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Abstract

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The flora and biogeography of the Atlantic Sahara have been little studied, and most of the corresponding literature was published between 1935 and 1950. The paucity of data on the region reflects, in part, the extreme climate in much of the Atlantic Sahara, but also logistical and geopolitical obstacles. Many biogeographical questions remain unresolved. This paper presents an analysis of 22,000 vascular plant records for southern Morocco, northern Mauritania, and western Algeria. The floristic richness of the Atlantic Sahara (s.str.) is estimated at 578 taxa and subspecies, 78 being endemic (s.l.), yielding an endemism rate of 13 %. Biogeographic and bioclimatic analyses suggest that this area, positioned between the Mediterranean and Afro-tropical regions, forms an important gradient; the Atlantic Sahara may thus be best characterized as an ecotone or transition zone, as it was proposed by White in 1986 for the Sahara as a whole. Based on our geostatistical analyses of climate data and plant occurrences, and supported by recent collections and field observations, we propose a new phytogeographical bioregionalization for the Atlantic Sahara, including four new subregions, conforming to the framework of "Ecoregions of the World".

Keywords

North Africa – Sahara – Biogeography – Delineation – Ecoregion – Endemism – Flora

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Introduction

The spatial distribution of species is central to understanding biogeography and monitoring environmental dynamics and biodiversity. Such data have become only more critical in the face of accelerating climate change, and this has been especially true in arid and semiarid regions (Cartereau et al., 2023). While big data has improved our ability to delimitate biogeographical regions for many parts of the world (e.g. Holt et al., 2013; Edler et al., 2017; Morrone, 2018), some regions remain highly data-deficient, more severely so than previously recognized (Boakes et al., 2010; Qian et al., 2018; Farooq et al., 2021). Compounding this problem, data that do exist for these regions are at times based on questionable taxonomy (Maldonado et al., 2015; Hortal et al., 2008).

The Sahara Desert is one such region marked by deep biogeographical ignorance (Brito et al., 2014; Médail & Quézel, 2018). Though the Sahara is the largest desert in the world, with an area of c. 8.5 million km^2, it has been the subject of few biogeographic studies using modern geostatistical approaches. The more recent bioregionalization studies of the Sahara-Sahel region have drawn on the concepts of bioregion or ecoregion (Olson et al., 2001; Dinerstein et al., 2017), analyzing climate data and the distributions of vertebrates (Brito et al., 2016; Soultan et al., 2020) or vascular-plants (Naia & Brito, 2021).

If the global boundaries of the Sahara and their contractions and expansions during past climatic events have been long considered (Engler, 1910; Maley, 2010), attempts to define biogeographical units within the Sahara based on plant occurrences have been particularly difficult, as evidenced in various maps offering provisional delineations (Quézel, 1965, 1978; Frankenberg, 1978; White, 1986; Le Houérou, 1995a, b). Most of these efforts relied on old and limited data (1935–1950), with few exceptions (e.g. Barry et al., 1988; Barry, 1989, 1990). The delineation of the western part of the Sahara, or Atlantic Sahara, is particularly complex due to the varying oceanic influence and intergradation of Mediterranean and tropical elements across the region. Recent world maps of ecoregions (Olson et al., 2001; Dinerstein et al., 2017), drawing largely on White's (1986) map of Africa, do not capture this heterogeneity, showing instead quite uniform units running east-west across the Sahara. This most likely reflects insufficient data, rather than the large scale of the maps. Greater resolution, in some cases, is available, for example in Costa et al. (2016), who describe new plant associations for the Sahel-Sahara area between Mauritania and Chad and propose limits for floristic regions.

The present study proposes a more precise delineation of the Atlantic Sahara, and we concur with Takhtajan (1986) that vascular plants offer the most useful bioindicators for defining robust biogeographical units (e.g. domains, sectors, districts and subregions), particularly when considering endemism (Rodrigues et al., 2015; Morrone, 2018).

One question, dating to the seminal work of Monod (1944), concerns whether the Atlantic Sahara should be considered part of the Saharo-Mediterranean domain or the Saharo-African domain. This distinction is biogeographically more significant than may first appear, as it implies more broadly its inclusion in either the Palearctic (Holarctic) realm or the Afro-tropical realm. The boundary between the Palearctic and the Afro-tropical realms on the African continent is still debated (Linder et al., 2012; Holt et al., 2013). Though the biota of the Sahara Desert has been considered by some to be Palearctic rather than Afro-tropical (e.g. Dinerstein et al., 2017), other studies have placed the boundary between these realms along the northern margin of the Sahara (Cox, 2001), or even along the Mediterranean coast (Kreft & Jetz, 2010). A recent study based on angiosperm phylogeny has even suggested a Saharo-Arabian realm (Liu et al., 2023). The biogeographical relationship between the Atlantic Sahara and the nearby Canary Islands is subject to similar debate (Médail & Quézel, 1999, 2018; Freitas et al., 2019; Riina et al., 2021). A robust determination of these boundaries and the species characterizing these different areas is crucial because it will be at these levels that the first floristic changes due to climate change will become apparent.

