



## The phytogeographical significance of S.W. Morocco compared to the Canary Islands

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Received 13 January 1998; accepted in revised form 6 October 1998

**Key words:** Biogeography, Endemism, Growth forms, Mediterranean region, North-Africa, Rupicolous communities, Tertiary refugia

### Abstract

A phytogeographical comparison of S.W. Morocco (the 'Argan area' western part of the Anti-Atlas mountains) and the neighbouring Canary Islands is performed in order to determine whether or not this original North-African area must be included in the Macaronesian sub-region. Patterns obtained with some species' life attributes (growth forms, succulence, dispersal) and biogeographical spectra show that, in spite of some similarities regarding climate, flora (presence of succulent species and endemics common to the two areas) and landscape in the lower zones (infra- and thermo-Mediterranean 'étages'), S.W. Morocco belongs to the Mediterranean sub-region. Characteristic features are the high percentages of Mediterranean indigenous annuals and phanerophytes, and the low level of adaptive radiation compared to the Canary Islands. Nevertheless, some parts of this Moroccan area have acted as major refugia for the Tertiary paleoflora (e.g., *Aeonium arboreum*, *Davallia canariensis*, *Dracaena draco* subsp. *ajgal*, *Sonchus pinnatifidus*), especially in the newly described rupicolous communities. Contrasting reliefs and fog precipitation induced by the nearby Atlantic Ocean explain the moderate impact, in these regions, of drastic climatic changes since the Pliocene period.

### Introduction

The coastal and subcoastal area of south-western Morocco is one of the most remarkable regions of North-Africa, because of its vegetation landscapes and also the unique nature of its flora. This region dominated by the Argan (*Argania spinosa*), the gum tree (*Acacia gummifera*) and various *Euphorbia* shrubs (*Euphorbia obtusifolia* subsp. *regis-jubae*, *E. balsamifera*) or cactiform *Euphorbia* (*Euphorbia officinarum* subsp. *echinus*, *E. beaumierana*, or even very locally here, *E. resinifera*), represents a specific entity from the physiognomic viewpoint, which authors following Braun-Blanquet & Maire (1924) have become accustomed to calling 'the Argan sector'. The gradual botanical exploration of this sector has particularly highlighted similarities between this region and the Canary Islands (Hooker 1878; Emberger 1925, 1939; Gatefossé 1941; Kunkel 1971; Peltier 1973,

1982; Barbero et al. 1982). For this reason, several authors have, from a biogeographical viewpoint, individualised it in a 'Moroccan-Macaronesian sector' (e.g., Jahandiez & Weiller 1932; Peltier 1982; Kim et al. 1996) whose precise significance and exact boundaries have nevertheless remained undefined. Peltier (1982) thus excludes the coastal part of these area of the North-African Mediterranean domain and, without stating it clearly, appears to include it in a Macaronesian and, more particularly, in a Canarian area, currently considered by Spanish authors (Rivas-Martinez et al. 1993) as defining a Canarian sub-region included in the Mediterranean region. The recent discovery of *Dracaena draco* on the western part of the Anti-Atlas (Benabid & Cuzin 1997) further underlines these affinities. Therefore we considered it interesting to attempt to define the exact biogeographical value of this region of S.W. Morocco (Figure 1), from a floristic viewpoint and with respect to the

vegetation structures. Rupicolous communities were particularly investigated because rocky habitats shelter more relict taxa than other communities and constitute evolutionary trap (Snogerup 1971).

## Methods

This phytogeographical analysis is partly based on several field trips by one of us (P.Q.) in S.W. Morocco since the 1950's, and more especially on a trip carried out in May 1996 in the western part of the Anti-Atlas (Figure 1). For the region considered, despite some recent phytocological works (Peltier 1982, 1983; Barbero et al. 1982; Quézel et al. 1995), there is still quite a lot of inexactness, particularly on the plant systematic, because very little precise research has been performed on the flora, and several localities – or even species – have yet to be confirmed. The main reference work on the flora of the region is still the 'Catalogue des plantes du Maroc' (Jahandiez & Maire 1931–1934; Emberger & Maire 1941); however, this is an old publication and still quite incomplete. On the other hand, in the Canary Islands, the flora can be now considered very well documented following various recent works (Santos-Guerra 1983; Bramwell & Bramwell 1990; Hansen & Sunding 1993) which tend, however, towards marked atomization of the species.

Analysis of phytogeographical patterns between the two regions cannot be reduced to a purely physiognomic approach, which is too global and schematic. In fact, precise analysis can only be performed by the comparison of homologous vegetation structures (equivalent from the point of view of physiognomy and ecology, but different according to the flora). This is possible since a quite complete syntaxonomic study has been performed for the natural plant communities of S.W. Morocco (Barbero et al. 1982; Peltier 1982, 1983, 1986; Peltier & Msanda 1995) and a nearly exhaustive syntaxonomic study has been performed for Tenerife (Rivas-Martinez et al. 1987, 1993) and La Palma (Santos-Guerra 1983), while the other Canary Islands are still relatively less researched.

It is obviously difficult to attempt an overall comparative analysis of all existing vegetation types. Therefore we shall limit ourselves to comparing a certain number of significant, well-defined communities in the main types of similar plant formations found in the African continent and in the Canaries. This is possible for zonal formations of the two lower 'étages' (belts or zones of vegetation described on the basis

of regional climate, altitude and topography), i.e., the infra-Canarian/infra-Mediterranean and thermo-Canarian/thermo-Mediterranean, and also for azonal coastal formations (Biondi et al. 1994) and thero-phyte grasslands. These communities were chosen more particularly in Tenerife (Rivas-Martinez et al. 1993), because there are only few precise studies of the eastern islands, apart from the works of Esteve-Chueca (1968), Fernandez-Galvan & Santos-Guerra (1984), Esteve-Chueca & Socorro-Abreu (1977), and Biondi et al. (1994). Furthermore, Tenerife was chosen to establish these comparisons because there is accurate data available related to the analysis of the vegetation on this island (in particular Rivas-Martinez et al. 1993), and also because it has evident climatic similarities that are not found in the eastern islands, which are much more arid or even more desertified than most of the Argan sector in Morocco. Climatological stations are mentioned in a form close to the Emberger-diagram (Emberger 1930), but the Emberger's bioclimatic coefficient ( $Q_2$ ) is replaced by annual precipitations ( $P$  in mm), according to the work of Stewart (1975) (Figure 2). Rupicolous communities exhibit high biogeographical value, but due to the absence of data about these communities in S.W. Morocco, we described four rupicolous communities; thus, 24 relevés were done between Ida-ou-Tanane and the mouth of the oued Noun, in order to compare them with those of the Canaries.

In order to refine the comparisons, we shall mainly consider the biogeographical criteria and certain aspects of the life-strategies of the species (growth forms, types of dissemination, succulence). On the biogeographical level, in all synthetic tables concerning the communities in question, the mediterranean-atlantic taxa and also the mediterranean-holarctic plants have been included within the mediterranean species. However, western Moroccan species have been counted separately within this element. The information on Canarian endemism is largely based on the data of Bramwell (1976) and Humphries (1979), complemented by Hansen & Sunding (1993). The growth forms of Moroccan taxa were established from the list drawn up by Peltier (1982), according to the conceptions of Raunkiaer (1934). The growth form spectra have been weighted according to presence-absence of the species. Although they do not give directly informations, growth forms can often provide significant data on the affinities between the flora of various regions (Raunkiaer 1934). This information become more precise again on comparing not

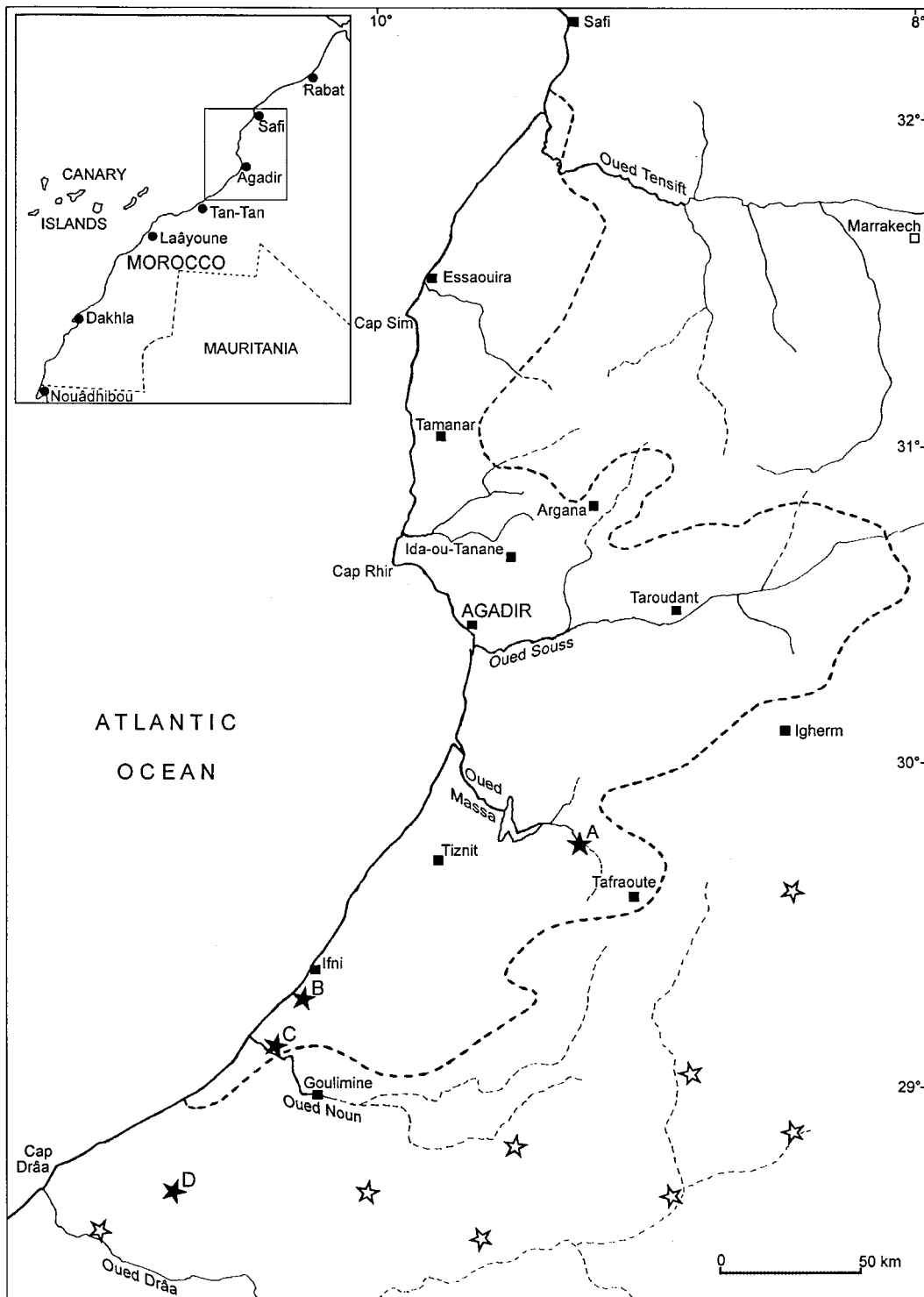


Figure 1. Location map of the S.W. Morocco area and the Canary Islands. For Moroccan localities a black square symbolizes a meteorological station and refers to data mentioned in Table 1. ---: Limits of the area of *Argania spinosa*. ☆: Isolated populations of *Argania spinosa*, according to Ehrig (1974). ★: Main Tertiary-Pleistocene refuges of plants in S.W. Morocco. A: gorges of Assif Oumarhouz; B: gorges of Oued Ouarsik; C: gorges of Oued Noun; D: gorges of Kheneg el Hamman.

