitated $CaCO_3$: (1) the bioclastic carbonates dissolved due to rain events can be subsequently re-precipitated with the return of typical conditions of high evapo-transpiration and aridity; (2) high biological activity can facilitate chemical precipitation of Ca^{2+} from volcanic rocks reacting with CO_2 from plants; and (3) fine-grained foreign carbonates from other regions (including Sahara) can be admixed via wind transport (Torres, 1995). The proportion of $CaCO_3$ in soils of the eastern islands ranges typically between 1 and 500 g/kg (0.1 to 50%), but may occasionally reach up to 950 g/kg (95%) (Torres, 1995). In addition, many fossil shells preserved in paleosols and dunes display a high proportion of carbonate coatings, which cover shells partially or totally (Yanes et al., in press).

Fuerteventura Island is the oldest of the islands of the Canary Archipelago and one of the few where the Oligocene volcanic and plutonic units crop out on the surface (Coello et al., 1992; Ancochea et al., 1996). Lanzarote Island is the second oldest island, where Miocene, Pliocene and Pleistocene volcanic materials are found (Carracedo and Rodríguez Badiola, 1993; Coello et al., 1992). La Graciosa Islet consists primarily of Upper Pleistocene–Holocene volcanics (Fúster et al., 1968; De la Nuez et al., 1997).

Although moisture-rich trade winds are present in the region, the eastern Canary Islands do not induce abundant rainfall. This is, most likely, due to the longitudinal orientation and low altitude of the islands. Consequently, in contrast to the western islands of the archipelago, their climate is arid-to-semi-arid. The precipitation is scarce and irregular (203 mm/m^2 year maximum), and long periods devoid of any precipitation further enhancing the arid-to-semi-arid character of local habitats (Dorta, 2005). Moreover, the warm and dry southeastern winds ("levante") from the neighboring Sahara desert induce high evaporation rates. Nevertheless, despite low levels of precipitation and high evaporative rates, the direct oceanic influence allows the islands to retain a moderately stable relative humidity, averaging around 70% annually. The temperature is relatively stable seasonally, with the mean annual value of ~20 °C (Dorta, 2005). Due to infrequent cloud cover, the islands receive substantial amounts of direct sun light averaging ~2800 h/year.

The vegetation is scarce and represents around 678 species, including about 42 endemic forms (Scholz, 2005). At least 67

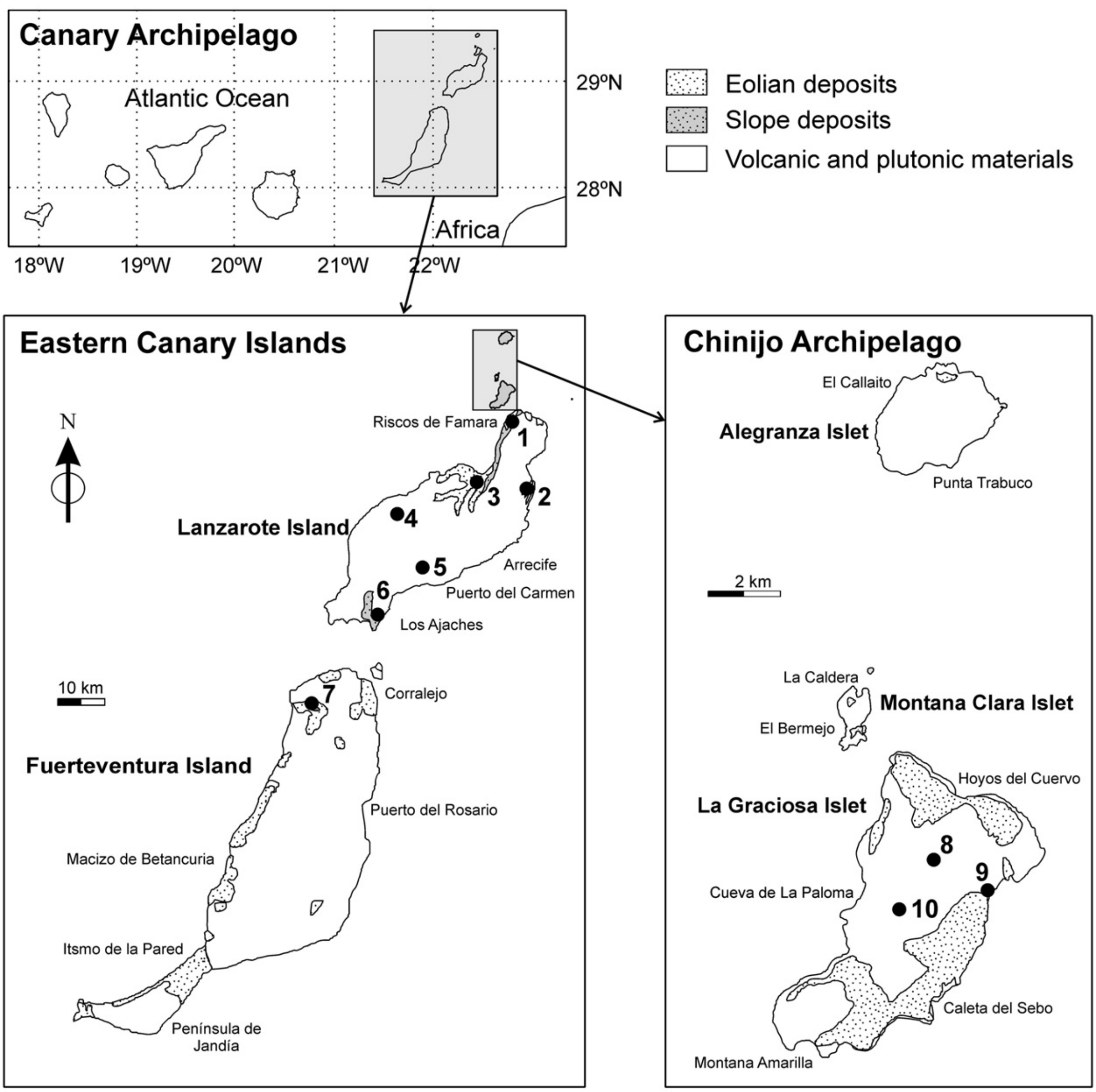

Fig. 1. Geographical location of Fuerteventura, Lanzarote and La Graciosa Islands, with sampling localities indicated by solid dots (modified after Ortiz et al., 2006). Localities are as follows: (1) Famara, (2) Mala, (3) Tao, (4) Tinajo, (5) Mácher, (6) Los Ajaches, (7) Montaña de la Costilla, (8) Agujas Grandes, (9) Morros Negros, (10) Montaña del Mojón.

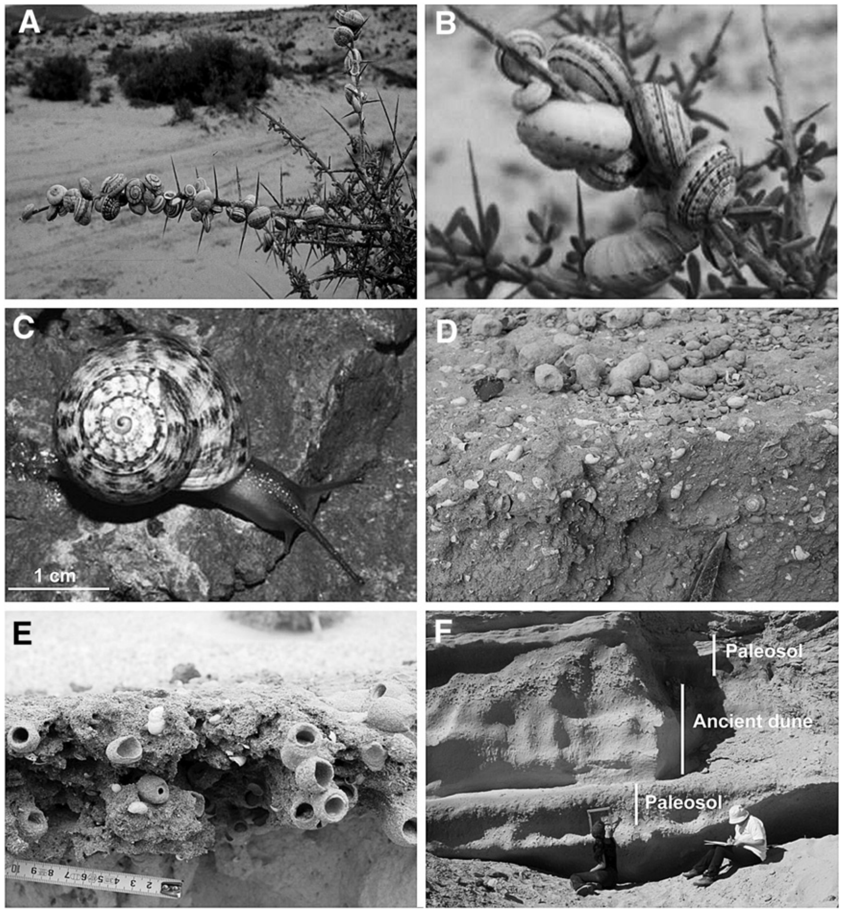

Fig. 2. (A–C) Photographs of multiple living individuals of the helicid *Theba geminata* from the north part of Fuerteventura Island. (D–F) Field photographs of Late Quaternary eolianite deposits (i.e., alternated ancient eolian dunes and paleosols) with abundant and well-preserved land snail shells (including *T. geminata*) from (D) Fuerteventura, (E) La Graciosa, and (F) Lanzarote islands.

species known from the islands are believed to represent C_4 photosynthesis pathway (Méndez et al., 1991; Rodríguez-Delgado et al., 1991; Méndez, 2001). However, the majority of the photosynthetic interpretations of plants have been based so far on ecophysiological studies without stable isotope data.