Although the nomenclature used to describe the phytogeography of the Atlantic Sahara has changed, it has been difficult to break away from the earlier classifications of Murat (1944), Monod (1944, 1957) and Quézel (1965). These diverge above all in the ranks that are applied for the various biogeographical entities. In his work *Les grandes divisions chorologiques de l'Afrique*, Monod (1957) recognized a Saharo-Mediterranean domain included in the Mediterranean region and he divided the western part of this domain into two subdomains (Saharo-Atlantic and Saharo-sub-Atlantic). Quézel (1965) defined this area as the "Oceanic Sahara domain" and placed it within the Saharo-Arabian region and the Holarctic realm (Quézel, 1978). Later, White (1986) proposed the terms "Saharan transition zone" and "Mediterranean transition zone" to emphasize the existence of an ecotone in this large African region situated between two major realms.

The current convention for mapping and managing biodiversity is to identify ecoregions, and this is the category that was used in the global synthesis of Olson et al. (2001) and Dinerstein et al. (2017). These last authors divided the Atlantic Sahara between two large ecoregions: "Saharan-Atlantic coastal desert" and "North-Saharan xeric steppe and woodland". Precise biodiversity data that would allow better capturing the biogeographical complexity of this area and afford greater resolution, however, have been limited. The partitioning of the Palearctic and Afrotropic realms, for example, is still largely based on climate data.

At the regional level, floristic delineations largely remain provisional or obscure, and there is little consensus. For example, while Fennane & Ibn Tattou (2005) and Fennane et al. (1999, 2007, 2014) propose a single region called "Maroc saharien (Ms)", Dobignard et al. (1992a, b) propose a compromise between earlier delineations (Fig. 1) but provide little data to support their choices. One area of agreement is the delineation of a littoral zone of the Atlantic Sahara, which is characterized by a Quaternary sedimentary geological substrate, 100 to 200 km in width and extending along the entire coast, and especially by the distinctive climate arising from regular oceanic mists and humidity (see Fig. 2G). In contrast, the biogeographical delineation for the internal zone overlapping the Reguibat granite ridge (Fig. 3B) and approaching the Central Sahara remains debated. Although the physiognomy of the desert vegetation might lead one to conclude that this region is homogeneous, a careful analysis of floristic composition, for example of the inselbergs (*guelb* in Arabic, Fig. 4H), shows the opposite.

Though many pieces remain to be filled in for a better understanding of the complex biogeographical puzzle of North Africa, most phytogeographical analyses for the continent still concern the sub-Saharan region (Linder, 2001; Linder et al., 2012; Küper et al., 2006). Delineating biogeographical units in the Sahara Desert using modern quantitative approaches such as clustering algorithms will provide vital tools for investigating the drivers of species distributions and identifying crucial areas for the conservation of biodiversity (Brito et al., 2014, 2016).

To partially fill these gaps, several field missions were undertaken in recent years (1988–2023) to remote areas of the Atlantic Sahara, and these have yielded valuable new botanical data and provided an expanded foundation for understanding the biogeography of this area. Significant rainfalls during this period also favored the discovery of new floristic elements, particularly for Afro-tropical species, which provided important keys for this analysis (Garcin, 2016, 2019, 2022; Chambouleyron et al., 2022). Incorporating these findings, and drawing from the existing literature and herbarium specimens, we have assembled one of the most extensive compilations of botanical data to date for the Atlantic Sahara.

The objectives of this work are: (1) to perform, for the first time, a precise assessment of plant biodiversity, distribution, and endemism for this long-neglected but key biogeographical area of Africa; (2) to propose a comprehensive biogeographical delineation of the Atlantic Sahara using a geostatistical approach based on plant occurrences and bioclimatic variables.

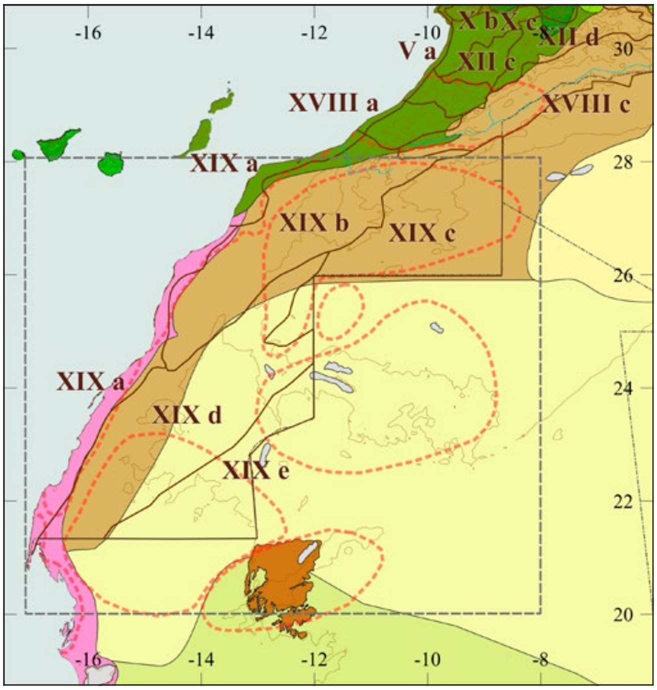

Fig. 1. – Biogeographical map of the Atlantic Sahara and neighboring areas proposed by Dobignard et al. (1992a): XIXa, Sahara littoral; XIXb, Sahara-hamaïdias; XIXc, Zemmour- Hamadas; XIXd, Sahara atlantique central; XIXe, Tiris-Tijirit.
[Based on the Ecoregion2017 map sensu Dinerstein et al., 2017]

Materials and methods

Study area

The Atlantic Sahara, as conceived in this study, refers to the large area of the Western Sahara that extends south of the Draa River valley, located between 20°N and 28°N latitude, approximately, and extending inland from the coast to about 8°W. Our analysis additionally includes data from beyond these boundaries, particularly to the north (to 30°N), so as to better apprehend the biogeographical transitions that define the region. This expanded area, which includes the Banc d'Arguin and the Adrar of Mauritania, has a total surface area of some 560,000 km² (Fig. 3A). The Saharan regions to the immediate east of the study area are true deserts, nearly devoid of vegetation. To the west, on the oceanic side, we excluded the Canary Islands, despite their interest and allied vegetation. Including them would have required considerable taxonomic revision to reconcile the continental and island floras.