Table 1. Bioclimatic data of S.W. Morocco (according to Donnadieu 1977, Peltier 1982 and Le Houérou 1989) and Canary Islands (according to Rivas-Martinez 1987 and Rivas-Martinez et al. 1993). m: minimal average of the coldest month of the year; M: maximal average of the warmest month of the year; M': maximal average of winter months.

Localities	Altitude (m)	Latitude N. (°)	Longitude W. (°)	Annual precipitations (mm)	m (°C)	M (°C)	M' (°C)
Morocco							
Safi	15	32.2	9.15	336	8.4	29.7	–
Essaouira	5	31.3	9.5	295	9.6	22.2	18.5
Tamanar	360	31	9.4	313	6.8	37.4	19.8
Argana	750	30.5	9.1	176	2.2	41.2	18.8
Ida-ou-Tanane	1310	30.4	9.3	493	4.8	33.8	14.3
Agadir	50	30.3	9.4	225	7.2	27.1	20
Taroudant	255	30.3	8.5	232	5.6	35.7	21.6
Igherm	1750	30.1	8.3	180	–0.1	33.4	10.8
Tiznit	225	29.4	9.4	189	7.3	31.2	20.9
Tafraoute	1050	29.4	9	192	2.8	38	19.6
Ifni	65	29.2	10.1	168	11.9	24.1	18.7
Goulimine	300	28.6	10	132	6.5	35.4	21.2
Canary Islands							
Arrecife (Lanzarote)	10	28.6	13.3	139	12.7	29	21.6
Los Estancos (Fuerteventura)	200	28.4	13.6	108	12	27.3	19
Tazacorte (La Palma)	131	28.3	17.5	326	13.6	–	20.9
Las Palmas (Gran Canaria)	6	28.1	15.2	145	15.6	26.9	20.8
Tafira (Gran Canaria)	375	28.2	15.3	366	8.5	–	16.2
La Laguna (Tenerife)	547	28.3	16.2	605	8.8	27.2	15.4
Sta. Cruz-de-Tenerife (Tenerife)	36	28.2	16.2	234	15.1	30.1	20.8

the overall flora, as did Shmida & Werger (1992) for the Canary Islands, but the homologous vegetation structures on biogeographical and ecological levels. In drawing up synthetic tables concerning the plant communities, accidental species (i.e., < 2 records for the whole relevés of the community) were not taken into account.

For endemics common to the Canaries and to Morocco, six main types of dispersal were chosen (Van der Pijl 1982): anemochory, endozoochory, epizoochory, hydrochory (dispersal by flowing water), ombrohydrochory (dispersal by rain) and barochory. This last category also covers plants whose means of dissemination are not known. Patterns of dispersal were determined on the basis of field observations and the indications of Monod (1974) and Bramwell (1985). Data on the succulence of species were compared to that concerning the Canaries, according to Shmida & Werger (1992) but, as opposed to these authors, we did not consider certain slightly fleshy

taxa as succulent (*Limonium*, *Urginea*, *Arum*, *Dip-cadi*, *Asphodelus*, *Polygonum maritimum*); introduced succulents (*Opuntia*, *Aloe*, *Agave*) were also excluded from the analysis.

## Results

### *Geographical and climatic boundaries*

There are ambiguities in the individualisation of an Argan sector or a Macaronesian sector, in S.W. Morocco, and these ambiguities first appear in the search for its boundaries. If we refer to the Argan, for which a precise distribution map was drawn up by Ehrig (1974), complementing the observations of Emberger (1924, 1925), the zone in question stretches from Safi to the mouth of the oued Draâ and includes, in addition to the coastal areas, the valley of the oued Souss, the southern slope of the western High Atlas and the northern and southern slopes of the western Anti-Atlas

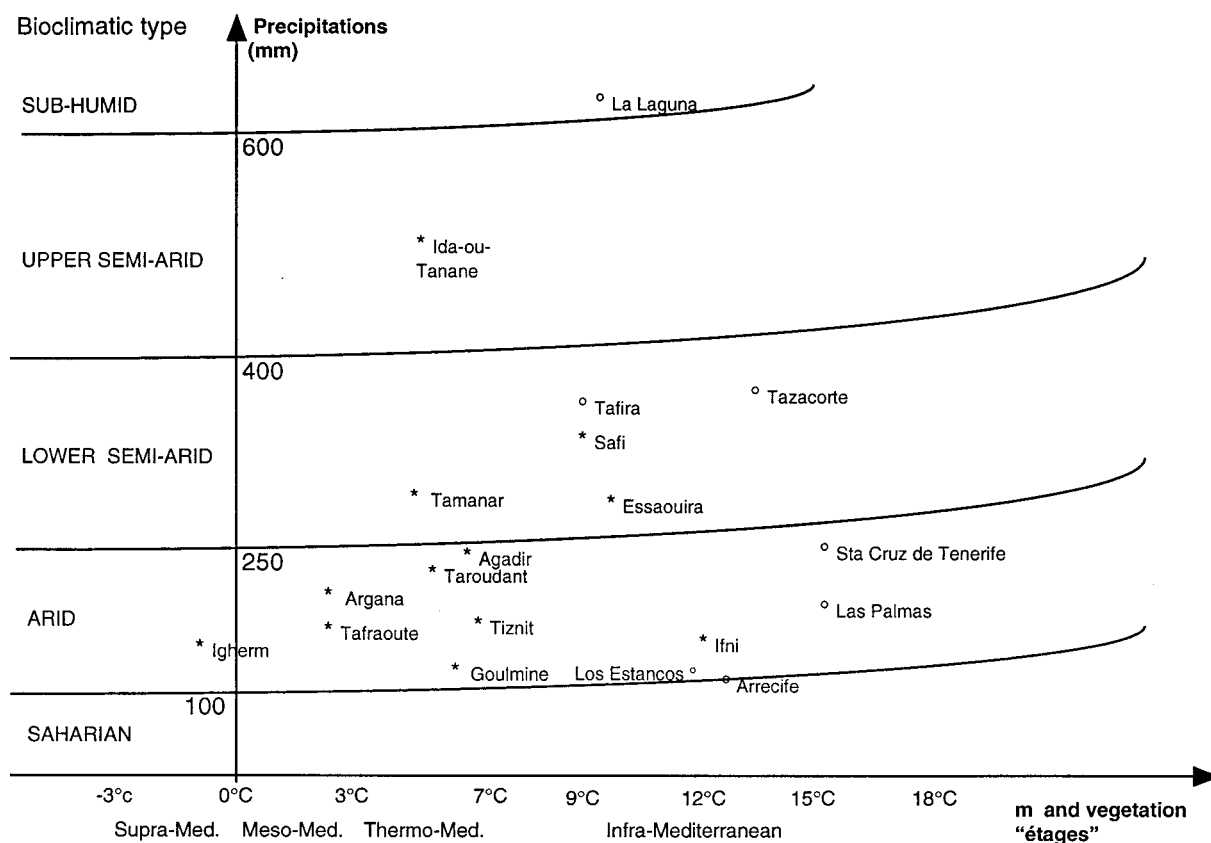


Figure 2. Bioclimatic diagram of S.W. Morocco (°) (datas according to Donnadiou 1977, Peltier 1982 and Le Houérou 1989) and the Canary Islands (\*) (datas according to Rivas-Martinez 1987 and Rivas-Martinez et al. 1993) localities. P: annual precipitations (in mm); m: minimal average of the coldest month of the year (°C).

up to altitudes of 1300–1500 m (Figure 1). However, in Morocco, the Argan has a certain number of isolated populations (but not relictual, according to the genetic analysis of cpDNA: El Mousadik & Petit 1996), particularly in the upper valley of the oued Grou to the south-east of Rabat (Emberger 1924), and on the northern slope of Beni Snassene (Tregubov 1963). To the south, it extends beyond the Moroccan-Algerian border (Tindouf hamada: Maire 1938), but it is then only found in alluvial berms along the side of wadis (Quézel et al. 1995), because of hydrological compensations. These isolated stations are found outside the sector where the Argan is theoretically present in continuous stands, or at least potential stands, if it has been destroyed by Man. Note that these boundaries coincide approximately with those of the cactiform *Euphorbia* (apart from *E. resinifera*). The 'Argan sector' covers an area of around 4 000 000 ha and the tree itself is present in an area of 820 000 ha.

Peltier (1982) limits the Macaronesian-Moroccan sector to a narrow coastal strip, but he does not define its northern and southern boundaries. However, his floristic approach would indicate that it extends at least to Essaouira in the north and to the oued Noun in the south. This author does not discuss the question of the coastal vegetation situated further south, where some Moroccan-Canarian endemic plants persist along the coast of the western Sahara as far as Cape Blanc (Râs Nouâdhibou) in Mauritania (Maire 1938; Hernandez-Pacheco et al. 1939; Barbero et al. 1982). Peltier (1982) stresses that the vegetation of this sector is located mainly on rocky and sandy substrates beside the ocean, and in the areas unfit for agriculture, which makes it difficult to determine its exact boundaries further inland.