Dense populations of land snails occur in direct associations with xerophytic plants (i.e., plants adapted to a limited supply of water and generally arid conditions), which are abundant in coastal dune areas and characterized by spiny morphologies. Typically, snails aggregate on plants during warmer parts of the day (Fig. 2A–B), where spiny morphology serves as protection and camouflage against predators, especially birds (field observations, 2003 and 2004).

3. Methodology

A total of 120 samples have been selected and processed for stable isotope analyses (Table 1): 17 snail shell samples from live-collected specimens of *T. geminata* (Fig. 2A–C), 17 samples of snail soft tissues from live-collected specimens of *T. geminata,* 10 samples of carbonate-rich sediments (including 3 bioclastic sand samples and 7 carbonate soil samples), 69 samples of plants, and 7 samples of rain water. The sampled localities are indicated on Fig. 1, and their geographical coordinates and elevation are summarized in Table 1.The stable isotope measurements have been carried out in the Stable Isotope Laboratory of the Estación Experimental del Zaidín (CSIC-Granada, Spain).

3.1. Systematic sampling and selection of species

The samples were randomly collected from ten localities (Fig. 1; Table 1) on three islands (Fuerteventura, Lanzarote and La Graciosa) of the Canary Archipelago, always below 300 masl (Table 1). All the samples were collected by the paleontology group of La Laguna University over a period of 3 years (2002–2004).

We have focused collecting efforts on *T. geminata* because this species is the most abundant and widespread land snail in the eastern Canary Islands (Gittenberger and Ripken, 1987; Gittenberger et al., 1992) and also occurs throughout the upper Quaternary eolian successions in the study area (Yanes et al., 2004, 2007, in press; Ortiz et al., 2006). *T. geminata* (Fig. 2A–F) is especially common in coastal areas below 300 masl and lives in coastally located (ocean influenced) arid-to-semi-arid environments. Its populations are typically found as concentrations in

Table 1
Summary of the 10 sampled localities, including information about the geographic coordinates, altitude (in masl) and the type and number of samples collected

Island	Sampling site	Latitude	Longitude	Elevation (masl)	# rain water samples	# plant samples	# carbonate sediment samples	# of living land snails (shell+soft tissue)
La Graciosa	Morros Negros	29°15′22″ N	13°29′16″ W	10		32		5
La Graciosa	Aguja Grande	29°15′10″ N	13°30′15″ W	200		28		2
La Graciosa	Montaña del Mojón	29°14′40″ N	13°31′10″ W	26		9		
Lanzarote	Tinajo	29°04′00″ N	13°40′47″ W	190	2			
Lanzarote	Macher	28°56′40″ N	13°41′15″ W	200	2			
Lanzarote	Tao	29°02′36″ N	13°36′51″ W	247	3			3
Lanzarote	Mala	29°05′43″ N	13°27′38″ W	25			10	
Lanzarote	Famara	29°07′00″ N	13°32′21″ W	100				2
Lanzarote	Los Ajaches	28°51′48″ N	13°46′20″ W	150				1
Fuerteventura	Montaña Costilla	28°41′16’’ N	13°58′09″ W	55				4

bushes (Fig. 2A–B). Our direct field observations suggest that *T. geminata* is active primarily at night, when the coolest and wettest conditions occur. *T. geminata* feeds primarily on higher plants, including grasses and bushes (direct field observations, 2004). In addition, based on data available for the congeneric species *Theba pisana* (e.g., Cowie, 1984), *T. geminata* is likely to have an annual to biennial cycle life.

T. geminata is a small helicid with globose-spherical shape (Fig. 2A–C). Although this endemic species is restricted to the Canary Archipelago only, its genus is widespread represented in the Mediterranean area, Western Europe and Northern Africa (Kerney and Cameron, 1979).

Adult snail specimens were live-collected from their natural habitats at the ten localities (Fig. 1; Table 1). All plant species noted at some collecting sites (24 identified species total) were also sampled. In addition, bulk samples of carbonate-rich sediments (i.e., bioclastic sands and carbonate soils) and rain water (collected at the time of rain event) were acquired at some sites (Fig. 1; Table 1).

It should be noted that the studied sites, because of their coastal and low-altitude location, do not display any notable seasonality in climate (i.e., temperature, sun light, humidity, and precipitation rates are all relatively constant through the year). Accordingly, the local vegetation also does not change notably on subannual-to-annual time scales. Similarly, the studied species of land snail display no noticeable shifts in their ecology, diet, or behavior: no hibernation periods have been noticed and the daily behavior (resting during the hottest ours of the day, plant foraging patterns, etc.) does not change substantially throughout the year. For all those reasons, the stable isotope signatures of individual shells are expected to be relatively homogenous throughout the shell (snails ingest the same vegetation and water under the relatively constant climatic conditions throughout the year). Consequently, given that no significant shifts in stable isotope signatures are expected within shells, and also given our goal of estimating the averaged environmental signal (and not a high-resolution seasonality), we have acquired for stable isotope analyses averaged aliquots obtained by grinding entire specimens. It should be also noted that the whole-shell sampling approach of a single or even multiple individuals represents a standard strategy used in stable isotope projects of land snails (e.g., Bonadonna and Leone, 1995; Bonadonna et al., 1999; Stott, 2002; Yates et al., 2002; Metref et al., 2003; Balakrishnan et al., 2005a,b; Zanchetta et al., 2005; but see Baldini et al., 2007), which makes our study directly comparable with the majority of similar studies done in other environmental settings previously.

3.2. Laboratory preparations and analysis

3.2.1. $^{18}O/^{16}O$ and $^{13}C/^{12}C$ ratios in aragonite shells, carbonate sediments and rain water

All isotopically analyzed carbonate samples (entire homogenized shells of adult individuals of *T. geminata* or aliquots of bioclastic sediments) were initially rinsed with deionized water, and then treated ultrasonically in deionized water to remove any adhering particles of organic matter or other debris. Subsequently, samples were dried in air at about 40–50 °C.

Table 2
Hydrogen and oxygen isotope values of meteoric water (MW) samples collected on the Lanzarote Island in February and March 2003

Sample ID	Sampling site	δD ‰ (V-SMOW)	δ^{18}O ‰ (V-SMOW)
MW_1	Tinajo	18	4.3
MW_2	Tinajo	−3	−1.2
MW_3	Macher	2	−0.7
MW_4	Macher	17	1.6
MW_5	Tao	−7	−1.9
MW_6	Tao	−6	−2.1
MW_7	Tao	−11	−2.6
	Mean	−5	−2.0
	SD	5	1.0

The mean and standard deviation (SD) values were computed excluding samples MW 1 and MW 4, which were collected between 10 and 20 h after the rain and had been affected by evaporation processes.

The possible organic matter adhered to the shell (i.e., remains of soft body and/or part of the periostracum) and to the carbonate sediments was removed by placing the sample in a bath of 5% sodium hypochlorite for 48 h (e.g., Stott, 2002). Then, the carbonate samples were rinsed with deionised water and dried in air at 40–50 °C.

The carbonates were then converted to CO_2 gas by reacting for 24 h in vacuum with 100% H_3PO_4 at 25 °C. The CO_2 samples were analyzed isotopically on a Gas Bench II connected to IRMS Finnigan Delta Plus XL mass spectrometer. Values were calibrated against the international standard NBS-18 (Carbonatite) and NBS-19 (Limestone) (National Bureau of Standards). The precision of analyses based on the measurement of multiple standard aliquots during the run of samples is generally better than 0.1‰ for both carbon and oxygen isotopes. The δ values are defined as:

$$\delta^{13}\mathrm{C} \text{ or } \delta^{18}\mathrm{O} = \left[\left(R_{\mathrm{sample}}/R_{\mathrm{standard}}\right) - 1\right] \times 1000 \text{ (in ‰ units)}$$

where $R = {}^{13}\mathrm{C}/{}^{12}\mathrm{C}$ or ${}^{18}\mathrm{O}/{}^{16}\mathrm{O}$ ratios. Carbon and oxygen isotope values of carbonate samples are reported relative to the international standard Vienna-Pee Dee Belemnite (V-PDB).