Historically, the name of this region has varied from Río de Oro on old Spanish maps to, more recently, Atlantic Sahara, Western Sahara, Oceanic Sahara, or Central-Oceanic Sahara. It can be juxtaposed to the Central-Western Sahara, which includes the interior of Mauritania, Mali, and western Algeria (see maps in Médail & Quézel, 2018). Here we retain the names Atlantic Sahara and Sub-Atlantic Sahara, as these are the most widely used and least restrictive in biogeographical

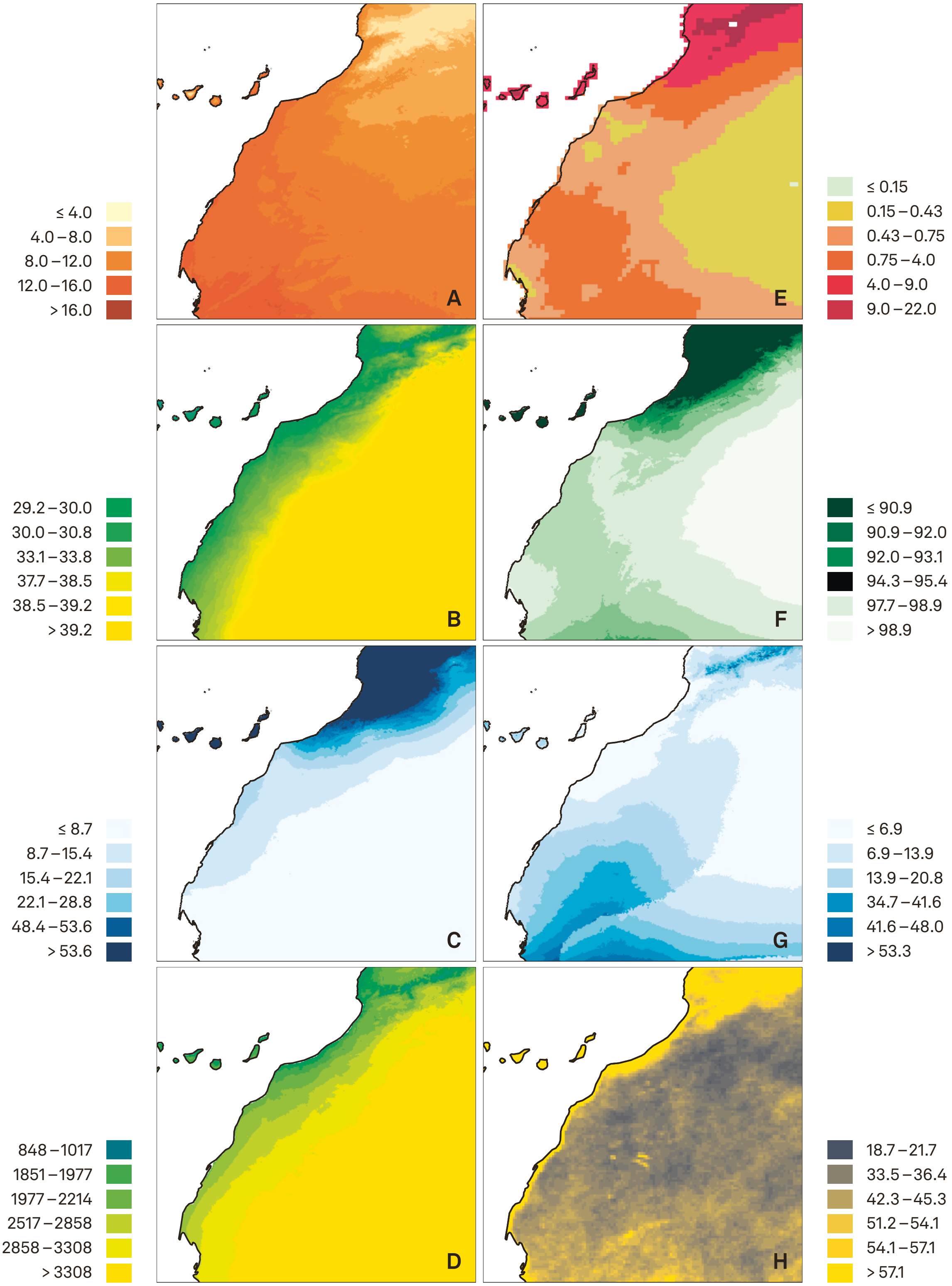

Fig. 2. – Spatial distribution of the main bioclimatic variables characterizing NW Africa and the Canary Islands. **A.** Minimum temperatures of the coldest month (Bio6); **B.** Maximum temperatures of the warmest month (Bio5); **C.** Mean precipitations of the coldest season (Bio19); **D.** Evapotranspiration (PET); **E.** PINA index, a measurement of aridity based on temperature and precipitation; **F.** Aridity index (ratio P/PET); **G.** Mean precipitation of the warmest season (Bio18); **H.** Average number of days with clouds in 2020 (Modal2_M_CLD_OT).
[**G:** based on WorldClim; **H:** see https://neo.sci.gsfc.nasa.gov]