The general climate of S.W. Morocco is similar to that of certain parts of the Canaries (apart from areas of laurel forest and high upland areas) (Table 1, Figure 2). According to the data supplied for the Ca-

naires by the Basic Atlas of the Canaries (1980) and by Rivas-Martinez et al. (1993), and for Morocco by Donnadieu (1977) and Peltier (1982), precipitation levels vary between 110 mm and 500 mm according to the location and the altitude. Mean annual temperatures vary between 17 and 24 °C, with higher values in a pre-Saharan zone (29.2 °C in Tafraoute); and the mean minimum temperature of the coldest month of the year ('m' *sensu* Emberger 1930) is between 5 and 12 °C in S.W. Morocco, according to the degree of continentality, while in the Canaries, oceanic influences raise the minima to between 9 and 16 °C (Figure 2). Another major factor that is much more difficult to evaluate consists of atmospheric humidity, fog and mist, which are always marked in an oceanic situation. For Agadir, however, Peltier (1982) shows that mean monthly relative humidity levels never fall below 83% (in Winter) at 6.00 h UT and 62% (in Spring) at 18.00 h UT; they are above 90% in the morning in Summer. In the Canaries, Kämmer (1974) mentions fog precipitations totalling 300 mm per year in laurel forests of Tenerife and La Gomera; but it is at higher altitudes, in the forests of *Pinus canariensis*, that these additional precipitations would be the highest (up to 2500 mm yr<sup>-1</sup>).

We must also mention an essentially bioclimatic approach that attempted to define this zone (Table 1). Benabid (1976) individualises an 'infra-Mediterranean' bioclimate whose climatic criteria are values of 'm' above 7 °C and high atmospheric humidity throughout the whole year. Michalet (1991) specifies that the infra-Mediterranean stations have a mean maximum January temperature (*M*) between 17.5 °C and 22 °C, while *M* varies between 15 °C and 17.5 °C in the thermo-Mediterranean stations. The boundaries of the infra-Mediterranean 'étage' are around those of the Argan, which however extends well into the thermo-Mediterranean 'étage'. Note that this bioclimatic interpretation has been chosen by the vast majority of ecologists working in this region (Barbero et al. 1982; Quézel et al. 1995). It has also been accepted for the Canaries, where an infra-Canarian bioclimate has been defined in accordance with identical criteria (Rivas-Martinez et al. 1987, 1993).

#### *Floristic criterion*

#### *Floristic richness*

Within the geographical boundaries that we have defined, it is evidently difficult to establish a precise total number of species, but Peltier (1982) evaluates

the floristic richness at 1240 taxa and 902 genera in the study area. In considering the coastal areas between Safi in the north and the mouth of the Draâ to the south (Figure 1), but eliminating zones with average altitudes of more than 1500 m, the totals are not very different, but probably a little augmented due to the occurrence of Saharan taxa that are practically absent from Peltier's inventory. We can thus reasonably estimate that the flora of S.W. Morocco totals 1400 species and subspecies.

#### *Endemism*

Endemic species *sensu lato* common to S.W. Morocco and the Canaries are not very numerous (Quézel 1978; Peltier 1973, 1982) and can be currently estimated at 28 taxa (Table 2). They include three species (*Asplenium* gr. *aethiopicum*, *Davallia canariensis*, *Laurus azorica*) that are found in the Canaries but also beyond S.W. Morocco; they have also been considered, because they are incontestably associated with the Macaronesian element.

Of these species, 15 (55%) are mainly associated with seaside areas or salty substrates of coastal areas (5 psammophilous, 3 present on sea rocks and cliffs, 7 on rock or sand). 10 taxa, or 37%, are associated with rocks and cliffs at low and medium altitudes. Two are represented in Morocco by subspecies or particular varieties: *Dracaena draco* subsp. *ajgal* and *Caralluma burchardii* var. *maura*.

Some endemo-vicarious or schizoendemic taxa (Favarger & Contandriopoulos 1961) must be mentioned (Maire 1932-1934; Peltier 1982): *Scilla latifolia* and *S. haemorrhoidalis*, *Lotus maroccanus* and *L. glaucus* + *L. mascaensis*, *Bubonium imbricatum* and *B. sericeum*, *Senecio anteuphorbium* and *S. kleinia*. Even if further information would be preferable for better identification of these vicariations, it appears difficult to establish a close relation – as does Peltier (1982) – between *Argania spinosa* and *Sideroxylon marmulano* (Sapotaceae), or between Moroccan cactiform *Euphorbia* and *E. canariensis*. However, *Aeonium arboreum* (the Moroccan species of *Aeonium* should be named *A. korneliuslemsii*, according to H.Y. Liu *in* Santos-Guerra 1997), which is found in an isolated location on the Rif coast, has affinities with *A. balsamiferum* (found in Lanzarote and Fuerteventura), and *Pulicaria lozanoi* has similarities with *P. canariensis* (present in Fuerteventura).

Even a brief analysis of endemism in S.W. Morocco and the Canaries underlines the considerable differences in endemism in these regions. In the Ca-

Table 2. List of endemic plants shared by S.W. Morocco and the Canary islands, with indications on growth forms, dispersal types, and ecological preferences.

Taxa	Growth forms	Dispersal	Habitat type
<i>Andryala pinnatifida</i>	chamaephyte	anemochory	maritime sands, dunes
<i>Artemisia ramosa</i>	chamaephyte	anemochory	low altitude rocky places
<i>Artemisia reptans</i>	chamaephyte	anemochory	maritime cliffs and rocks
<i>Asparagus pastorianus</i>	nanophanerophyte	endozoochory	low altitude rocky places, dunes
<i>Asplenium</i> gr. <i>aethiopicum</i>	geophyte	ombrohydrochory	mid altitude siliceous cliffs and rocks
<i>Astydamia latifolia</i>	hemicryptophyte	hydrochory	maritime cliffs and rocks
<i>Atriplex glauca</i> var. <i>ifniensis</i>	chamaephyte	barochory	maritime rocks and sands
<i>Bupleurum handiense</i>	nanophanerophyte	barochory	maritime sands
<i>Caralluma burchardii</i>	chamaephyte	anemochory	low altitude shrubby places
<i>Chenoleoides tomentosa</i>	chamaephyte	barochory	maritime rocks and sands
<i>Davallia canariensis</i>	geophyte	ombrohydrochory	low and mid altitude siliceous cliffs and rocks
<i>Dracaena drago</i>	phanerophyte	endozoochory	mid altitude siliceous cliffs and rocks
<i>Drusa glandulosa</i>	hemicryptophyte	epizoochory	low and mid altitude siliceous cliffs and rocks
<i>Euphorbia obtusifolia</i> subsp. <i>regis-jubae</i>	nanophanerophyte	epizoochory	low altitude rocky places, maritime cliffs
<i>Frankenia ericifolia</i> subsp. <i>ericifolia</i>	chamaephyte	hydrochory	maritime rocks and sands
<i>Helianthemum canariense</i>	chamaephyte	barochory	maritime cliffs and rocks, rocky slopes with Argan
<i>Hypericum coadunatum</i>	nanophanerophyte	anemochory	mid-altitude moist rocks
<i>Laurus azorica</i>	phanerophyte	endozoochory	mid altitude cliffs
<i>Lobularia canariensis</i> subsp. <i>marginata</i>	chamaephyte	barochory	maritime rocks and sands, mid altitude rocks
<i>Mairetis microsperma</i>	therophyte	barochory	maritime sands, dunes
<i>Nauplius graveolens</i> subsp. <i>odorus</i>	chamaephyte	anemochory	maritime and low altitude sandy places
<i>Phagnalon calycinum</i> (= ? <i>P. hansenii</i> )	chamaephyte	anemochory	maritime rocks
<i>Polycarpha nivea</i>	chamaephyte	barochory	maritime rocks and sands
<i>Rhus albidia</i>	nanophanerophyte	endozoochory	maritime rocks and sands, mid-altitude rocky places
<i>Rumex vesicarius</i> var. <i>rhodophysa</i>	chamaephyte	anemochory	low altitude rocky places
<i>Sonchus pinnatifidus</i>	chamaephyte	anemochory	low and mid altitude cliffs and rocks
<i>Traganum moquinii</i>	nanophanerophyte	anemochory	maritime sands, dunes
<i>Zygophyllum fontanesii</i>	nanophanerophyte	hydrochory	maritime rocks and sands

aries (an area of 7273 km<sup>2</sup>) there are 600 endemics in the broad sense in a flora comprised of 1782 species, i.e., a rate of endemism of 37.9% (Shmida & Werger 1992; Médail & Quézel 1997). In Morocco, in an area about ten times greater, the flora counts around 1400 taxa, and endemics represent less than 120 species and subspecies, i.e., around 9% of the total flora. Peltier (1982) finds a total of 140 endemic species and subspecies in his study area, including a sizeable number of Mediterranean orophile or sub-orophile taxa that are absent from the area considered in our study.

Generic endemism is modest in S.W. Morocco. However, this area contains (Quézel 1978) the genera *Hesperolaburnum*, *Traganopsis*, *Sclerosciadium*, *Hannonia*, *Ighermia*, or even *Ismelia* (genetically very closely related to *Chrysanthemum*, according to Francisco-Ortega et al. 1995). *Argania* and *Warionia*

*nia* extend much further outside the area to the north and east, and *Vagarria* to the south, while the genus *Mairetis* is common to S.W. Morocco and in the Canaries. The affinities of these genera, which are still sometimes questioned, must be looked for mainly in Mediterranean or Saharan genera (*Traganopsis*, *Mairetis*, *Ighermia*) or tropical African genera (*Argania*, *Warionia*). In the Canaries, generic endemism is much more developed (Bramwell 1976; Humphries 1979) and there are 17 genera strictly in the Canaries and around 14 endemic Macaronesian genera.

As regards specific endemism of S.W. Morocco, many significant biogeographical facts can be underlined:

– The vast majority of endemic species are of mediterranean origin. The richest genera include: *Teucrium* (6), *Bubonium* (4), *Centaurea* (4), *Limonium* (4),

*Senecio* (3), *Scilla* (3), *Lotus* (3), *Fumaria*, *Ononis*, *Coronilla*, *Astragalus*, *Bupleurum*, *Limoniastrum*, *Echium*, *Satureja*, *Thymus*, *Jasonia*.