The rain water samples were flushed with 0.4% CO_2 in He. After adding a small aliquot of 100% H_3PO_4 acid, samples were left to equilibrate at 25 °C temperature for 48 h before being analyzed. Samples were analyzed on a Gas Bench II connected to an IRMS Finnigan Delta Plus XL mass spectrometer. Oxygen isotope values of meteoric waters are reported relative to the international standard Vienna-Standard Mean Ocean Water (V-SMOW). Precision was ±0.1‰ based on the reproducibility of multiple measurements of IAEA-OH-1 and IAEA-OH-2 international water standards among samples.

3.2.2. ${}^{13}C/{}^{12}C$ ratios in plants and soft tissues of land snails

Snail soft tissues and plants were dehydrated in air at about 40–50 °C and then homogenized and converted to powder, so each analyzed aliquot represented an entire-averaged (=homogenized) specimen. For each sample, a small aliquot (~5 mg) of the organic matter was placed into a tin capsule and weighed. Then, the capsule was crimped and analyzed on a Carlo Erba Elemental Analyzer (NA1500), where combustion (oxidation and then reduction) of the sample occurred. The CO_2 produced after combustion was analyzed using the IRMS Finnigan Delta Plus XL mass spectrometer. Values are reported in ‰ relative to the international standard Vienna-Pee Dee Belemnite (V-PDB). Multiple aliquots of the international standards IAEA-C-3 (cellulose) and IAEA-CH-6 (sucrose) were analyzed as a check on the analytical precision throughout the analyses, which was ±0.1‰ for δ^{13}C in plants and soft tissues of land snails.

3.2.3. ${}^{2}H/{}^{1}H$ ratios in rain water

Isotopic rain water data were collected between February and March of 2003 at three localities on the Lanzarote Island (Fig. 1; Table 1): Tinajo, Macher and Tao. δD of precipitation was measured by a TC/EA connected to IRMS Finnigan Delta Plus XL mass spectrometer. Analytical precision for the procedure (i.e., reproducibility of multiple of IAEA-OH-1 and IAEA-OH-2 international water standards analyzed among samples) was ±1.5‰.

The isotopic compositions of precipitation were simulated by the Rayleigh-type isotope circulation model and the isotopic fractionation between H and O is proportional, following the Meteoric Water Line, where $\delta\mathrm{D} = 8\ \delta^{18}\mathrm{O} + 10$ (Craig, 1961). Values are reported in ‰ relative to the international standard Vienna-Standard Mean Ocean Water (V-SMOW).

4. Results and discussion

4.1. Isotopic composition of the rain water

The rain water values from Lanzarote island range between −2.6‰ and +4.3‰ (V-SMOW) (Table 2). The majority of the samples plot linearly along the Meteoric Water Line (MWL) (Fig. 3A). Only the two samples collected between 10 and 20 h after the precipitation event (MW-1 and MW-4) displayed additional fractionation due to evaporation (Dansgaard, 1964). For that reason, these two samples have not been used when preliminarily estimating the mean stable isotope value of the rain water in the study area.

The small overall number of rain water samples analyzed (only 5 reliable samples out of the 7 analyzed) is due to the rarity of rain events throughout the duration of the project, as expected given the arid-to-semi-arid climate of the eastern Canary Islands (Dorta, 2005). However, the consistent pattern obtained from samples collected right after rain events makes it possible to provide a preliminary evaluation of the isotopic composition of the rain water in the study area.

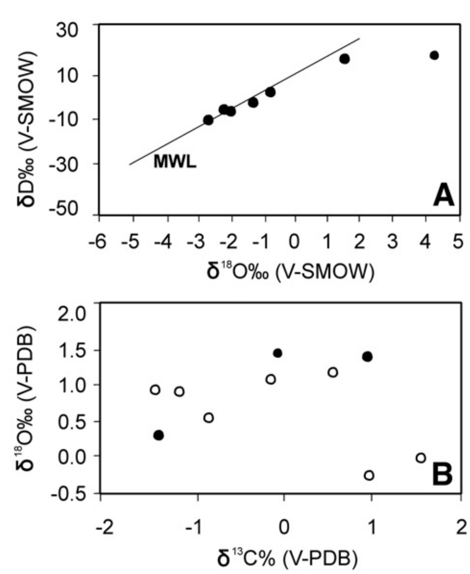

Fig. 3. (A) Isotopic composition of rain water from the Lanzarote Island collected in February–March of 2003. The Meteoric World Line (MWL) is based on the equation of Craig (1961) for meteoric waters. (B) Bivariate plot of the oxygen isotopic composition graphed against the carbon isotopic composition of the local carbonate sediment samples from Mala, Lanzarote Island. Black circles represent bioclastic sand carbonates and white circles represent soil carbonates.

Table 3
Carbon isotopic composition of 24 plant species from La Graciosa Islet

Plant species	n	$\delta^{13}C$ ‰ (V-PDB)		Plant type	Reference
		Mean	SD		
Atriplex glauca L.	3	−14.5	0.9	C_4	Jiménez et al. (1983)*
Beta sp.	1	−29.0		C_3	This paper
Carrichtera annua (L.) DC.	4	−25.6	1.8	C_3	This paper
Chenoleoides tomentosa (Lowe) Botsch.	3	−14.4	0.9	C_4	Jiménez et al. (1983)*
Cuscuta planiflora Ten.	1	−25.8		C_3	This paper
Echium lancerottense Lems & Holzapfel	2	−25.9	0.4	C_3	Méndez (2001)*
Euphorbia regis-jubae Webb & Berthel.	2	−24.6	0.0	C_3	This paper
Graminaceae	1	−25.7		C_3	This paper
Ifloga spicata (Forssk.) Sch. Bip.	4	−22.5	1.5	C_3	This paper
Cakile maritima Scop.	1	−24.5		C_3	This paper
Launaea arborescens (Batt.) Murb.	3	−26.0	1.6	C_3	This paper
Lycium intricatum Boiss.	1	−13.0		C_4	This paper
Limonium papillatum (Webb & Berthel.) Kuntze	1	−25.1		C_3	This paper
Mesembryanthemum crystallinum L.	2	−17.0	1.1	CAM	Willert et al. (1977)*
Mesembryanthemum nodiflorum L.	6	−18.8	2.0	CAM	Morales et al. (1982)*
Nicotiana glauca R. C. Graham	1	−23.8		C_3	Méndez (2001)*
Ononis sp.	1	−25.0		C_3	This paper
Plantago sp.	4	−25.2	2.2	CAM	Méndez (2001)*
Polycarpaea nivea (Aiton) Webb	9	−24.3	1.3	C_3	Méndez (2001)*
Reseda lancerotae Webb & Berthel. *ex* Delile	1	−27.0		C_3	Méndez (2001)*
Salsola vermiculata L.	3	−13.8	0.5	C_4	Echevarria et al. (1988)*
Spergularia sp.	3	−24.5	1.5	C_3	This paper
Suaeda vera Forssk. ex J. F. Gmel	6	−20.7	4.2	CAM	This paper
Suaeda mollis Delile.	6	−14.4	0.9	C_4	This paper

Symbols: n—number of individuals analyzed; SD—standard deviation. The previous studies about the photosynthesis of these species are indicated as well. Asterisks mark studies based on ecophysiological analysis (without stable isotope data).

These preliminary estimates of mean stable isotope values of the rain water are −5±5‰ (V-SMOW) for δD and −2±1‰ (V-SMOW) for δ^{18}O, respectively. The values are consistent with the oceanic and low-latitude setting of the islands as suggested by Rozanski et al. (1993). That is, in the case of near equatorial oceanic location, most/all clouds are derived relatively locally from nearby ocean water masses. Consequently, the oxygen isotopic composition of rain water in such settings usually tracks closely the composition of the surrounding oceanic water masses (Rozanski et al., 1993).