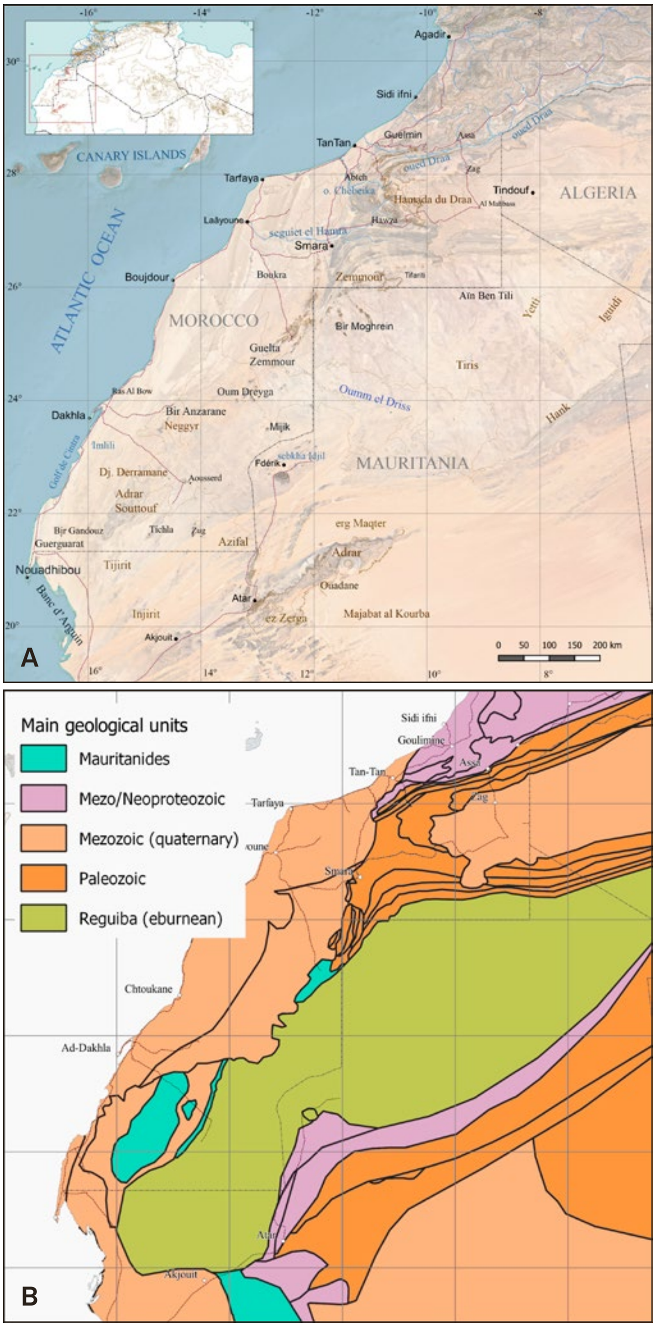

Fig. 3. – A. Geographical map of the Atlantic Sahara; **B.** Simplified geological map showing the main geological units. [Based on Michard et al., 2010]

terms, and they avoid any reference to national boundaries or geopolitical divisions, which in some cases are contested.

The Atlantic Sahara has a complex geological structure (Fig. 3B). Part of the region rests on the northern end of the crystalline basement of the Reguibat ridge, which on the surface manifests as *guelbs* and extends to Guinea. The western part of the Atlantic Sahara is marked by sedimentary layers of the Cretaceous-Tertiary period (Laayoune basin), while the eastern part is made up of a Precambrian layer. The area of Guelta Zemmour is geologically distinct, dating from the Paleozoic, and is situated within the sedimentary regions described above (Villeneuve et al., 2015). The present relief has largely been formed by northeasterly wind erosion since the Precambrian period, leading to the formation of vast plateaus (called *rich*, in Arabic) made of sandstone, clay, or limestone. Areas of sharper relief, for example the Adrar, have been shaped significantly as well by water erosion. At lower elevations, there are many vast plains covered with eolian sand, where only crystalline blocks emerge (e.g. the *guelbs* in the Azefal and Tiris regions), and clayey depressions (*sebgha* or *sebkra*, in Arabic) where the region's limited precipitation accumulates (e.g. the sebgha Ijill region).

The distinctive feature of the Atlantic Sahara is its hyperaridity (Le Houérou, 1995a), similar to the rest of the Sahara, but here somewhat attenuated by humidity and cloud cover intruding from the Atlantic Ocean. The zone is located between the arid Mediterranean region to the north, with more than 100 mm/year of rainfall (maximal rain in the winter), and the Sahelian region to the south, with 60–70 mm/year (maximal rain in the summer) (Fig. 2C, F). The period of maximum vegetation growth is between October and December, which also corresponds to the cooler months. Although precipitation or water availability is the greatest determining factor for vegetation, the minimum temperature of the coldest month also appears to be important (Dubief, 1963; Quézel, 1965). Apart from the immediate influence of salt spray along the coast (reaching perhaps 1–5 km), the major differences in floristic composition between the coastal zone and inland zones can be explained by the importance of mists and fogs (Fig. 2G) which can likely extend a hundred kilometers or more, as described by Sauvage (1951) and Barry (1990) for Bir Moghrein (Mauritania). The variation in rainfall recorded in historic times is also considerable. For example, between 1951 and 1966 rainfall was abundant. Then, from 1970 until 2003 (except for 1988) there was a severe drought. Annual variation can be high, as indicated by the rainfall trends for Bir Moghrein in Mauritania: annual rainfall reached 23.7 mm in 1945, then 68 mm in 1946, and similarly 68.3 mm in 2018, then 22.5 mm in 2019. Comparisons of average rainfall over longer periods, for example between 1926 and 1950 according to Dubief (1963) and then from 1960–2000 according to WorldClim (Fick & Hijmans, 2017), suggest a trend toward increasing aridity.