– A certain number of endemics of tropical origin already indicated by Sauvage (1948) and Mathez (1974) must be mentioned, because many show marked distinctions from closely-related species: *Sporobolus lanuginellus*, *Leptochloa ginae*, *Kralikelia hesperidum*, *Commelina rupicola*, *Kalankoe faustii*, *Caralluma* spp., *Pentzia hesperidum*.

– Endemics of Saharo-Arabian origin are absent from the Canaries and rare in S.W. Morocco; however, mention must be made of *Traganopsis glomerata*, *Anvillea platycarpa* and *Fagonia harpago*.

#### *Life-strategies of taxa*

For the whole flora of S.W. Morocco, 66 succulent taxa have been counted, that is, 58 with succulent leaves and 22 with succulent stems (Figure 3); 14 species have both succulent leaves and stems. The most commonly found genera include *Sedum* (12 taxa), *Salsola* (7), *Caralluma* (5), *Euphorbia* (4) and *Suaeda* (4); cactiform *Euphorbia* (*Euphorbia officinarum* subsp. *echinus* and *E. beaumierana*) and *Senecio anteuphorbium* play the most important physiognomic and landscape role. In Morocco, succulent taxa are found in three major habitats; 31 taxa (67%) are dependent on coastal and juxta-coastal biotopes of varying degrees of salinity, 8 preferentially in pre-Saharan sectors of the southern zone, while 27 species are located on cliffs or rocky slopes (*Sedum*, *Umbilicus*, *Caralluma*, *Euphorbia*). The distribution by growth forms shows that around 40% of succulent taxa are chamaephytes. Annuals are also well represented (31% of taxa with succulent leaves and 41% with succulent stems), while nanophanerophytes make up around 20% of the total contingent of succulent taxa. In the Canaries, there are 156 succulent taxa (Shmida & Werger 1992, modified), including 114 with succulent leaves and 42 with succulent stems (Figure 3). As in Morocco, ligneous taxa predominate irrespective of the type of succulence, and therophytes with fleshy leaves reach a noteworthy percentage (21%).

Examination of certain features of the species' life attributes of Macaronesian endemic plants common to the Canaries and to S.W. Morocco (Table 2) underlines that the majority of species are perennials with ligneous stems (chamaephytes + nanophanerophytes + phanerophytes: 81%), while only one taxon (*Mairetis microsperma*) is an annual. Herbaceous plants rep-

resent a contingent reduced to 5 plants. These endemics are preferentially anemochorous (37%) and barochorous (26%), while zoochorous species are very infrequent (5 taxa or 18.5%) but include the two trees (*Dracaena draco* subsp. *ajgal* and *Laurus azorica*) dispersed by ornithochory in this contingent. Overall, three quarters of these taxa can be dispersed over a long distance (by anemochory, zoochory or hydrochory).

#### *Plant communities criterion*

If we limit ourselves to a simple landscape approach, S.W. Morocco and the Canaries have major physiognomic resemblances that are mainly perceptible in the lower vegetation zones in cactoid formations. But, even at this level of analysis, the zonation of vegetation already shows appreciable differences (Achhal et al. 1980; Barbero et al. 1982; Willdpret de la Torre & Arco-Aguilar 1987; Rivas-Martinez et al. 1993). Examination of Table 3 clearly underlines that there are major physiognomic affinities between the infra-Mediterranean and infra-Canarian 'étages', and they remain perceptible in the thermo-Mediterranean and thermo-Canarian 'étages' in arid and semi-arid environments, while laurel forest is absent from S.W. Morocco. However, in the zones above these, the differences are fundamental: forests of sclerophyll oaks in Morocco, pine-woods of *Pinus canariensis* and communities of high leguminous shrubs (*Spartocytisus*, *Adenocarpus*) in the Canaries.

Therefore, in the following analysis, we compare a certain number of more significant plant communities at low and medium altitudes in S.W. Morocco and the Canaries, considering, within the azonal, zonal and particularly rupicolous communities, the vegetation structures that offer comparable ecological and physiognomic characteristics (Table 4).

#### *Azonal communities*

This consists in particular of psammophilous formations, which are all juxta-coastal, and halophilous formations. Psammophilous formations are not greatly developed in the Canaries and we chose *Euphorbia paraliasi-Cyperetum kalli* Sunding 1972 present in the central and eastern islands (Sunding 1972; Biondi et al. 1994), and in Morocco (Peltier 1982), *Chrysanthemo carinatae-Senecietum hesperidi* Peltier 1982 in the juxta-coastal dunes, and *Bubonio imbricati-Centaureetum gentilii* in fixed dunes, present in the region situated south of Agadir. As regards halophilous



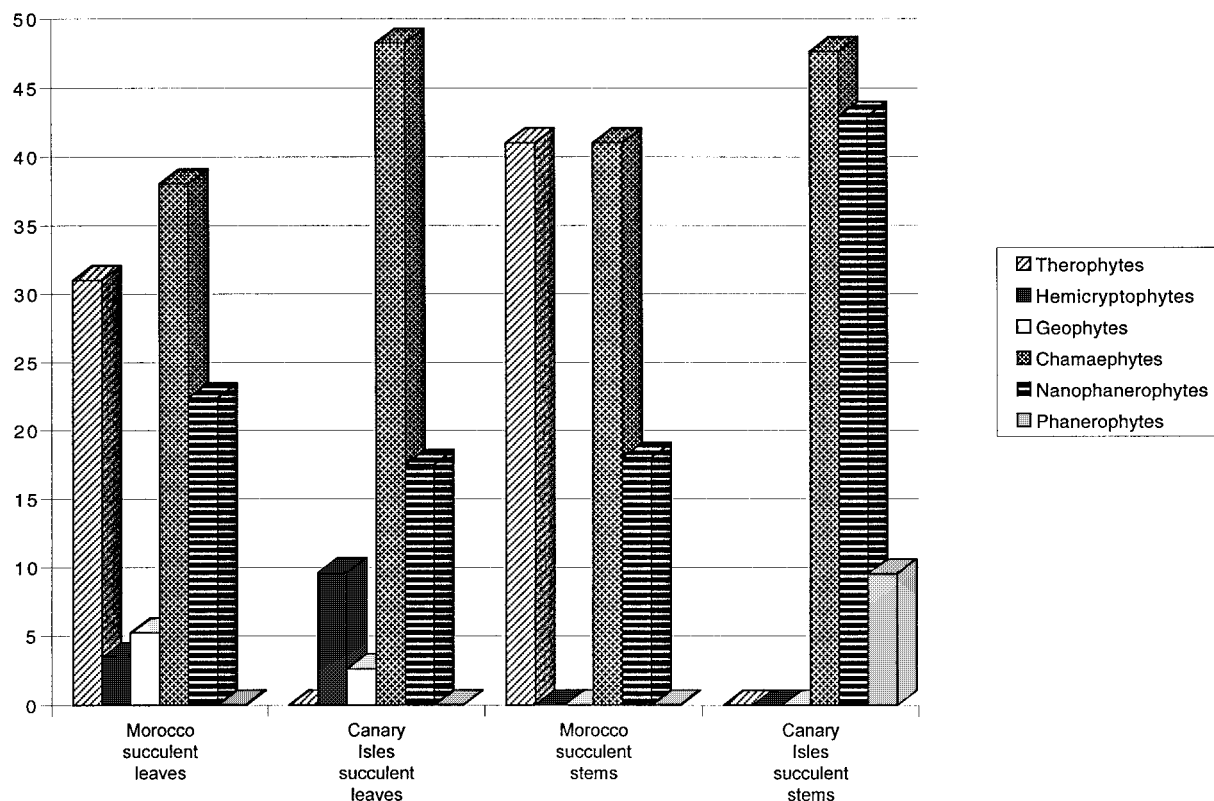


Figure 3. Percentage of leaves or stems succulence in S.W. Morocco (respectively  $n = 58$  and  $n = 22$ ) and the Canary Islands (respectively  $n = 114$  and  $n = 42$ ) floras, according to the growth forms. Data for Canarian plants are from Shmida & Werger (1992), modified.

Table 3. Comparison of the vegetation 'étages', in S.W. Morocco and the Canary Islands.

S.W. Marocco	Canary Islands
<i>Infra-mediterranean 'étage'</i> Succulent shrubs ( <i>Euphorbia</i> , <i>Caralluma</i> , <i>Senecio anteuphorbium</i> ) with <i>Argania spinosa</i>	<i>Infra-canarian 'étage'</i> Succulent ( <i>Euphorbia</i> , <i>Aeonium</i> , <i>Senecio</i> , <i>Caralluma</i> ) and sclerophyllous shrubs
<i>Thermo-mediterranean 'étage'</i> Pre-forest with <i>Argania</i> , <i>Tetraclinis</i> , <i>Pistacia</i> , <i>Olea maroccana</i> , <i>Juniperus turbinata</i> (semi-arid and sub-humid)	<i>Thermo-canarian 'étage'</i> – Pre-forest with <i>Olea cerasiformis</i> , <i>Juniperus</i> <i>canariensis</i> , <i>Pistacia</i> , <i>Rhamnus</i> (semi-arid) – Laurel forest with <i>Laurus</i> , <i>Persea</i> , <i>Ocotea</i> , <i>Myrica</i> , <i>Erica</i> (sub-humid and humid)
<i>Meso-mediterranean 'étage'</i> <i>Quercus rotundifolia</i> forest	<i>Meso-canarian 'étage'</i> <i>Pinus canariensis</i> forest
<i>Supra-mediterranean 'étage'</i> <i>Quercus rotundifolia</i> forest	<i>Supra-canarian 'étage'</i> Leguminous shrubs ( <i>Spartocytisus</i> , <i>Adenocarpus</i> ) and herbs

Table 4. Physiographical and climatological data about zonal and rupicolous communities used for phytogeographical and growth forms comparisons.