4.2. Isotopic composition of the local vegetation

The carbon isotope values vary greatly across sampled plant species (Table 3; see also Appendix A): from −29.0‰ up to −13.0‰ δ^{13}C (V-PDB), indicating heterogeneous vegetation

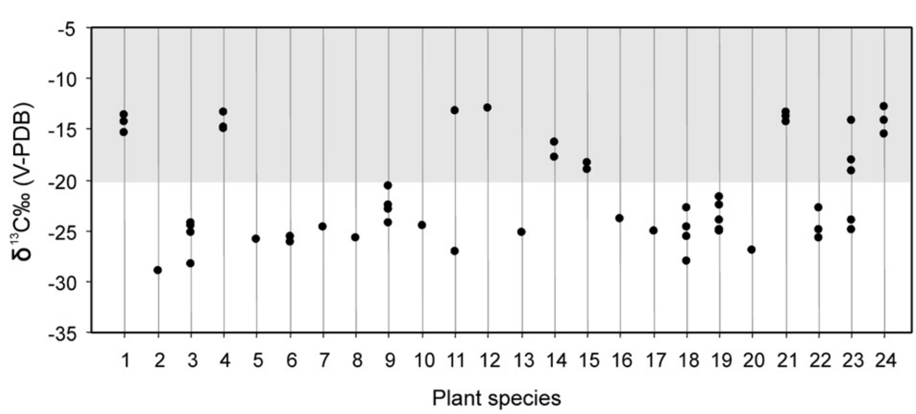

Fig. 4. Isotopic δ^{13}C composition of plant species identified at the sampling sites on La Graciosa Islet. The grey band represents the values of δ^{13}C expected for C_4-type plants, generally between −10‰ and −14‰ (V-PDB). Plants with the most negative values of δ^{13}C are interpreted as C_3-type vegetation, which typically displays δ^{13}C values between −21‰ to −35‰ (V-PDB). The plant species are as follows: (1) *Atriplex glauca,* (2) *Beta* sp., (3) *Carrichtera annua,* (4) *Chenoleoides tomentosa,* (5) *Cuscuta planiflora,* (6) *Echium lancerottense,* (7) *Euphorbia regis-jubae,* (8) *Gramineacea*, (9) *Ifloga spicata,* (10) *Cakile maritima,* (11) *Launaea arborescens,* (12) *Lycium intricatum*, (13) *Limonium papillatum*, (14) *Mesembryanthemum crystallinum*, (15) *Mesembryanthemum nodiflorum*, (16) *Nicotiana glauca*, (17) *Ononis* sp., (18) *Plantago* sp., (19) *Polycarpaea nivea*, (20) *Reseda lancerotae*, (21*) Salsola vermiculata*, (22) *Spergularia* sp., (23) *Suaeda vera*, and (24) *Suaeda mollis*.

Table 4
Carbon stable isotope values of carbonate-rich sediments (i.e., bioclastic sands and carbonate soils) collected in Lanzarote Island

Sample	Sampling site	Sediment-type	$\delta^{18}O$ ‰ (V-PDB)	$\delta^{13}C$ ‰ (V-PDB)
OCS_1	Mala	Bioclastic sands	1.4	0.0
OCS_2	Mala	Bioclastic sands	1.4	0.9
OCS_3	Mala	Bioclastic sands	0.3	−1.4
OCS_4	Mala	Carbonate soils	0.9	−1.1
OCS_5	Mala	Carbonate soils	0.9	−1.4
OCS_6	Mala	Carbonate soils	1.2	0.6
OCS_7	Mala	Carbonate soils	1.1	−0.1
OCS_8	Mala	Carbonate soils	0.6	−0.8
OCS_9	Mala	Carbonate soils	0.0	1.6
OCS_10	Mala	Carbonate soils	−0.3	1.0
		Mean	0.8	−0.1
		SD	0.6	1.1

Symbols: SD—standard deviation.

encompassing both C_3 and C_4 type plants (Table 3; Fig. 4). Out of the 24 sampled species, at least five have values ($\delta^{13}C$ between −14.5‰ and −13.0‰ (V-PDB), with a mean value of −14.0‰ [V-PDB]), consistent with C_4 photosynthesis. Fifteen species show more negative values ($\delta^{13}C$ between −29.0‰ and −23.8‰ (V-PDB), with a mean value of −25.5‰ [V-PDB]), consistent with C_3 photosynthesis pathway. At least four plant species (*Mesembryanthemum crystallinum*, *M. nodiflorum*, *Plantago* sp. and *Suaeda vera*) show a notable variation in their carbon isotope composition (standard deviation generally higher than 2‰ $\delta^{13}C$), and a mean $\delta^{13}C$ values close to −20‰ (ranging from −22.5‰ to −17‰ [V-PDB]), the value range relatively far from the typical average carbon stable isotope value for C_4 (−12‰ [V-PDB]) and C_3 (−27‰ [V-PDB]) plants (e.g., Farquhar et al., 1989). Because of that, we classified them as plants that follow CAM photosynthesis pathway (Table 3; Fig. 4; see also Appendix A).

The relatively variable $\delta^{13}C$ signatures observed across samples representing the same species of plants and a specific photosynthesis pathway (C_4 or C_3), have been attributed previously to "Water-Use Efficiency " (WUE) or hydrologic stress (i.e., ecophysiological measure quantifying the ratio of net CO_2 uptake from the atmosphere during photosynthesis versus net water loss; e.g., Farquhar et al., 1982, 1989). Thus, the concentration of CO_2 inside the plant (and consequently, the carbon isotope discrimination) depends on the rate of photosynthesis and the opening of the stomatal pores. The plants exposed to water stress (dryness periods, prolonged sun exposure, sandy [dry] soils, etc.) protect themselves from evapo-transpiration problems by closing their stomatal pores. This behavior prevents diffusion of CO_2 into the leaf. Consequently, all available CO_2 is used during photosynthesis making it impossible for Rubisco to discriminate against $^{13}CO_2$. Therefore, the plant material with closed stomatal pores (during dryness periods) will display more positive values of carbon isotopes than the plant material with open stomatal pores (during periods when water stress is absent) (Farquhar et al., 1982, 1989).

Differences in water stress across individual plants, induced by local habitat variation in sun exposure, rain water access, and other parameters, may thus translate into intra-specific variability in $\delta^{13}C$ signatures. High variation in the $\delta^{13}C$ values observed for some species in this study (i.e., *Carrichtera annua*, with a standard deviation of ±1.83‰ in $\delta^{13}C$ values) may be due to such differential water stress.

While the photosynthesis of the eastern Canarian vegetation was studied previously by other authors (e.g., Willert et al., 1977; Morales et al., 1982; Jiménez et al., 1983; Tenhunen et al., 1983; Echevarria et al., 1988; Méndez, 2001), the majority of these studies were mostly based on ecophysiological evaluation. Our results, which allow us to independently classify plant species using stable isotopes, are consistent with those obtained in ecophysiological studies (Table 3). In addition, we provide a metabolic evaluation for 14 plant species that, as far as we know, have not been classified previously (Table 3).

In summary, the vegetation of the land snail habitat is heterogeneous, including ~21% of C_4-type plants, ~62% of C_3-type plants and ~17% of CAM plants (Table 3; Fig. 4; see also Appendix A). The simultaneous presence of C_3, C_4 and CAM plants translates into the vegetative landscape that provides herbivores with a highly heterogeneous carbon isotope menu. In addition, a secondary isotopic variability, induced by water stress, appears to affect at least some of the species.

4.3. Isotopic composition of local substrate carbonates

Samples of carbonate-rich sediments (n=10) collected in Mala (Fig. 1; Table 1) ranged from −0.3‰ to +1.4‰ $\delta^{18}O$ (V-PDB), with a mean of +0.8±0.6‰ $\delta^{18}O$ (V-PDB) (Table 4; Fig. 3B). The relatively narrow range of $\delta^{18}O$ values of these grains, which primarily represent bioclastic sands (n=3) and carbonate soils (n=7), is not surprising given the low climatic seasonality of the Canary Islands and the oxygen isotope composition of the open oceanic waters surrounding the archipelago. The carbon isotope values also display a narrow range of values, ranging from −1.4‰ to +1.6‰ $\delta^{13}C$ (V-PDB) and averaging −0.1±1.1‰ $\delta^{13}C$ (V-PDB) (Table 4).

Although the analyzed samples represent two distinct substrate types: eolian dunes (n=3) and carbonate soils (n=7), neither $\delta^{13}C$ nor $\delta^{18}O$ appear to differ notably between the two settings (Fig. 3B). Consequently, isotopic estimates based on the full dataset pooled across both substrates (n=10; Table 4) are considered here to be the best empirical proxy for

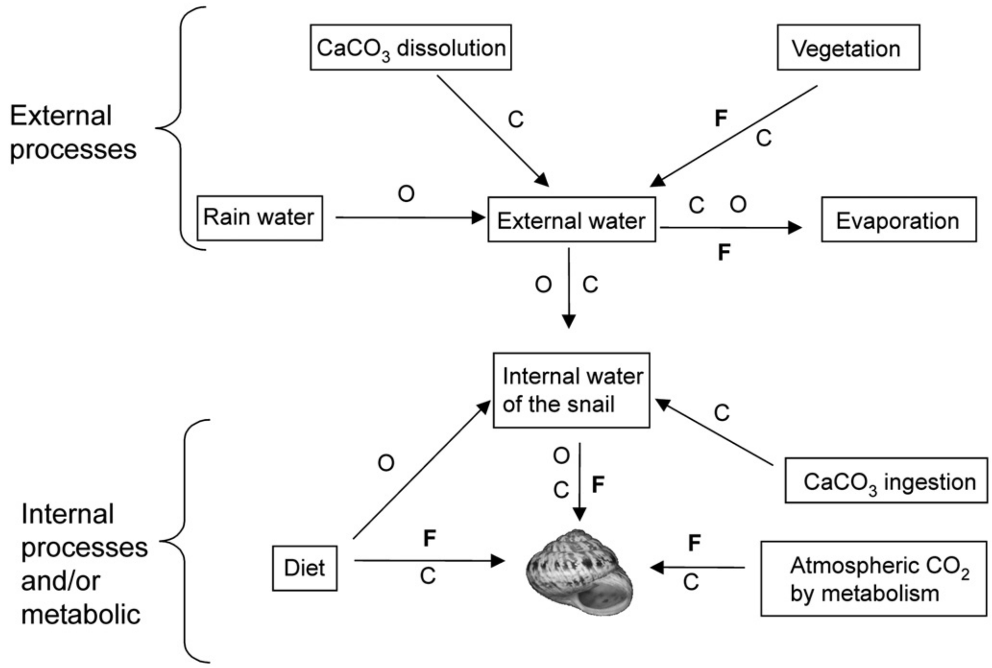

Fig. 5. A flowchart summarizing the major sources of carbon and oxygen that can contribute to the stable isotope composition of the land snail shells. The letter "F" indicates those processes during which a fractionation of oxygen (O) or carbon (C) occurs (modified after Yates et al., 2002).