Brief history of plant biogeographical studies in the Atlantic Sahara

The foundational publications on the biogeography of plants in the Atlantic Sahara were published between 1935 and 1950, though the first botanical collections in the region go

Fig. 4. – Landscapes of the Atlantic Sahara. **A.** Atlantic coast (28°N); **B.** Shrubby steppe with *Launaea arborea* (Tan-Tan, 28.5°N); **C.** Desertic Steppe with *Traganum nudatum* (East of Dakhla, 23°4N); **D.** Desertic Steppe (Cintra); **E.** Desertic Savana with *Acacia* (Southern Guelta Zemmour, 25°N); **F.** *Caroxylon* on mound in a Wadi (Seguiet El Hamra, 27°N); **G.** Sebkhra with a small border of *Tamarix* (black Zemmour, 25.6°N); **H.** Guelb with *Panicum turgidum* desert (Azefal, 21.3°N); **I.** Arid Steppe/reg (black Zemmour, 25.9°N); **K.** Adrar of Mauritania and *Acacia tortilis* savanna (North Adrar, El Beyed, 21.7°N).
[Photos: **A–C, E–F:** C. Chatelain; **D:** A. Garcin]

back further; the naturalist and explorer René Chudeau, for example, set out from Mauritania and reached Bir Guendouz in 1908. These early studies left several open questions.

Maire & Wilczek (1935) were probably the first to recognize a division between an Atlantic Sahara, occupying "a variable depth, reaching and exceeding 40 km at certain points", and a sub-Atlantic Sahara "which extends inland to a great distance from the coast". Zolotarevsky & Murat (1938) made an early effort to subdivide the northwestern Sahara. They distinguish, within the Mediterranean domain, an oceanic Sahara and a sub-oceanic Sahara as subdomains, and their map shows the Saharo-African domain (denoted as Sahelian) as including Bir Moghrein and the Aousserd regions. Later, Murat (1944) and Monod (1944) pertinently proposed biogeographic boundaries along a north-south gradient running parallel to the Atlantic coast (Fig. 5A, B), and both recognized a coastal sector "11". Monod (1944), and later Adam (1962), debated whether this sector had either a stronger Saharo-Mediterranean or Saharo-African affiliation (Saharo-African domain = the Sahelo-Saharan domain of Zolotarevsky & Murat, 1938). The same question was again raised by Monod (1952) concerning the Banc d'Arguin and the Adrar of Mauritania, which may form the southern limit of the oceanic/sub-oceanic Sahara. Earlier, Guinea (1945, 1948) had published a relevant study of the flora and vegetation of the former Spanish Sahara, including a comprehensive map of vegetation (Fig. 5C). In the tumultuous political context of that period, however, his work perhaps did not receive the attention it deserved. Twenty years later, Quézel (1965) presented an analysis from a biogeographical perspective of the vegetation of the entire Sahara, defining the region of the Atlantic Sahara as the "domaine du Sahara océanique", but his study was based on previous authors observations. From 1970 to 2003, in addition to increased political instability, a long period of drought settled on the Sahara and Sahel, further complicating the study of the flora and vegetation of this large area. Nevertheless, during this period Lauer & Frankenberg (1977) contributed to the knowledge of the northern limits of the Afrotropic realm (referred there as Paleotropical), and Frankenberg (1978) published a map of biogeographical sectors for the Sahara. This map, though not well known, agrees with the map of Guinea (1945) in that both highlight a north-south biogeographical gradient.

Floristic data

The floristic data analyzed here represent the most exhaustive compilation of vascular plant (species and subspecies) occurrences to date for the Atlantic Sahara (Fig. 6, Appendix 2). Records have been compiled from reliable historical inventories, herbarium specimens, field trips by the authors between 1988–2022 (Fig. 6B), and published sources: Guinea (1945, 1948), Rungs & Sauvage (1945), Sauvage (1946, 1949), Monod (1952, 1988), Dubuis et al. (1960), Faurel & Simmoneau (1960), Mathez & Sauvage (1974), Gauthier-Pilters (1975), Edmonson et al. (1988), Fennane (1989), Barry (1989, 1990), Quézel et al. (1995) and Vernet & Chatelain (2022). The field expeditions added many new collections and observations, particularly for the coastline from Mauritania to Tarfaya city, the hinterland of Dakhla city, and the area of Guelta Zemmour. For the southern part of the study area, below 21°N and mainly in Mauritania, we included data from Daget (2014) for the vicinity of Atar, Adam (1962) for Inchiri, Monod (1952, 1968) for the Adrar, and the herbarium specimens of Bruneau de Miré, who made important collections in the region in 1948. The nomenclatural of the plant taxa is based on the *African Plant Database* (APD, 2024).