	Altitudinal range (m)	Precipitations/ year (mm)	Thermic zone	Bioclimate	Vegetation 'étage'	Substrate
Zonal communities						
<i>Ceropegio fuscae</i> – <i>Euphorbietum balsamiferae</i>	50–300	100–180	warm	arid	infra-canarian	basaltes
<i>Periploco laevigatae</i> – <i>Euphorbietum canariensis</i>	30–200	180–300	warm	arid/semi-arid	infra-canarian	basaltes
<i>Euphorbio beaumieranae</i> – <i>Arganietum spinosae</i>	30–300	250–350	warm	arid	infra-mediterranean	eruptive rocks - limestone
<i>Euphorbio echini</i> – <i>Arganietum spinosae</i>	30–250	150–300	warm	arid	infra-mediterranean	eruptive rocks - limestone
<i>Junipero canariensis</i> – <i>Oleetum cerasiformis</i>	200–750	300–500	warm-temperate	arid/semi-arid	thermo-canarian	basaltes
<i>Cistetum symphytifoliae</i> – <i>monspeliensis</i>	600–1100	400–600	temperate	arid/semi-arid	thermo-canarian	basaltes
<i>Oleo maroccanae</i> – <i>Arganietum spinosae</i>	400–1000	300–450	temperate	arid/semi-arid	thermo-mediterranean	eruptive rocks - limestone
<i>Tetraclino articulatae</i> – <i>Arganietum spinosae</i>	800–1100	300–500	temperate	arid/semi-arid	thermo-mediterranean	limestone - pelites
Rock communities						
<i>Soncho radicati</i> – <i>Aeonietum tabulaeformis</i>	100–800	300–500	warm	arid/semi-arid	infra-canarian	basaltes
<i>Aeonietum lindleyi</i>	200–400	200–300	warm	arid/semi-arid	infra-canarian	basaltes
<i>Davallio canariensis</i> – <i>Dracaenetum ajgal</i>	500–1400	300–500	temperate	arid/semi-arid	thermo-mediterranean	quartzites
<i>Scillo latifoliae</i> – <i>Saturejetum monanthae</i>	100–400	150–200	warm	arid	infra-mediterranean	quartzites - sandstones

communities envisaged in the Canaries, we chose *Frankenio capitatae-Zygophylletum fontanesii* Rivas-Martinez et al. 1993 of Tenerife and Gran Canaria, and in Morocco, *Arthrocnemetum indici* Br.-Bl. 1928 (in Peltier 1982), present on the banks of the Souss and Massa wadis. We only have few relevés concerning coastal cliffs, which however contain very specific vegetation. It was only possible to select the community with *Pentzia hesperidum* and *Limoniastrum weygandiorum* (Quézel 1965) of the Aoreora region in southern Morocco. From the viewpoint of phytosociological hierarchy, all the structures mentioned belong to atlantic or mediterranean-atlantic units: *Ammophiletea* Br.-Bl. and Tüxen 1943, *Crithmo-Staticetea* Br.-Bl. 1947, but the latter belong more especially to the alliance *Frankenio-Astydamion latifoliae* Santos 1976, which includes the vegetation of the coastlines of the Canaries and of S.W. Morocco.

Although these do not correspond to azonal structures, we also analysed some therophyte grasslands, particularly, in the Canaries, *Hypochaeridi glabrae-Tuberarietum guttatae* Rivas-Martinez et al. 1993 and '*Stipetum canariensis macaronesticum*' Esteve-Chueca & Socorro-Abres 1977, and on the continent, *Stipo retortae-Notoceretum bicornis* Peltier 1983, because the results obtained are quite comparable to the previous ones.

#### Zonal communities

In the infra-Canarian 'étage' of Tenerife we selected *Ceropegio fuscae-Euphorbietum balsamiferae* Rivas-Martinez et al. 1993, in its typical sub-association type corresponding to an arid bioclimate, and *Periploco laevigatae-Euphorbietum canariensis* Rivas-Martinez et al. 1993, probably the most characteristic community of this zone, in arid and semi-arid bioclimates. In S.W. Morocco, we selected for the infra-Mediterranean 'étage', *Euphorbio beaumieranae-Arganietum spinosae* Barbero et al. 1982 situated rather to the north of Agadir in arid or semi-arid bioclimates, and *Euphorbio echini-Arganietum spinosae* Barbero et al. 1982, widespread throughout the south of the Souss and in the Anti-Atlas in an arid bioclimate (Barbero et al. 1982).

In the thermo-Canarian 'étage' we selected *Junipero canariensis-Oleetum cerasiformis* Rodriguez et al. 1990, in an upper semi-arid bioclimate, and *Cistetum symphytifoliae-monspeliensis* Rivas-Martinez et al. 1993 which is rather a stage of degradation of the previous community, in a semi-arid bioclimate. On the continent, we considered *Oleo*

*maroccanae-Arganietum spinosae* Barbero et al. 1982 of southern slope of Ida-ou-Tanane, in a higher semi-arid and lower sub-humid bioclimates, and *Tetracchino articulatae-Arganietum spinosae* Fennane 1987, which is especially developed on the southern slope of the western High Atlas, in the same types of bioclimates.

The Canarian communities studied are all included in *Kleinio-Euphorbietea canariensis* (Rivas-Goday and Esteve 1965) Santos 1976, and in the orders of *Kleinio-Euphorbietalia canariensis* (Rivas-Goday and Esteve 1965) Santos 1976 in the infra-Canarian and in *Oleo-Rhamnetalia crenulatae* Santos 1983 in the thermo-Canarian 'étage'. All the Moroccan communities mentioned belong to the *Acacio gummiferae-Arganietalia* Barbero et al. 1982, centred on the region studied, but extending quite far to the east of it. The floristic structures of the above communities allow them to be unquestionably included within the *Quercetea ilicis*. However, some authors, and recently Peltier (1982), prefer to include the Moroccan formations with cactiform *Euphorbia* in the *Kleinio-Euphorbietea canariensis*, reserving the order of *Acacio-Arganietalia* for vegetation structures with *Argania spinosa*. This position cannot be supported on a syntaxonomic basis, because all the Moroccan communities mentioned still have a strong contingent of Mediterranean species related to *Quercetea ilicis* in the broad sense, and the floristic affinities between the Canarian and Moroccan communities are very limited.

#### Rupicolous communities

Rupicolous communities in the Canaries are now well documented. While communities that belong to the holarctic class of *Asplenietea trichomanis* (Br.-Bl. 1934) Oberdorfer 1977, in old walls, or *Anomodonto-Polypodietaea* Rivas-Martinez 1975, at the bottom of rocks, are still present, most of the rocky vegetation of the Canaries and also of Madeira, belong to an endemic class, *Greenovio-Aeonietea* Santos 1976, within which several communities have been described that are very rich in endemic species, often of limited distribution. The most significant rupicolous elements are related to Crassulaceae and particularly to the genera *Aeonium*, *Aichryson*, *Monanthes*, *Greenovia* and to chamaephytic Asteraceae (*Sonchus* and *Tolpis*).

In Morocco, on the other hand, while the communities of the Atlas have been studied in the high altitude (Quézel 1952, 1957), the problem has been barely approached at lower zones. According to the

existing data, it appears that the majority of these North-African communities in Morocco must belong to the *Asplenieta trichomanis* and also marginally to the other two classes mentioned above. Within the *Asplenieta*, the order of *Potentilletalia caulescentis* Br.-Bl. 1926 is represented in the Atlas mountains by the endemic alliance *Violion saxifragae* Quézel 1952. Elsewhere, the order of *Tinguarretalia siculae* Daumas et al. 1952 has been described in Algeria (Daumas et al. 1952) for the vegetation of limestone rocks at low and medium altitudes; the presence of this order in Morocco had been reported at the time. Perez-Latorre et al. (1996) brought this unit to the rank of sub-order. The *Poterion ancistroidis* Br.-Bl. 1934 represents the most widely distributed alliance in Morocco. However, in S.W. Morocco, there is quite rich rupicolous vegetation, where a Canarian-Moroccan species, *Sonchus pinnatifidus*, is relatively frequent, as well as *Aeonium arborescens*, which could have allowed possible comparison with the *Greenovio-Aeonieta*.

The 24 relevés carried out on limestone or siliceous rocks between Ida-ou-Tanane and the mouth of oued Noun show unquestionable uniformity (Tables A1 and A2), and must belong to *Asplenieta trichomanis* and to *Tinguarretalia*. They can be incorporated in a new alliance – *Celsio antiatlanticae-Aeonium arborescentis* nov. all. (Typus: *Davallia canariensis-Dracaenetum ajgal* Benabid & Cuzin 1997, stat. nov.) whose characteristic plants are: *Celsia longirostris* subsp. *antiatlantica*, *Aeonium arborescens*, *Sonchus pinnatifidus*, *Bituminaria bituminosa* var. *rotundifolia*, *Davallia canariensis*, *Polygala balansae* var. *foliosa*, *Jasonia hesperidum*, *J. antiatlantica*, *Perralderia coronopifolia* subsp. *purpurascens*, *Andrachne maroccana* and *Ranunculus spicatus* subsp. *rupestris* var. *maroccanus*. To these we added, as transgressive species, *Warionia saharae*, more associated with stony grounds than cliffs, and transgressive of *Acacio-Arganietalia*, and *Selaginella rupestris* subsp. *balansae*, which extends quite far to the east (siliceous High Atlas and Rif). For the moment, four associations can be defined.

(1) *Davallia canariensis-Dracaenetum ajgal* Benabid & Cuzin 1997, stat. nov. (Table A1, relevés 1 to 8; Typus: relevé 4)

In their initial article relating the discovery of *Dracaena draco* in Morocco, Benabid & Cuzin (1997) defined under this name a community where the Dragon-tree is well represented, and they included this formation in *Acacio-Arganietalia*. A field expe-

dition convinced us that there were closely linked two communities, one for which the name given by Benabid & Cuzin (1997) was retained, and another with *Argania spinosa*, corresponding to *Euphorbio echini-Arganietum spinosae* in a particular variant. The latter is present in the crevasses and at the foot of quartzite cliffs, of which many plants take refuge in the rocks themselves. The Dragon-tree formation is located in remote gorges that are difficult to explore in the Assif Oumarhouz mountain, between 400 and 1400 m, and is especially well developed in north-facing locations (Figure 4). It is characterized by *Dracaena draco* in its endemic sub-species *ajgal*, *Davallia canariensis*, and various endemics of the Kest massif: *Teucrium weneri*, *Leontodon garnironii* and also *Asplenium* gr. *aethiopicum*, a *Caralluma* with long decumbent stem closely related to *C. joannis*, and on a local level, *Phagnalon atlanticum* var. *rehamnorum*. Although the botanical survey is still quite incomplete, this is probably one of the most remarkable rupicolous communities of S.W. Morocco. It prospers in the infra- and thermo-Mediterranean 'étages', and in an upper semi-arid or even locally sub-humid bioclimates.