the isotopic composition of the carbonate sediments in the study area. These estimates are used below (see the mass balance equation in Section 4.4.3) to assess the effect of foreign carbonate (ingested by snails during their growing periods to aid shell secretion or accidentally during feeding) on the $\delta^{13}C$ of *T. geminata* shells.

4.4. Isotopic composition of living land snails

The variation in $\delta^{13}C$ and $\delta^{18}O$ values in land snail shells could be related to several external factors (Fig. 5) associated with the environmental conditions, diet type or soil type. The potential role of these external factors in the specific context of the study area is explored in detail below.

4.4.1. $\delta^{18}O$ of aragonite shells and its relation to local rain water

Aragonite shells of the land snail *T. geminata* varied over a narrow range of $\delta^{18}O$ values: from −0.3‰ to +2.5‰ (V-PDB) (Table 5). This restricted range is remarkable when compared with the much wider spread of oxygen isotope values reported for shell carbonates in natural settings globally—previous studies of modern land snails from various regions yielded values ranging from −11.7‰ to +4.5‰ $\delta^{18}O$ (V-PDB)

Table 5
Carbon isotope values of the soft tissue and carbon and oxygen isotope values of shells of 17 individuals of the gastropod *Theba geminata* live-collected on La Graciosa, Lanzarote and Fuerteventura islands

Sample ID	Island	Sampling site	Soft tissue	Aragonite shell	
			$\delta^{13}C$ ‰ (V-PDB)	$\delta^{13}C$ ‰ (V-PDB)	$\delta^{18}O$ ‰ (V-PDB)
LS_1	La Graciosa	Morros Negros	−23.9	−4.4	1.9
LS_2	La Graciosa	Morros Negros	−22.7	−3.6	1.5
LS_3	La Graciosa	Morros Negros	−16.9	−3.5	0.1
LS_4	La Graciosa	Morros Negros	−12.0	1.7	0.6
LS_5	La Graciosa	Morros Negros	−17.3	−4.3	0.6
LS_6	La Graciosa	Aguja Grande	−18.2	−4.6	0.8
LS_7	La Graciosa	Aguja Grande	−19.3	−1.7	1.4
LS_8	Lanzarote	Famara	−27.2	−8.0	1.0
LS_9	Lanzarote	Famara	−19.0	−4.4	1.6
LS_10	Lanzarote	Tao	−22.8	−7.2	2.5
LS _11	Lanzarote	Tao	−24.2	−7.7	−0.3
LS _12	Lanzarote	Tao	−23.1	−7.6	0.2
LS_13	Lanzarote	Los Ajaches	−15.8	−4.6	0.7
LS _14	Fuerteventura	Montaña Costilla	−21.6	−6.0	1.3
LS_15	Fuerteventura	Montaña Costilla	−20.5	−6.7	0.9
LS_16	Fuerteventura	Montaña Costilla	−23.5	−6.1	0.0
LS_17	Fuerteventura	Montaña Costilla	−25.8	−9.4	0.5

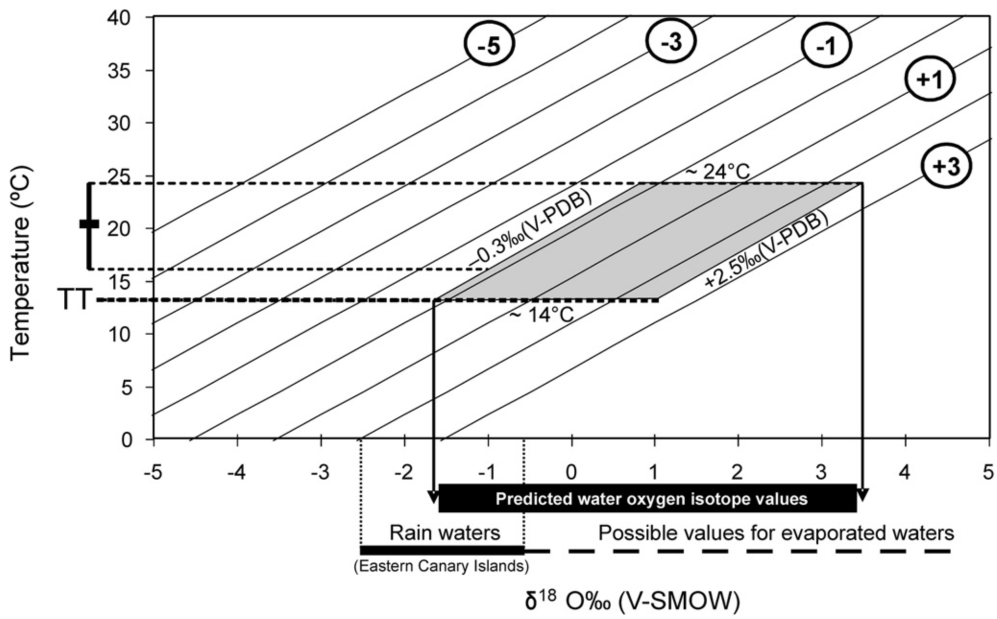

Fig. 6. Hypothetical range of oxygen isotopic composition values for aragonitic shells of land snail precipitated in equilibrium with rain water at a given temperature. The diagonal solid lines indicate theoretical δ^{18}O values of shells in equilibrium with waters with different δ^{18}O values and different temperatures, using the equation of Grossman and Ku (1986). The grey diamond area represents the observed range of values of δ^{18}O in *Theba geminata* shells and the possible range of temperatures for the eastern Canary Islands. The black rectangle along the *x*-axis represents the predicted range of δ^{18}O values expected for waters possible over the possible range of temperature and δ^{18}O aragonite shell values. Below the black rectangle along *x*-axis (predicted range of δ^{18}O water values), the observed δ^{18}O values of rain waters from the study area are plotted as a continuous black line. The prolonged dashed line indicates possible values of δ^{18}O for evaporated (fractionated) waters. Note that the most negative δ^{18}O aragonite values are closest to the observed δ^{18}O rain water values. Abbreviations: TT—mean temperature during a storm event.

(Balakrishnan et al., 2005a and references therein). The notable variability observed globally reflects a combined effect of latitudinal variation in the isotopic composition of the rain water, seasonal variations (especially pronounced for continental settings), and various local environmental effects (Rozanski et al., 1993). However, the range of values reported here is remarkably narrow even when compared to variation observed within single regions (but see Baldini et al., 2007). For example, snail shells from the Southern Great Plains (USA) sampled by Goodfriend and Ellis (2002) varied in oxygen isotope values from −5‰ to +0.5‰ (V-PDB). Similarly, a study performed in coastal settings of Italian Peninsula by Zanchetta et al. (2005) documented a much wider range of oxygen isotope values (from −3.3‰ to +1.7‰ [V-PDB]) than reported here.

The much tighter clustering of δ^{18}O values observed here is consistent with the suppressed seasonality so characteristic of the low-latitude oceanic islands (see also Baldini et al., 2007) such as the Canary Archipelago. This pattern is also reassuring in supporting recent studies relating oxygen isotopic composition of land snail shells to that of local precipitation (e.g., Goodfriend and Ellis, 2002; Zanchetta et al., 2005). And while some pioneering efforts to relate oxygen isotopic composition of snail shells and local precipitation had failed (e.g., Goodfriend and Magaritz, 1987), several more recent studies showed that δ^{18}O isotopes of snail shells may be related to local meteoric waters (e.g., Goodfriend and Ellis, 2002; Balakrishnan and Yapp, 2004; Zanchetta et al., 2005).