For purposes of our analysis, two data sets were assembled. A first dataset concerns the Atlantic Sahara s.str. (20°N to 28°N, and 8°W to the coast) and includes 13,740 observations corresponding to 578 taxa. The second dataset, aiming to position the Atlantic Sahara within a larger biogeographical context, corresponds to an area extending further to the north and east (20°N to 30°N, and to 8°W) with 922 taxa. For the region above 28°N, we incorporated data from the Emirates Center for Wildlife Propagation (Morocco), herbarium collections of Joël Mathez from the Tarfaya area (1963–1964), phytosociological observations by Quézel et al. (1995) from the Draa, and the records of Bendaanoun (1991) from the estuaries of Wadi Massa and Souss. We also included specimens from P and MPU herbaria, while we excluded data from FLOTROP-GBIF (Taugourdeau et al., 2019) because they cannot be validated taxonomically. The total dataset for this extended area comprises 22,000 occurrences (Table 1, Fig. 6C) and constitutes the largest dataset currently available for this poorly studied region.

For each species, we assigned a chorological type: Sudano-Sahelian (T, subsumed to Afro-tropical), Saharo-Sindian (SS), Mediterranean (Me), or Saharo-Mediterranean (Mes), and some secondary types as littoral, cultivated, azonal, pantropical, etc. These assignations were based on the overall range of the species, as reported in Adam (1962) and Lebrun (1977, 1981, 1998). Endemic species (from a biogeographic perspective, not in relation to national boundaries) were identified by checking general distribution maps in the *African Plant Database* (APD, 2024) and Plants of the World Online (POWO, 2024). We consider a taxon to be endemic if it is either restricted to the study area (strict endemic) or if it conforms to one of the following (subendemic) distributions: (1) present both in and to the north of the Atlantic Sahara, but not extending beyond the High Atlas Mountains (e.g. *Convolvulus trabutianus*, see Fig. 7 [author(s) of the taxa cited in the text are indicated in Appendix 2]); (2) restricted to the region of the Moroccan Saharan coast in the study area, but also found in the Canary islands (e.g. *Astydamia latifolia*, see also Fig. 7); or (3) having a range extending partially to more arid regions to the east, or more humid regions to the south (e.g. *Jatropha chevalieri*, Fig. 7).

Biogeographical clustering

The biogeographical delineation of the Atlantic Sahara was based on a cluster analysis and the presence or absence of plant species within 0.5° cells (Fig. 8). We used the unweighted pair-group method with arithmetic mean (UPGMA), with Ward.D as the agglomeration method to produce more compact clusters (Kreft & Jetz, 2010; Bloomfield et al., 2018; Castro-Insua et al., 2018). Ward.D was based on a βsim distance matrix and is not affected by taxonomic differences between cells (Marshal et al., 2020), and we used the *Vegan, hclust* and *dendextend* modules of R-cran (Oksanen et al., 2020).

A grid resolution of 1° to 2° (100−200 km) is generally used for analyses at a continental scale (Linder et al., 2012), whereas for a country or region a resolution of 0.2° to 0.5° (20 to 50 km) is generally applied, as was done by Abdelaal et al. (2020) for Egypt. In our case, the use of a 0.5° cell brings out the best definition given the distribution of observations. Some cells are empty, reflecting an entire lack of observations. To facilitate the cluster analysis, only cells with more than 5 species were retained. We also removed cultivated and non-native species (e.g. *Datura stramonium, Nicotinia glauca, Prosopis juliflora, Sesamum* spp., and *Sinapis* spp.) as well as species exclusively located in small springs or *gueltat* (*Adianthum capillus-veneris, Marsilea aegyptiaca*, etc.), representing a total of 38 spp. The number of groups retained was based on an ANOSIM test with a probability greater than 0.001. Identification of constituent and indicator species was carried out by way of the *labdsv* module of R-Cran (Roberts, 2019) at the major group level and then at the cluster level.

We initially tested a clustering approach based on Jaccard-type similarity matrices, but this revealed large variations in

Table 1. – Origin of the principal contributors to the floristic data in the areas of the Atlantic Sahara with their references, areas, number of collections and/or observations with the year intervals in square brackets, and references. Abbreviation: ECWP = Emirates Center for Wildlife Propagation.

Contributors	Area	Number of data
Adam (1962)	Mauritania	887 coll. [1956–1958]
Barry (1989, 1990)	Hank, Bir Moghrein, F'Dérik	344 obs. [1986]
Bruneau de Miré (unpubl. data)	Atar and the region of Tourine	74 obs. [1948]
Bruneau de Miré (in Sauvage, 1951a)	Bir Moghrein	74 obs. [1947–1948]
Chambouleyron et al. (unpubl. data)	Draa, Tantan, south Morroco	872 obs. [2011–2019]
Chatelain et al. (unpubl. data)	Smara, Aousserd, Mauritania	1411 coll. [2015–2018]
Dobignard (1992)	Smara, Boukra	310 coll. [1988–2017]
Dubuis et al. (1960)	Seguiet el Hamra	281 obs. [1959]
ECWP (unpubl. data)	Tata	7360 obs. [2013–2019]
Garcin (2016, 2019, 2022)	Saharan Morroco	2427 obs. [2001–2023]
Gauthier-Pilters (1975)	Bir Moghrein	69 obs. [1971]
Guinea (1945, 1948)	Zug	40 obs. [1943–1944]
Ibn Tatou (in Qninba et al., 2020)	Dakhla Imlili	68 obs. [2012]
Attioui & Lemmel (2020)	Saharan Morroco, Banc d'Arguin	1860 obs. [2017–2023]
Mathez & Sauvage (1974)	Tarfaya	450 obs. [1963–1970]
Médail et al. (unpubl. data)	Adrar Souttouf and Dakhla area	343 obs. [2019]
Monod (1952, 1988)	Adrar	442 obs. [1923–1977]
Quézel et al. (1995)	Draa, Tata, Agadir	1129 obs. [1992]
Sougy (in Vernet & Chatelain, 2022)	Yetti, Bir Moghrein, Iguidi	389 coll. [1952–1954]
Various: Chudeau (1910), Jury (2007), Ollivier (1935–1939), Podlech (1986, 1990) (unpubl. data)	Saharan Morroco	470 obs. et coll. [1910–1990]