(2) *Jasonia antiatlanticae-Saturejetum arganietorum* nov. ass. (Table A1, relevés 9 to 15; Typus: relevé 10)

Floristically less well individualised than the previous community, this formation appears to colonise mainly the south-western slope of the Anti-Atlas, particularly in the regions of Tighmi and Tafraoute, on limestone and volcanic substrates, without any notable differences in plant composition in relation to the substrate. Especially present in north-facing locations, it is developed between 200 and 500 m in the infra-Mediterranean 'étage' and in a semi-arid bioclimate. Only the species that were used to name it, and *Pulicaria glandulosa*, seem to be able to characterise it. The characteristics of the superior units are quite well represented, but the companion species and particularly the species of *Acacio-Arganietalia* are much less frequent than in the previous association. It is probably in this grouping that *Lafuentea jeanpertiana* appears on the limestone cliffs of Tazeroualt, a little further to the south.

(3) *Scillo latifoliae-Saturejetum monanthae* nov. ass. (Table A2, relevés 1 to 7; Typus: relevé 4)

Distributed more in the south, this community is found particularly in a sub-littoral situation between Ifni and oued Draâ. We were able to study it near the mouth of the oued Ouarsik and S.W. of Goulimine



Figure 4. Dragon-tree (*Dracaena draco* L. subsp. *ajgal* Benabid et Cuzin) community of the gorges of the Assif Oumarhouz mountain (Anti-Atlas), between 400 and 1400 m.

(Khanguet). We also included here two unpublished relevés done by Maire in the gorges of the oued Noun, and a list drawn up by Mathez (1974) in the locality of *Commelina rupicola*. Located on sandstone in an arid infra-Mediterranean bioclimate, this community is mainly characterized by *Scilla latifolia*, *Satureja monantha* and *Leptochloa ginae*, as well as the rare *Kalanchoe faustii*, *Commelina rupicola*, *Enteropogon rupestris*, *Abutilon albidum* and *Thymus hesperidum*. While the characteristic species of the alliance are still strongly present, those of the order and class are quite rare. Note that, in this community, we included the two relevés published under the name of *Crepidi pinnatifidae-Warionietum saharae* Barbero et al. 1982, which we then included to the *Acacio-Arganietalia*.

(4) *Teucrietum tananici* nov. ass. (Table A2, relevés 8 to 10; Typus: relevé 9)

Three relevés done in the limestone rocks around Immuuzer-des-Ida-ou-Tanane can define a particu-

lar association of limited distribution, and with low plant richness. Only *Teucrium tananicum* and *Satureja macrosiphon* can define this restricted community situated in the semi-arid thermo-Mediterranean 'étage'.

To compare rupicolous communities of the Canaries and of S.W. Morocco, we considered the following in the Canaries: *Soncho radicati-Aeonietum tabulaeformis* Santos-Guerra and Fernandez-Galvan 1983 of the semi-arid infra-Canarian 'étage' of the northern slope of Tenerife, and *Aeonietum lindleyi* Voggenreiter in Rivas-Martínez et al. 1993 of the arid infra- and thermo-Canarian 'étages' of the southern slope of this island. In Morocco, we selected *Davallio canariensis-Dracaenetum ajgal* and *Scillo latifoliae-Saturejetum monanthae*.

### Phytogeographical types

For azonal communities, the results (Table 5) generally highlight that the widely distributed species (Mediterranean and west-Macaronesian, cosmopolitans) are predominant, especially in coastal formations, to the extent that some communities are common to the Canaries and to coastal areas of Morocco. This is the case in particular for *Frankenia ericifoliae-Astydamietum latifoliae* Lohmeyer & Trautmann 1970. Further inland, specific local features appear.

In these azonal communities:

- endemics *sensu stricto* are virtually inexistent in the Canaries, while on the Moroccan coastline, they reach high values between 16 and 30%.
  - in the Canaries, the proportion of Canarian taxa (20–30%) is comparable to that of plants common to the Canaries and S.W. Morocco, and the latter are much more numerous in the islands than on the continent.
  - Mediterranean taxa are two or three times less abundant in the islands than on the continent, where the Saharo-Mediterranean element is more represented.
- Within therophytes grasslands, Mediterranean taxa alone represent 92% of species in Tenerife, and 75% in Morocco, where there is a rather important contingent of Saharo-Mediterranean (17%) taxa. The endemism rate of these communities is low, between 1 and 4%.

Even if zonal communities of low and medium altitudes show a certain physiognomic convergence, examination of Table 5 confirms the clear disparity between the biogeographical spectra of the two regions:

- Strictly endemics have higher values in Morocco (7 to 26%) than in the Canaries (2.5 à 9.8%). Endemism is more marked in *Euphorbia echini-Arganietum*, located in the zone north of Agadir.
- Endemic species and those common to the two regions are about twice as numerous in the infra-Mediterranean and infra-Canarian 'étages' than in the thermo-Mediterranean and thermo-Canarian 'étages'.
- Canarian taxa represent between 40 and 60% of species in the Canarian communities, while they are, of course, absent from Morocco.
- Mediterranean taxa in the broad sense are clearly predominant in Morocco (between 60 and 85%), while in the Canaries, they represent between 17.5 and 20% in chamaephytic formations.
- Mediterranean-tropical taxa are more numerous in the Canaries (5 to 16.4%) than in Morocco (2.9 à 8.5%), while the inverse is true for taxa of

Mediterranean-Saharan origin, which represent a contingent of 6 to 10.6% on the continent, but are absent from the Canaries.

For rupicolous communities, the percentages of local endemics are higher in relation to the azonal and zonal formations, both in the Canaries (17 à 21%) and in Morocco (14 à 23%). The rate of species common to the two areas is small, except for the sub-maritime community *Scillo latifoliae-Saturejetum monantha*, where it reaches 7.5%. If we examine the most frequent biogeographical types, the distortion is very clear between the two regions: in the Canaries, more than half (52 to 55%) of the rupicolous species belongs to strictly Canarian and Macaronesian elements, while Mediterranean taxa predominate in Morocco and culminate at 76% in the case of *Davallio canariensis-Dracaenetum ajgal*.

### Growth-forms

Using the same communities as for biogeographical analysis, the spectra of growth forms obtained are shown in Table 6.

For azonal communities, the rarity of therophytes in the Canaries is still perceptible (around 5% in formations of *Euphorbia paralias* or of *Frankenia capitata*), while annuals represent around 50% of species on juxta-coastal sands of Morocco. As above, hemicryptophytes and nanophanerophytes have the highest rates in the islands. For post-cultivation formations with annuals, as for grasslands included in *Tuberarietea*, the situation is virtually identical in Morocco and in the Canaries: everywhere, annuals represent around 70% of the plant diversity, with a maximum of 91% for grassland of *Hypochaeris glabra* and *Tuberaria guttata*.

Within zonal plant communities, the results obtained for the four analysed formations in infra-Canarian and infra-Mediterranean 'étages' and in the same climatic environment are very comparable. However, the presence of a significant rate of phanerophytes (around 11.5%) in Moroccan communities underlines the role of trees (*Argania*, *Acacia*, *Rhus*, etc.) in this zone in Morocco, while the infra-Canarian 'étage' has practically none. In the thermo-Canarian and thermo-Mediterranean Moroccan 'étages', this difference decreases but the percentage of trees remains higher in Morocco. On the other hand, the percentages of chamaephytes and nanophanerophytes become different; chamaephytes are predominant in Morocco (around 30%) as opposed to 5–6% in the Ca-

Table 5. Plant communities phytogeographical spectra, in S.W. Morocco (M) and the Canary Islands (C).

	Region	Species number	Endemic	Canary Islands	Macaronesian region	Canary-S.W. Morocco	Medit. & W. Morocco	Tropical & Medit.-Tropical	Sahara-Medit.	Cosmopolite
Azonal communities										
Euphorbio paraliasi-Cyperetum kalli	C-M	19	0	21	5.2	31.6	31.6	0	0	10.5
Chrysanthemo carinatae-Senecietum hesperidi	M	30	20	0	0	13.3	56.7	3.3	0	6.7
Bubonio imbricati-Centaureetum gentilii	M	44	15.9	0	0	6.8	61.3	4.5	6.8	4.5
Frankenio capitatae-Zygophylletum fontanesii	C	21	0	31.8	4.5	22.7	27.3	0	0	13.6
Arthrocnemetum indici	M	7	0	0	0	14.3	71.4	0	0	14.3
Limoniastrum weygandiorum community	M	32	29	0	0	12.9	35.5	3.2	19.3	0
Hypochaeridi glabrae-Tuberarietum guttatae	C	35	1.2	3.8	0	0	92.4	1.2	0	1.2
Stipo retortae-Notoceretum bicornis	M	53	3.8	0	0	0	75.4	0	17	3.8
Stipetum capensis macaronesicum	C	56	6.3	4.2	4.2	2.1	61.2	4.2	12.6	4.2
Zonal communities										
Ceropegio fuscae-Euphorbietum balsamiferae	C	61	9.8	41	1.6	8.2	19.7	16.4	0	3.3
Periploco laevigatae-Euphorbietum canariensis	C	58	8.6	50	6.9	5.1	18.9	8.6	0	3.4
Euphorbio beaumieranae-Arganietum spinosae	M	57	13.5	0	0	7.7	61.5	7.7	9.6	0
Euphorbio echini-Arganietum spinosae	M	34	26.5	0	0	5.9	55.9	2.9	8.8	0
Junipero canariensis-Oleetum cerasiformis	C	61	6.7	58.3	6.7	1.7	18.3	6.7	0	1.7
Cistetum symphytifoliae-monspeliensis	C	40	2.5	60	5	2.5	17.5	5	0	7.5
Oleo maroccanae-Arganietum spinosae	M	47	8.5	0	0	42	68	8.5	10.6	0
Tetraclino articulatae-Arganietum spinosae	M	67	7.3	0	0	0	85.3	1.5	5.9	0
Rock communities										
Soncho radicati-Aeonietum tabulaeformis	C	42	21.4	47.6	4.7	2.4	9.5	7.1	0	7.1
Aeonietum lindleyi	C	36	16.7	47.2	8.3	0	16.7	8.3	0	2.8
Davallio canariensis-Dracaenetum ajgal	M	85	14	0	0	1.2	76.4	5.9	2.3	0
Scillo latifoliae-Saturejetum monanthae	M	51	22.6	0	0	7.5	54.7	11.3	1.9	1.9

Table 6. Plant communities growth forms spectra, in S.W. Morocco (M) and the Canary Islands (C). Th/Hb: therophytes and bi-annual hemicryptophytes; Hv: perennial hemicryptophytes; G: geophytes; Ch: chamaephytes; NPh: nanophanerophytes; Ph: phanerophytes; PhL: lianescent phanerophytes; Pa: parasites.