Indeed, some type of relation can also be anticipated theoretically. Balakrishnan and Yapp (2004) reviewed briefly land snail physiology to evaluate the possible vital effects that occur during their life cycle. Land snails are susceptible to dehydration by loosing water via evaporation from the integument. The extent of water loss depends primarily on the relative humidity of the ambient environment. Consequently, land snails typically rest during daytime and forage at night. They tend to be most active during and immediately after rain events. Because local precipitation is the primary source of water for snails, it seems reasonable to assume that snails growth (secretion of the shell) takes place usually at times of relatively warm and moist conditions when snails tend to be active (Balakrishnan and Yapp, 2004). Consequently, oxygen isotopic composition of the shell may potentially record that of meteoric water at the time of precipitation (note: this prediction assumes that fractionation takes place from water to shell, as has been argued by others [e.g., Goodfriend and Ellis, 2002; Balakrishnan and Yapp, 2004; Zanchetta et al., 2005]).

This anticipated relation has been also supported empirically in a recent study of Zanchetta et al. (2005). Those authors showed correlatives between the oxygen stable isotopic composition of the local rain water and snail shells collected together from various terrestrial habitats around the Italian Peninsula.

We have constructed a hypothetical model that includes oxygen isotopic composition of land snail aragonite shells in equilibrium with water of a given isotopic composition at a given temperature (Fig. 6). Thus, three variables are included in this model: (1) The hypothetical oxygen isotopic compositions of aragonite shells, which are represented by solid diagonal lines and range from −5 to +3‰ (V-PDB) on Fig. 6. (2) A possible range of δ^{18}O values of water (from −5 to +5‰ vs. V-SMOW) represented by the *x*-axis on Fig. 6. (3) A large range of possible temperatures (from 0 to 40 °C), displayed as *y*-axis on Fig. 6. To construct this model we applied these variables to the equation proposed by Grossman and Ku (1986): $[T(°C) = 19.7 - 4.34 (\delta^{18}O_{aragonite} - \delta^{18}O_{water})]$ for the aragonite–water system.

Thanks to the fact that the relationships among these three variables (=temperature, $\delta^{18}O_{aragonite}$ and $\delta^{18}O_{water}$) are well understood (Grossman and Ku, 1986), the constructed hypothetical model can be useful to predict expected values in paleoclimatic and paleoenvironmental studies. To test the utility of this hypothetical model, we use below the empirical data from the eastern Canary Islands presented in this study.

The continuous black line along the *y*-axis (Fig. 6) indicates the possible range of temperature values observed for the eastern Canary Islands (between 14 and 24 °C, with an annual mean value of 20 °C; based on Dorta, 2005). The grey diamond inside the plot (Fig. 6) indicates the $\delta^{18}O$ range values extracted from aragonite shells of *T. geminata* specimens (based on 17 individuals from three eastern islands). Consequently, by knowing the temperature range in the study area and the observed range of $\delta^{18}O$ measured for aragonitic shells; we can predict the expected $\delta^{18}O$ values of waters at the time when the snails precipitated their carbonate shell. This prediction is shown as a black rectangle along the *x*-axis on Fig. 6.

We can test the reliability of the predicted $\delta^{18}O$ results of waters (based on the expected temperature range and the observed $\delta^{18}O$ values of snail shells) by comparing those predications (black rectangle along *x*-axis on Fig. 6) against the observed oxygen isotopic values measured for the rain water samples collected from the study area (continuous black line along the *x*-axis of Fig. 6). The dashed extension of this black line represents possible values of evaporated (fractionated) waters. As is clear from the overlap between the predicted values (black rectangle) and the observed values (solid black line), the model constrained by shell $\delta^{18}O$ and temperature provides a partly correct prediction of the observed range of the $\delta^{18}O$ values of rain water (Fig. 6). Specifically, the predicted isotopic composition of the rain water was at least 1‰ more positive than the observed values (compare the continuous part of the black line against the black rectangle, both plotted along the *x*-axis on Fig. 6). This is consistent with previous studies of snail shells from other regions, which showed a notable positive shift in shell $\delta^{18}O$ (between 2 and 8 ‰) when compared to $\delta^{18}O$ of local rain water (e.g., Lécolle, 1985; Goodfriend and Magaritz, 1987).

Based on the hypothetical model we propose that the most negative values of $\delta^{18}O$ extracted from multiple aragonite shells collected in the same fossil horizon (=same age) should be used in paleoclimatic estimates because the most negative values of oxygen isotopes from the shell are closer to the oxygen isotope values of the local rain waters, while the most positive values seem to be associated with evaporated (fractionated) waters.

When the temperature is colder (i.e., between 14 and 16 °C), the precipitated hypothetical shell carbonates should record primarily the oxygen isotopic signal of the rain water, while when the temperature is warmer (i.e., between 16 and 24 °C), the shell carbonate should mainly record the evaporated water signal, with the higher (more positive) $\delta^{18}O$ values (Fig. 6).

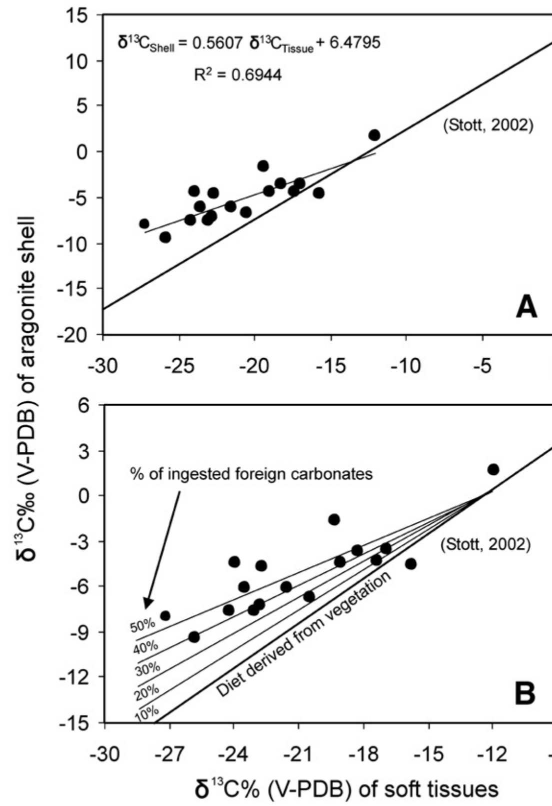

Fig. 7. (A) Bivariate plot of the isotopic composition of carbon graphed for aragonite shell versus soft tissue of live-collected specimens of *Theba geminata*. The straight solid line based on equation of Stott (2002) for the helicid gastropod *Helix aspersa* cultured in the laboratory setting without access to carbonate substrate. (B) Isotopic Mass Balance correcting for the ingestion of foreign carbonates (bioclastic sands in the case of the study area) that could have contributed to the shell aragonite. The lines marking different % of foreign carbonate in the diet calculated using the mean isotopic value of the soil carbonates (Table 4) and the equation of Stott (2002) for snails with a carbonate-free diet. Symbols: R^2—coefficient of determination measuring the strength of association between two plotted variables.

Consequently, we can expect that the lower values of $\delta^{18}O$ in the aragonite shells should occur at times of greater availability of rain water. Shell samples close to −0.3‰ (V-PDB) may record rain water events (Fig. 6), while those more positive may correspond to shell growth at times between rain events, when more positive evaporated water and/or alternatively, plant water contributed to the snail diet (Dongman et al., 1974; Burk and Stuiver, 1981). The contribution of plant water, in particular, could explain the unexpected enrichment of up to several per mil of $\delta^{18}O$ observed in some of the sampled aragonite shells from the same locality in the study area.

4.4.2. $\delta^{13}C$ of aragonite shells and its relationship with the local vegetation

The carbon isotopic composition extracted from snail shell carbonates from the eastern Canary Islands ranges from −9.4‰ to +1.7‰ (V-PDB). The wide range of carbon isotope values suggests that the snails have followed a mix diet, consuming both C_3 and C_4 plant types, and probably some percentage of foreign carbonates from the surrounding sediments. This result implies that the helicid *T. geminata* is capable of consuming indiscriminately both plant types. The variation in $\delta^{13}C$ across specimens can thus provide a measure of metabolic heterogeneity in local vegetation.

All in all, the carbon isotope composition of the snail shell carbonate may be useful for reconstructing the composition of the local vegetation (C_3–C_4 plants). Because C_3 plants tend to dominate during wetter and colder conditions and C_4 plants tend to be more abundant during drier and warmer conditions, the carbon isotope signatures of snail shells may potentially provide environmental and climatic insights.

Previous studies of aragonite shells of land snails in natural settings have reported values ranging from −13.5‰ to +1.7‰ $\delta^{13}C$ (e.g., Balakrishnan et al., 2005a; Baldini et al., 2007). The most positive $\delta^{13}C$ values (+1.7‰ vs. V-PDB in this particular study) suggest that some of the individual snails consumed, almost exclusively, C_4-type plants (Table 5). These positive values point to persistent abundance of this plant type in local habitats, which is not surprising given the semi-arid environment of the study area.