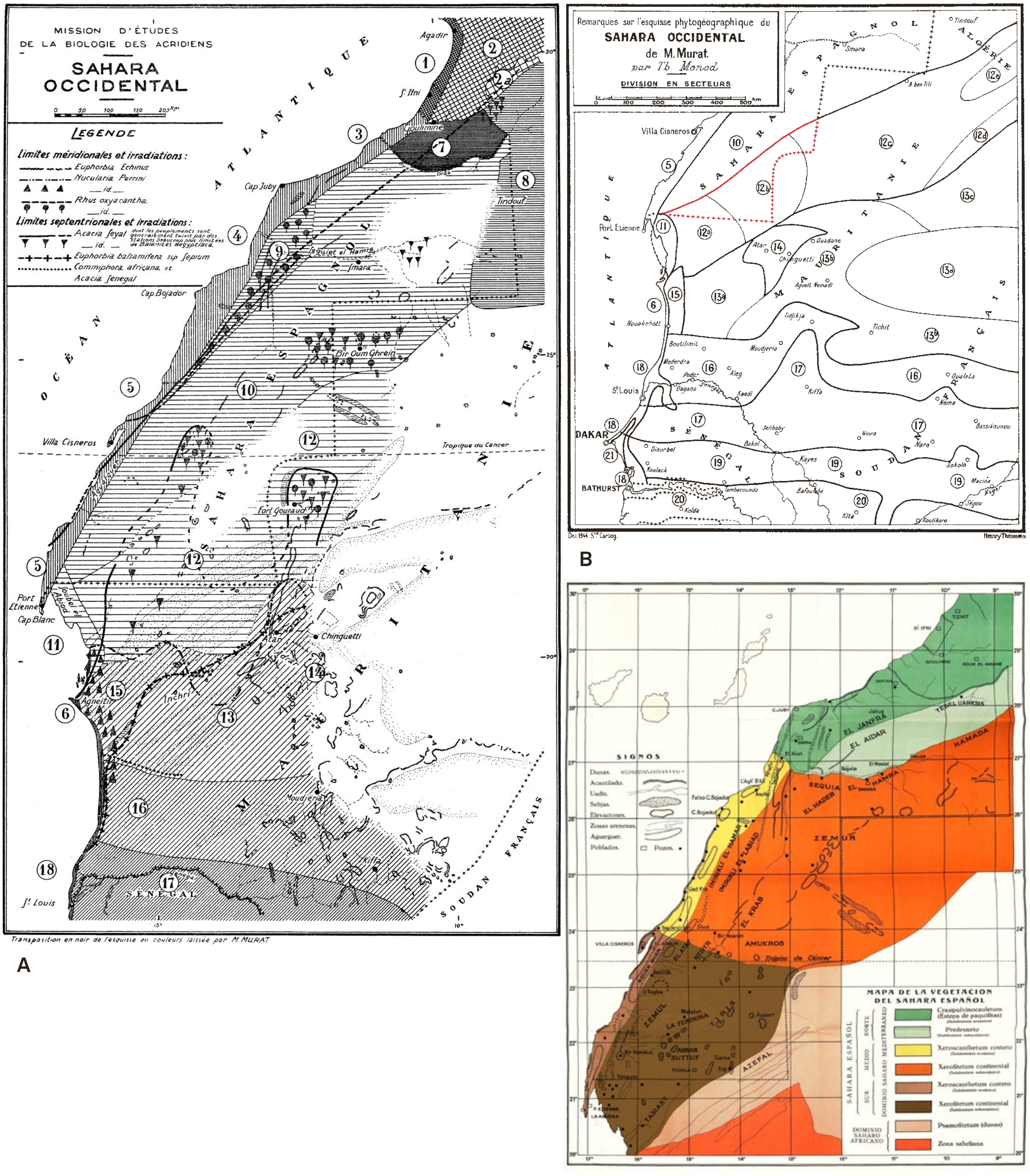

Fig. 5. – Earliest biogeographical maps of the Atlantic Sahara. **A.** Sectors defined by MURAT (1944): ⑤: Aguerguer (coastal); ⑨: Seguiet el Hamra sector; ⑩: central sector; ⑪ Banc d'Arguin; ⑫ Azifal-Tijirit; **B.** Map of the biogeographic sectors by MONOD (1944), in red its "unkown sector" ⑫; **C.** Vegetation map of GUINEA (1945).