	Region	Species number	Th/Hb	Hv	G	Ch	NPh	Ph	PhL	Pa
Azonal communities										
Euphorbio paraliasi–Cyperetum kalli	C–M	19	5.2	10.5	5.2	52.6	26.3	0	0	0
Chrysanthemo carinatae–Senecietum hesperidi	M	30	53.3	0	6.7	40	0	0	0	0
Bubonio imbricati–Centaureetum gentilii	M	44	50	4.5	9	36.4	0	0	0	0
Frankenio capitatae–Zygophylletum fontanesii	C	21	4.7	33.3	0	14.3	47.6	0	0	0
Arthrocnemum indici	M	7	14.3	14.3	0	57	14.3	0	0	0
Limoniastrum weygandiorum community	M	32	12.5	12.5	0	50	25	0	0	0
Hypochaeridi glabrae–Tuberarietum guttatae	C	35	91.4	0	2.8	5.7	0	0	0	0
Stipo retortae–Notoceretum bicornis	M	53	64.1	3.8	7.5	11.3	9.4	3.8	0	0
Stipetum capensis macaronicum	C	56	75	0	3.5	10.7	10.7	0	0	0
Zonal communities										
Ceropegio fuscae–Euphorbietum balsamiferae	C	61	5.2	15.8	7.9	21	44.7	0	5.2	0
Periploco laevigatae–Euphorbietum canariensis	C	58	2.4	14.3	4.7	16.7	54.8	0	7.1	0
Euphorbio beaumieranae–Arganietum spinosae	M	57	5.7	13.5	5.7	21.1	36.5	11.5	3.8	1.9
Euphorbio echini–Arganietum spinosae	M	34	0	2.9	11.7	14.7	47	11.7	8.8	2.9
Junipero canariensis–Oleetum cerasiformis	C	61	0	13.1	8.2	6.5	55.7	9.8	6.5	0
Cistetum symphytifoliae–monspeliensis	C	40	0	15	12.5	5	57.5	7.5	2.5	0
Oleo maroccanae–Arganietum spinosae	M	47	6.4	6.4	6.4	29.8	21.3	21.3	6.4	2.1
Tetraclino articulatae–Arganietum spinosae	M	67	20.9	2.9	7.4	31.3	22.4	13.4	1.5	0
Rock communities										
Soncho radicati–Aeonietum tabulaeformis	C	42	4.7	14.3	16.6	28.6	35.7	0	0	0
Aeonietum lindleyi	C	36	5.5	13.9	19.4	8.3	47.2	0	5.5	0
Davallio canariensis–Dracaenetum ajgal	M	85	1.2	14.1	10.6	28.2	24.7	15.3	5.9	0
Scillo latifoliae–Saturejetum monanthae	M	51	3.9	19.6	11.7	21.6	37.2	3.9	0	1.9

naries, while the rates of nanophanerophytes are twice as high in the Canaries. As regards herbaceous species, although hemicryptophytes are much more numerous in the Canaries (13 to 15%) than in Morocco (3 to 6%), therophytes are absent from the islands, in contrast with the Moroccan situation.

In rupicolous communities, the particularities shown by the various growth forms and identified in the zonal communities are found again, although to a lesser extent: phanerophytes are present in Morocco and absent from the Canaries. It could be different if the Canarian communities with *Dracaena draco* still exist in the Canary islands, but the Dragon-tree is now a very relictual species (only few individuals in the wild), and nowadays, none community with *Dracaena* cannot be described and others trees are

very scarce in these rocky habitats. There is also a slight predominance of chamaephytes in Morocco and of nanophanerophytes in the Canaries and, in all cases, therophytes (1 to 5%) play a very minor role. One should also note the importance of herbaceous perennials (hemicryptophytes and geophytes) which represent almost a third of the biological spectra of rupicolous communities in Morocco.

## Discussion

The studied area of S.W. Morocco, that is the zone of potentially continuous stands of Argan in the infra- and thermo-Mediterranean 'étages', constitutes a very specific region from a floristic viewpoint. From a physiognomic viewpoint, the presence of succulent



species implies a close relationship with certain areas of the Canaries that are climatically and ecologically very similar. On the floristic level, this impression seems to be confirmed by the presence in these two areas of a certain number of common or vicarious species.

For these reasons, some authors (e.g., Peltier 1982; Biondi et al. 1994; Kim et al. 1996) believed it was necessary to include this Argan sector to the Macaronesian domain and referred to a 'Macaronesian-Moroccan sector'. As one of us (Quézel 1995) recently pointed out, after several authors had analysed the origin and establishment of the Canarian flora (e.g., Sunding 1979; Bramwell 1985), this interpretation is in fact paradoxical. The Moroccan area considered has evidently served as a principal source-territory for plant colonisation of the Canary Islands, since the emergence of the oldest islands in the archipelago (Fuerteventura: 20.7 Mya, Lanzarote: 15.5 Mya, according to Kim et al. 1996), which are precisely the closest to the African coast. Furthermore, recent molecular phylogenies (e.g., Francisco-Ortega et al. 1995, 1996, 1997; Kim et al. 1996) show that many of Macaronesian plants had a Mediterranean origin. Currently, most authors (Bramwell 1985; De Nicolas et al. 1989; Shmida & Werger 1992; Quézel 1995) stress the essential role played by long-distance dispersal of species in the organisation of communities in Macaronesia. Thus, among the colonising plants necessary for the establishment of the present flora in the Canaries, 83% are dispersed over long distances (Bramwell 1985). Therefore, starting at the first half of the Miocene, the Canaries were supplied by the neighbouring African flora. Their present flora was gradually constituted according to the climatic and biogeographic vicissitudes in the western part of North-Africa since at least the beginning of the Miocene, but especially since the Pliocene period (Quézel & Barbero 1993). As stated by Huntley (1991), the main response of the taxa to climatic changes is more a strategy of migration than one of adaptive evolution, although the latter can be rapid in an insular situation (e.g., in Macaronesia, the speciation process of *Argyranthemum* began only in the middle Quaternary, between 1.2 Mya and 0.7 Mya according to Francisco-Ortega et al. 1996, 1997). Furthermore, according to paleoecological records, Clark et al. (1998) have recently underlined the rapid migrations of many temperate trees, 'well beyond that expected from the average dispersal distance'. Therefore the real 'Canarian plant conservatory' that was thus established

was only the result of this long-distance colonisation (De Nicolas et al. 1989), on islands where the major quaternary climatic fluctuations probably only had a quite limited impact, at least in the central and western islands. Note, however, that Kim et al. (1996) explain the recent adaptive radiation (between 4.2 and 2.3 Mya) of *Sonchus* subg. *Dendrosonchus* in the Canaries by Pliocene climatic and ecological upheavals induced by the first glaciation (2.8 Mya) in the northern hemisphere and the start of desertification of the Sahara (2.5 Mya). The key factors responsible for gradual speciation of plants in Macaronesia are: (i) ecological diversity (an often marked altitudinal gradient, contrasting bioclimates on different slopes, volcanic activity); (ii) general climatic stability due to the oceanic climate; and especially (iii) insular isolation. Together, all these factors favoured the radiative speciation process (Humphries 1979), and divergence following inter-island colonization (Francisco-Ortega et al. 1997), particularly frequent in the Canaries, notably in the Crassulaceae (Lems 1960) belonging to the *Aeonium* genera (35 species and subspecies), *Monanthes* (17), *Aichryson* (14), *Greenovia* (4), within the chamaephytic Asteraceae: *Sonchus* (24), *Cheirolophus* (16), *Tolpis* (8), and especially *Argyranthemum* (33; Humphries 1976; Francisco-Ortega et al. 1997), but also *Echium* (31), *Sideritis* (26), *Satureja* (22), *Limonium* (22) and *Lotus* (21).

S.W. Morocco, much more affected by Plio-Quaternary climatic changes, gradually lost virtually all its tertiary paleoflora, in particular species of laurel forest, the most demanding as regards hydrological criteria. However, because of the oceanic influences and the Atlas relief, this area of Morocco also acted as a refuge, although on a much more modest scale, particularly for African thermo-xerophile elements that are also present in the Canaries (cactiform *Euphorbia* and shrubs, *Caralluma*, *Aeonium*, *Dracaena*, *Senecio anteuphorbium*, etc.). The gorges of Assif Oumarhouz in the western Anti-Atlas, where a population of several thousand *Dracaena draco* subsp. *ajgal* has been discovered recently (Benabid & Cuzin 1997), are probably the most representative case for North-Africa of a refuge for tertiary flora (Figure 4). S.W. Morocco also received more recent inputs of species of Saharan or even dry tropical origin, which are absent from the Canaries (*Acacia*, *Argania*, *Kalanchoe*, *Leptochloa*, *Pentzia*, *Commelina*). In all these situations, depending on the length of isolation and the genetic potentials of the species, endemism developed at different rates, but the phenomenon of adaptive radiation is almost

totally absent from S.W. Morocco, except perhaps in juxta-coastal situations (*Limonium*, *Lotus*).

Cooper (1997) underlines that cliff habitats with the greatest species diversity are likely to be subject to less extremes of environmental variability. For Moroccan rupicolous communities, we must stress the high number of species where, in addition, accidentals have not been taken into account. Thus *Davallio canariensis-Dracaenetum ajgal* contains 85 species, and *Scillo latifoliae-Saturejetum monantheae* contains 53. These values confirm the classic refuge role played by these rupicolous habitats (Snogerup 1971) for all the flora of the region, including species of tropical origin that sometimes have their only Moroccan population there (Mathez 1974; Benabid & Cuzin 1997). Outside the zone studied, some of these plants have a few isolated populations in the whole of Morocco, which underlines their residual character. This is the case in particular for *Argania spinosa* in Beni-Snassene and S.W. of Casablanca, *Aeonium arborescens* on the Rif coastline, and even *Laurus azorica* in the Ksiba Atlas (Barbero et al. 1981).