4.4.3. $\delta^{13}C$ of body tissue snails and its relationship with the carbonate shell

The carbon isotope values of the body tissue ranged from −27.2‰ to −12.0‰ (V-PDB). Because the isotopic composition of snail body tissue tends to be enriched only slightly (by ~1‰) relative to the isotopic composition of ingested plants (DeNiro and Epstein, 1978; Stott, 2002), these highly variable results imply that individuals of *T. geminata* must have consumed variable amounts of C_3 and C_4 plant types. This interpretation is consistent with the interpretation of carbon isotope results of the shell carbonates outlined above.

However, when $\delta^{13}C$ values of the body tissue are compared to those observed for the shell carbonate, some of the shell carbonate values appear to be more positive than expected (Table 5). Calculations based on experimental laboratory data of Stott (2002) predict more negative values than those observed in our samples (Fig. 7A). This departure suggests that the snail diet may have also included inorganic and/or organic carbonates ingested by snails from the local substrate (e.g., Goodfriend, 1987). Radiocarbon analysis has shown that some land snail species can incorporate as much as 33% of such carbonates into their diet, especially in areas rich in carbonate substrates (Goodfriend and Hood, 1983; Goodfriend, 1999; Goodfriend and Ellis, 2002; Ortiz et al., 2006). Consequently, $\delta^{13}C$ of the fossil land snail shells from environments rich in carbonates (as is the case for the eastern Canary Islands), may overestimate the proportion of C_4 type plants in snail diet if not corrected for carbonate ingestion.

We can model the isotopic impact of variable carbonate ingestion using a “mass balance” equation (Fig. 7B):

$$\delta^{13}C_{\text{shell}} = \frac{\left(\delta^{13}C_{\text{shell from plant}} + \%C_{\text{consumed plant}}\right) + \left(\delta^{13}C_{\text{foreign carbonate}} + \%C_{\text{ingested carbonate}}\right)}{\left(\%C_{\text{consumed plant}}\right) + \left(\%C_{\text{ingested carbonate}}\right)}.$$

This “mass balance” equation can be empirically constrained using (1) the hypothetical value of the $\delta^{13}C$ of the shell carbonate derived exclusively from the consumed vegetation, using the following equation by Stott (2002) adjusted for an $R^2=1$: $\delta^{13}C_{\text{shell}}=\delta^{13}C_{\text{plant diet}}*0.94847+12.278$; and (2) the mean $\delta^{13}C$ value (−0.1‰ [V-PDB]) of the foreign carbonates from the dunes and soils in the eastern Canary Islands (Table 4).

This empirically constrained modeling suggests that most of the sampled specimens must have ingested notable amounts of foreign carbonates (between 20% and 40% of their diet) (Fig. 7B). These estimates are not unreasonable given (1) comparable estimates previously published based on radiocarbon analyses (see above) and (2) the ubiquitous presence of carbonate substrates (including bioclastic sands and soil carbonates) in the study area.

While carbonate ingestion undermines radiocarbon dating (e.g., Goodfriend, 1987), it is still possible to estimate the percentage of C_4-type plants consumed by land snails that inhabit carbonate-rich substrates. The plant diet of *T. geminata* can be identified using two different proxies: (1) isotope composition of the soft tissues; and (2) isotope composition of the aragonite shell. The fact the carbon isotope composition of both body tissues and shell carbonates show a very good correlation (Pearson correlation: $r=0.81$; $p=0.00009$; $n=17$) suggests that they record the same signal (Fig. 7A).

One caveat here is that it is possible that land snail specimens, which had been consuming C_4-type plants through most of their life, changed their diet to C_3-type plants short time before sampling (for example, this could be due to snail movement across heterogeneous vegetation or recent change in dominant plant type). Such a diet shift would change carbon isotopic composition of the soft tissue toward more negative values, but would not have altered the more positive $\delta^{13}C$ values of the shell carbonate. If the diet shift was from C_3-type plants to C_4-type plants, the resulting isotopic difference between the tissue and the shell could be misinterpreted as the signature of the foreign carbonate ingestion.

The carbon isotopic data extracted from both soft tissues and aragonite shells (Table 5) suggest that the land snail *T. geminata* consumes arbitrarily both C_3 and C_4 plants. This hypothesis has been postulated based on the great variability in carbon stable isotopes observed among the analyzed snails (Table 5; Fig. 7A). In addition, the carbon isotope variability among the analyzed snails greatly exceeds variability that could be generated by variable carbonate ingestion alone (see Fig. 7B). That is, individual snails vary notably in the proportion of C_3/C_4/CAM plants that they consumed: land snail with more negative values of $\delta^{13}C$ of shell have consumed more C_3-type plants, while those with less negative values have consumed mainly C_4 plants (e.g., Stott, 2002; Goodfriend and Ellis, 2002; Metref et al., 2003) and/or foreign carbonates (e.g., Goodfriend, 1987). The differences in carbon isotopic composition observed among shells most likely reflect local heterogeneity in vegetation, with different snails feeding on slightly different patches of plants. Consequently, the analysis of numerous fossil snail shells for carbon isotopes can provide insights into past habitats and their environmental characteristics. Changes in the averaged carbon isotopic composition of fossil shell samples observed throughout stratigraphic horizons (=age intervals) may be used to study changes in (or stability of) local vegetation through time, while variation in the carbon isotopes across specimens collected from the same stratigraphic unit (same age) may provide a measure of small-scale heterogeneities in plant distribution within the reconstructed habitat in a given time interval. This approach may be particularly powerful in carbonate-free settings, where interpretative ambiguities that may be induced by carbonate ingestion are minimized.

The Water Use Efficient (WUE) plants, which include C_4 and CAM-type vegetation, have been related to warm and sunny climates, where the night temperature never decreases below 8 °C (Teeri and Stowe, 1976). They have evolved in atmospheres with limited amounts of CO_2 (Sage, 2004), including C_4-type plants that appeared 12 Ma ago and became widespread as late as 6 Ma ago. Consequently, land snails with relatively more positive $\delta^{13}C$ values of shell and soft tissues (Table 5; Fig. 7A), likely had a higher proportion of C_4 plants in their diet, which in turn indicate more arid environments with a more severe water stress and lower density of the vegetation. Conversely, the relatively more negative values in $\delta^{13}C$ suggest greater amounts of C_3 plants, a more humid environment, less severe water stress, and higher density of vegetation (e.g., Goodfriend and Ellis, 2002). However, due to variation in shell diet among individual snails collected from the same present-day sites or the same fossil horizons, the reconstruction of dominant vegetation and associated climatic and environmental conditions should be based on a mean isotope value estimated using numerous specimens. Moreover, because soft tissue data are not accessible for fossil snails, the extant and variability of carbonate ingestion cannot be fully evaluated. Consequently, the interpretation should be limited to relative comparisons through time and space. For example, it may be reasonable to interpret a shift through time toward more positive *mean* values of carbon isotopes in snail shells as evidence of a temporal shift toward plant communities with a higher proportion of C_4 plants, which in turn implies drier conditions. However, it may be more debatable to argue numerically what was the proportion of C_4 plants in the community or how dry exactly the climate was.

5. Summary

1. The low-altitude vegetation of the eastern Canary Islands is heterogeneous ecophysiologically. It includes C3, C4, and CAM-type plants with $\delta^{13}C$ values ranging from −29.0‰ to −13.0‰ (V-PDB).
2. Out of 24 species found in sampled communities, five plant species (~21%) display $\delta^{13}C$ values in a range typifying C4-type plants: −14.5‰ and −13.0‰ (V-PDB). These species include *Atriplex glauca*, *Chenoleoides tomentosa*, *Salsola vermiculata*, *Lycium intricatum* and *Suaeda mollis*. The majority of $\delta^{13}C$ values fall between −29.0‰ and −23.8‰ (V-PDB) indicating that most of the plant species (~62% of the community) can be classified as C3-type plants. These include *Beta* sp., *Carrichtera annua*, *Cuscuta planiflora*, *Echium lancerottense*, *Euphorbia regis-jubae*, Graminaceae, *Ifloga spicata*, *Cakile maritima*, *Launaea arborescens*, *Limonium papillatum*, *Nicotiana glauca*, *Ononis* sp., *Polycarpaea nivea*, *Reseda lancerotae* and *Spergularia* sp. The remaining ~17% of species (*Mesembryanthemum crystallinum*, *M. nodiflorum*, *Plantago* sp. and *Suaeda vera*) likely present CAM photosynthesis pathway ($\delta^{13}C$ values fall between −22.5‰ and −17‰ [V-PDB] and display generally high standard deviation).
3. The first preliminary approximation of the stable isotope composition of rain water samples from Lanzarote Island (Canary Archipelago) is provided in this study. Oxygen isotope values range from −2.6‰ to −0.7‰ (V-SMOW), with a mean value of −2±1‰ (V-SMOW). Such a narrow range (close to oxygen isotope composition of sea water) is consistent with the low-latitude, oceanic setting of the study area. Preliminary hydrogen isotope results range between −11‰ and +2‰ (V-SMOW), with a mean of −5±5‰ (V-SMOW).
4. The carbonate-rich sediments (including bioclastic sands and carbonate soils) record a carbon isotopic composition that ranges from −1.4‰ to +1.6‰ (V-PDB), with a mean value of −0.1±1.1‰ (V-PDB). The stable isotopes of oxygen range from −0.3‰ to +1.5‰ (V-PDB), with a mean value of +0.8±0.6‰ (V-PDB).
5. Shells of the land snail *T. geminata* displayed a remarkably narrow range of oxygen isotope values: −0.3‰ to +2.5‰ $\delta^{18}O$ (V-PDB). This outcome is consistent with non-seasonal climatic patterns typical to low-latitude oceanic islands and the low-altitude coastal location of all studied sites.
6. The most negative $\delta^{18}O$ values in land snail shells are likely the most accurate records of local rain water composition, whereas the most positive ones may indicate either evaporation induced signatures or, alternatively, land snail diet rich in water-stressed plants. Consequently, we propose that the most negative values of $\delta^{18}O$, out of the range of values that may be recorded by multiple aragonite shells collected from within the same fossil horizon, should be used in paleoenvironmental and paleoclimatic reconstructions.
7. The most positive $\delta^{13}C$ values in modern land snail shells (+1.7‰ $\delta^{13}C$ [V-PDB]) indicate that some snail specimens in the Canary Islands must have consumed, nearly exclusively, C4-type plants.
8. A mass balance equation based on stable isotopes of carbon from carbonates (i.e., aragonite shell and carbonate sediments) indicates that the majority of the analyzed specimens have ingested between 20 and 40% of foreign carbonates (carbonate-rich sediments). Therefore, when used in radiocarbon dating, land snail specimens with the most negative $\delta^{13}C$ values should be targeted to minimize the bias induced by foreign (older) carbonates.
9. When data are averaged across all analyzed specimens to minimize diet variation due to location or behavioral variation, *T. geminata* specimens do not display a preferred diet between C3/C4 CAM-type plants in natural conditions. Thus, this helicid gastropod should be a useful tool for reconstructing paleoenvironments of the Canary Islands as long as multiple specimens are analyzed per each sampled fossil horizon.