However, despite the physiognomic and historical affinities between the two regions, the biogeographical interpretation of a flora must take into account all its components. In S.W. Morocco, the 1400 taxa present in the region in question only include a very small number of species in common with the Canaries, or even vicarious species (2 to 3% at the most), including many in a coastal situation. One should not exclude the recent establishment of certain species coming from the Canaries, since, for example, 75% of endemics common to the two regions are long-distance dispersed. Even if future taxonomic investigations may slightly raise the number of common taxa, this would never justify the inclusion of S.W. Morocco in the Macaronesian sub-region (Rivas-Martinez et al. 1987, 1993). Similarly, it is not possible, as did Peltier (1982), to limit this 'Moroccan-Macaronesian sector' to a narrow sub-coastal strip, since more than half the zonal and rock vegetation communities (Tables A1 and A2) are precisely in this zone, which must therefore be accorded the same biogeographical status. Only certain azonal communities on marine and coastal sands have a clearly higher percentage of species common to Morocco and the Canaries: more than 60% (i.e., 19 species) in *Euphorbio paraliasi-Cyperetum kalli*, and 50% (i.e., 22 species) in *Franke- nio capitatae-Zygophylletum fontanesii*, communities that are present in the Canaries and the Moroccan

coast, or even in the circum-Mediterranean area for the former.

Examination of the biogeographical types and some species' life attributes (growth forms, succulence and dispersal) also underline these disparities. Irrespective of the communities analysed, the taxa of mediterranean origin are generally at least twice as numerous in Morocco, where the Saharo-Mediterranean element is also apparent. In the Canaries, on the other hand, Canarian and Macaronesian species are clearly predominant, except in the therophyte grasslands where the invasion of mediterranean taxa must be explained, as in other regions (particularly California, according to Heady 1977), by historical anthropozoogenic disturbances. The spectra of growth forms show the importance in Morocco of phanerophytes and, to a lesser degree, chamaephytes, while, in the Canaries, nanophanerophytes and hemicryptophytes are generally better represented. Therophytes, well represented in zonal and especially azonal communities of Morocco, play a very limited role in the islands. In addition, the spectra of growth forms obtained for Canarian communities are quite different to those for the entire flora of the Canaries (Shmida & Werger 1992), where it is still clear that therophytes are under-represented in comparisons with the Mediterranean world (Freitag 1971; Quézel 1985). The differences between the work of Shmida & Werger (1992) and our study are mainly due to the fact that all the vegetation structures analysed here are in the infra- and thermo-Canarian arid and semi-arid 'étages'. In these low levels, laurel forests, but also higher areas where phanerophytes become more abundant, and where chamaephytes are greatly predominant over nanophanerophytes, are excluded. Most Moroccan succulent species are found in the coastal belt where marine and semi-desert influences are mixed, as on the coastlines of the Canaries (Rivas-Goday & Esteve 1965; Shmida & Werger, 1992) and the Arabian peninsula (Deil 1991). But the census of succulent species shows that this life-strategy in Morocco (around 5% of species) is half than in the Canaries, despite the physiognomic role played by cactiform *Euphorbia* and *Senecio anteuphorbium*.

Therefore, on the basis of the phytogeographical spectra and species' life attributes, the Moroccan region studied must be only considered from the historical and biogeographical viewpoints as a specific sector – the S.W. Moroccan sector of the North-African Mediterranean domain – and not at all as a Macaronesian enclave in Morocco.

## Acknowledgements

We are grateful to Prof. Benabid (Rabat) and his team for the organisation of the field trip carried out in May 1996 in the western part of the Anti-Atlas. We thank Prof. U. Deil (Freiburg) who made helpful comments on a preliminary draft of the manuscript.

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Table A2. Location of rupicolous communities relevés. *Scillo latifoliae-Saturejetum monanthes* nov. ass.: Relevés 1 & 2: gorges of Kheneg el Hamman, S.W. of Goulimine, near the track of El Ayoun du Draa. Relevés 3 & 4: gorges of Oued Noun (Maire ined. 1937). Relevé 5: gorges of Oued Ouarsik, S.W. of Ifni (Mathez 1974). Relevés 6 & 7: rocks located at 10 and 15 km, S.W. Ifni (Barbero et al. 1982). *Teucrium tananici* nov. ass.: Relevés 8 to 10: calcareous rocks near Immouzer-des-Ida-ou-Tanane. Substrate: Qz: quartzites; Ca: calcareous rocks; Gr: sandstone; Dol.: dolomite rocks.

Relevé number	1	2	3	4	5	6	7	8	9	10
Altitude (m)	400	450	150	150	30	280	300	700	750	700
Aspect	SW	E	S	SW	S	W	SW	N	NW	N
Slope (°)	70	65	60	80	-	80	70	90	90	80
Substrate	Qz	Qz	Gr.	Gr.	Dol.	Qz	Qz	Ca.	Ca.	Ca.
Relevé area (m <sup>2</sup> )	100	100	200	200	-	200	200	100	100	100
Total cover (%)	25	30	30	40	-	40	50	40	40	30
Taxa number	9	15	9	16	28	25	23	17	23	16
<b>Characteristic species</b>										
<i>Scilla latifolia</i>	1.1	1.2		1.2	x	+	1.2			
<i>Satureja monantha</i>	1.1	1.1	+	1.2	x					
<i>Kalanchoe laciniata</i> subsp. <i>faustii</i>				1.2	x		1.2			
<i>Leptochloa ginae</i>		1.1			x					
<i>Thymus hesperidum</i>				1.2	x					
<i>Abutilon albidum</i>				1.2						
<i>Commelina rupicola</i>					x					
<i>Enteropogon rupestris</i>					x					
<i>Teucrium tananicum</i>								2.3	1.2	1.2
<i>Satureja macrosiphon</i>								2.3	1.2	
<b>Species of the Celsio-Aeonion arborescentis</b>										
<i>Sonchus pinnatifidus</i>	+	+		1.1	x	+	+			+
<i>Polygala balansae</i> var. <i>foliosa</i>	1.2	1.2	1.2		x			1.1	1.1	1.1
<i>Bituminaria bituminosa</i> var. <i>rotundifolia</i>	1.2	+		1.2					1.2	1.2
<i>AEonium arborescens</i>		+2	+	1.2			+2			
<i>Warionia saharae</i>		1.1		1.2		+2	1.2			
<i>Celsia longirostris</i> subsp. <i>antiatlantica</i>		1.1						+	+	
<i>Perralderia coronopifolia</i> subsp. <i>purpurascens</i>		1.2	1.2		x					
<i>Davallia canariensis</i>			+				1.2			
<i>Andrachne maroccana</i>									1.2	1.2
<b>Species of the Tinguarretalia siculi</b>										
<i>Calendula suffruticosa</i>		+	1.2						2.2	1.2
<i>Phagnalon saxatile</i> subsp. <i>purpurascens</i>	1.2	+		+						
<i>Lavatera maritima</i>			1.1	1.2					1.2	
<i>Silene patula</i> subsp. <i>patula</i> var. <i>hesperia</i>				1.2				2.3	1.2	
<i>Galium bourgaeianum</i>								1.2	1.2	1.2
<i>Satureja hochreutineri</i>								+	+	
<i>Sedum dasyphyllum</i> subsp. <i>glandulosum</i>									1.2	+
<i>Scrophularia arguta</i>								1.2		
<i>Dianthus lusitanicus</i>									1.2	
<b>Species of the Asplenietea trichomanis</b>										
<i>Cheilanthes vellea</i>	+	+								
<i>Capparis spinosa</i>		1.2		1.2						
<i>Phagnalon saxatile</i> subsp. <i>saxatile</i>								1.1		1.2
<i>Umbilicus rupestris</i>									1.1	1.1
<i>Asplenium ceterach</i>									+	+
<i>Sedum sediforme</i>								1.2		
<b>Species of the Acacio-Arganietalia</b>										
<i>Senecio anteuphorbium</i>	1.2	+	+	1.2	x		2.3	1.1		
<i>Euphorbia officinarum</i> subsp. <i>echinus</i>	+		1.2	1.2	x	3.3	2.2			
<i>Argania spinosa</i>					x	2.2	2.3		+2	
<i>Asparagus pastorianus</i>				1.2		1.1	+2			
<i>Striga gesnerioides</i>					x	+	+			
<i>Caralluma commutata</i> subsp. <i>hesperidum</i>					x	+	2.3			
<i>Euphorbia obtusifolia</i> subsp. <i>regis-jubae</i>					x	2.2	1.2			
<i>Periploca angustifolia</i>						2.2	1.2			
<i>Coronilla ramosissima</i>						+			1.2	
<i>Chamaecytisus mollis</i>									1.2	+
<i>Genista ifniensis</i>							1.2			
<i>Linaria sagittata</i>						+				
<i>Bupleurum dumosum</i>										+
<i>Digitaria commutata</i> subsp. <i>nodosa</i>					x					

Table A2. Continued.

Teucrium collincola					x					
<b>Species of the Quercetea ilicis</b>										
Ephedra altissima					x	+	1.2			
Coronilla viminalis							1.2	+	1.2	
Ballota hirsuta								+	+	1.2
Arisarum vulgare							1.2	+		+
Prasium majus							+	1.1		1.1
Lycium intricatum					x	1.2				
Rhamnus lycioides subsp. atlantica						+				1.1
Withania frutescens						+				
Asparagus horridus							+			
Crambe filiformis								1.1		
Cerantonia siliqua									+	
<b>Others species</b>										
Fagonia cretica					x	+	1.2			
Echium petiolatum					x					1.1
Tetrapogon villosus							+2	1.2		
Scilla maura							1.1		+	
Lotus jolyi							+	+		
Convolvulus trabutianus							2.2			
Salsola oppositifolia							1.2			
Andropogon distachyos							1.2			
Urginea maritima							+1			
Dactylis glomerata subsp. hispanica								1.2		
Cenchrus ciliaris					x					
Traganopsis glomerata					x					
Salsola vermiculata					x					
Salsola glomerata					x					
Limonium fallax					x					
Vagaría ollivieri					x					