Acknowledgements

This work has been supported by the projects BOS2003/00374, of the Spanish Ministerio de Ciencia y Tecnología and CGL2006-

01586/BTE, of the Spanish Ministerio de Educación y Ciencia (Spanish Government). We thank R. Barone, F. LaRoche and B. Rodríguez-Martín for help in plant species identifications, and M.L. Quesada, F. LaRoche, E. Martín-González, D. Liché and R.F. Armas for their help in the sample collection. Additional thanks go to M.S. Jiménez for useful comments about ecophysiological issues of the analyzed plants. We also thank A. Rodríguez-Sánchez for helping in laboratory analyses, and D. Huminicki, J.D. Rimstidt, C. S. Romanek and E. Reyes for constructive comments on the earlier drafts of this report. In addition, we thank two anonymous reviewers for detailed and constructive comments that greatly improved the quality of this manuscript.

Appendix A. δ^{13}C values of the plant tissue samples

Sample ID	Island	Sampling site	Species	δ^{13}C ‰ (V-PDB)
PL_1	La Graciosa	Aguja Grande	*Beta* sp.	−29.0
PL_2	La Graciosa	Aguja Grande	*Carrichtera annua*	−28.2
PL_3	La Graciosa	Aguja Grande	*Echium lancerottense*	−26.1
PL_4	La Graciosa	Aguja Grande	*Euphorbia regis-jubae*	−24.7
PL_5	La Graciosa	Aguja Grande	Graminaceae	−25.7
PL_6	La Graciosa	Aguja Grande	*Ifloga spicata*	−20.6
PL_7	La Graciosa	Aguja Grande	*Cakile maritima*	−24.5
PL_8	La Graciosa	Aguja Grande	*Launaea arborescens*	−27.1
PL_9	La Graciosa	Aguja Grande	*L. arborescens*	−24.9
PL_10	La Graciosa	Aguja Grande	*Mesembryanthemum crystallinum*	−16.3
PL_11	La Graciosa	Aguja Grande	*Mesembryanthemum nodiflorum*	−22.2
PL_12	La Graciosa	Aguja Grande	*M. nodiflorum*	−18.9
PL_13	La Graciosa	Aguja Grande	*M. nodiflorum*	−18.5
PL_14	La Graciosa	Aguja Grande	*M. nodiflorum*	−15.9
PL_15	La Graciosa	Aguja Grande	*Plantago* sp.	−25.6
PL_16	La Graciosa	Aguja Grande	*Polycarpaea nivea*	−25.4
PL_17	La Graciosa	Aguja Grande	*P. nivea*	−25.2
PL_18	La Graciosa	Aguja Grande	*P. nivea*	−25.1
PL_19	La Graciosa	Aguja Grande	*P. nivea*	−24.5
PL_20	La Graciosa	Aguja Grande	*P. nivea*	−23.9
PL_21	La Graciosa	Aguja Grande	*Reseda lancerotae*	−27.0
PL_22	La Graciosa	Aguja Grande	*Salsola vermiculata*	−14.4
PL_23	La Graciosa	Aguja Grande	*Spergularia* sp.	−25.7
PL_24	La Graciosa	Aguja Grande	*Suaeda vera*	−23.6
PL_25	La Graciosa	Aguja Grande	*S. vera*	−18.1
PL_26	La Graciosa	Aguja Grande	*Suaeda mollis*	−15.1
PL_27	La Graciosa	Aguja Grande	*S. mollis*	−14.8
PL_28	La Graciosa	Aguja Grande	*S. mollis*	−14.2
PL_29	La Graciosa	Montaña del Mojón	*Atriplex glauca*	−15.4
PL_30	La Graciosa	Montaña del Mojón	*Chenoleoides tomentosa*	−14.9
PL_31	La Graciosa	Montaña del Mojón	*L. arborescens*	−13.2
PL_32	La Graciosa	Montaña del Mojón	*Lycium intricatum*	−13.0
PL_33	La Graciosa	Montaña del Mojón	*M. nodiflorum*	−18.3
PL_34	La Graciosa	Montaña del Mojón	*Plantago* sp.	−28.0
PL_35	La Graciosa	Montaña del Mojón	*Plantago* sp.	−22.8
PL_36	La Graciosa	Montaña del Mojón	*S. vermiculata*	−13.8
PL_37	La Graciosa	Montaña del Mojón	*S. vermiculata*	−13.4
PL_38	La Graciosa	Morros Negros	*A. glauca*	−13.7
PL_39	La Graciosa	Morros Negros	*C tomentosa*	−15.0
PL_40	La Graciosa	Morros Negros	*E. lancerottense*	−25.6
PL_41	La Graciosa	Morros Negros	*E. regis-jubae*	−24.6
PL_42	La Graciosa	Morros Negros	*I. spicata*	−24.2
PL_43	La Graciosa	Morros Negros	*I. spicata*	−22.9
PL_44	La Graciosa	Morros Negros	*Limonium papillatum*	−25.1
PL_45	La Graciosa	Morros Negros	*M. nodiflorum*	−19.0
PL_46	La Graciosa	Morros Negros	*Plantago* sp.	−24.6
PL_47	La Graciosa	Morros Negros	*P. nivea*	−25.0
PL_48	La Graciosa	Morros Negros	*P. nivea*	−21.7
PL_49	La Graciosa	Morros Negros	*Spergularia* sp.	−24.9
PL_50	La Graciosa	Morros Negros	*Spergularia* sp.	−22.8
PL_51	La Graciosa	Morros Negros	*S. vera*	−24.9
PL_52	La Graciosa	Morros Negros	*S. vera*	−24.0
PL_53	La Graciosa	Morros Negros	*S. vera*	−14.2
PL_54	La Graciosa	Morros Negros	*S. mollis*	−15.5
PL_55	La Graciosa	Morros Negros	*S. mollis*	−14.2
PL_56	La Graciosa	Morros Negros	*S. mollis*	−12.8
PL_57	La Graciosa	Morros Negros	*Nicotiana glauca*	−23.8
PL_58	La Graciosa	Morros Negros	*Ononis* sp.	−25.0
PL_59	La Graciosa	Morros Negros	*I. spicata*	−22.5
PL_60	La Graciosa	Morros Negros	*P. nivea*	−22.6
PL_61	La Graciosa	Morros Negros	*S. vera*	−19.1
PL_62	La Graciosa	Morros Negros	*A. glauca*	−14.2
PL_63	La Graciosa	Morros Negros	*C. annua*	−25.2
PL_64	La Graciosa	Morros Negros	*C. annua*	−24.5
PL_65	La Graciosa	Morros Negros	*C. annua*	−24.2
PL_66	La Graciosa	Morros Negros	*C tomentosa*	−13.4
PL_67	La Graciosa	Morros Negros	*Cuscuta planiflora*	−25.8
PL_68	La Graciosa	Morros Negros	*M. crystallinum*	−17.8
PL_69	La Graciosa	Morros Negros	*P. nivea*	−25.0

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