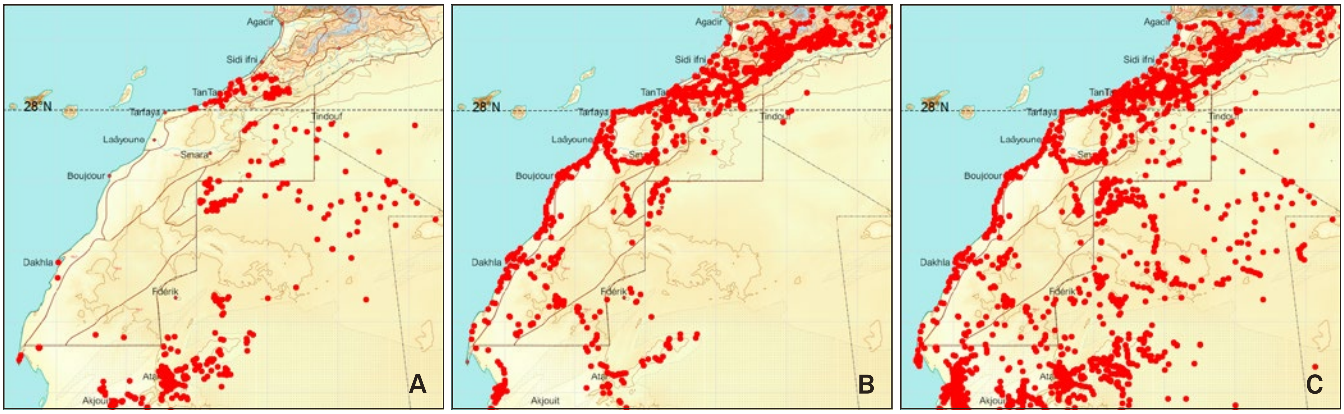

Fig. 6. – Maps of plant observations recorded during the main botanical expeditions performed in the Atlantic Sahara and adjacent areas. **A.** 1937–1961; **B.** 1988–2022; **C.** All 22,000 observations.

clustering when adding or removing certain cells. We opted instead for a Beta sim dissimilarity matrix, which gave more consistent results (Marshal, 2020; Marshal et al., 2020). We found that adding data at the periphery of the study area (that is, applying the analysis to a wider context) leads to a very different result, particularly in terms of the degree of similarity of the oceanic (coastal) group with the Mediterranean group. The study of gradients always depends on the scale chosen and the portion of the gradient studied.

All the statistics and percentages concerning endemism or biogeographical affinity were calculated at the level of the 8 clusters; that is the data from the corresponding cells were aggregated and averaged. The cells of 50 × 50 km, taken individually, vary considerably due to their limited surface area and their differing degrees of sampling.

Bioclimatic data

The bioclimatic data derives from two distinct sources; the first is the WordClim-V2 project (Fick & Hijmans, 2017), the second is Terra MODIS satellite images [https://neo.sci.gsfc. nasa.gov], with a ground resolution of 250 m. Among the many available variables, we selected the average cloud cover (Cloud Mask product MOD35) and insolation (CERES: Clouds and the Earth's Radiant Energy System) to consider the role of mists (and thereby of possible unregistered precipitation) which are a predominant factor in the coastal zone (Fig. 2H).

Several bioclimatic indices based on WorldClim-V2 data were calculated using the Envirem module for R-cran (Bemmels, 2017), including annual evapotranspiration potential (Mokhtari et al., 2014) (Fig. 2D), and the PINA index (Fig. 2E), which measures aridity based on both temperature and precipitation (Deniz et al., 2011). We also considered: minimum rainfall values for the drier months (Fig. 2C); the Emberger Q index, although this appears more useful in the Mediterranean (Mokhtari et al., 2014); the Thornthwaite aridity index (Fig. 2F); and the continentality index, the one index that does not consider rainfall. These variables were organized in raster format, and the climatic indices were aggregated (by nearest neighbor) conforming to the resolution used for the cluster analyses, either 0.5° or 1°, and then processed in a Canonical Correlation Analysis (CCA) to identify the climatic factors most linked to the distribution of certain groups of species. Of the 23 variables tested, we excluded 10 which were closely correlated with one another, retaining then 13 climatic variables (Fig. 9).

We did not consider topographic or geological variables. These are difficult to interpret at the level of cells (which can be heterogeneous, for example including both sandy zones and *guelbs*), and our focus was on gradients over a large area. For similar reasons, we have not included wind, despite its being a powerful force on both the landscape and vegetation. Wind intensity varies locally and correlates closely with topography; average yearly values are close to 48 km/h on the coast and 24 km/h inland (Davis et al., 2023).

All maps and spatial analyses were produced using R-cran and QGIS.org 3.4.13 (QGIS, 2019).

Results

Plant diversity of the Atlantic Sahara

An initial diversity analysis of the Atlantic Sahara at a broad scale, including peripheral areas (extending to 30°N) and with a resolution of 1° (for a total of 60 cells, Fig. 8A), showed a clear floristic boundary near the Draa valley. Indeed, north of 28°N, the floristic richness of the 1° grid cells ranges from some 214 to 338 spp./cell for the best surveyed zones, whereas in the south this richness is typically between 50 and 150 species, other than for the region of Atar, in Mauritania, with 178 species. For this larger area we identified a total of 922 species, 343 more than in the Atlantic Sahara s.str. (extending to 28°N). These additional species at the northern limit derive largely from Mediterranean families such as *Crassulaceae, Iridaceae, Linaceae, Oleaceae, Papaveraceae,*

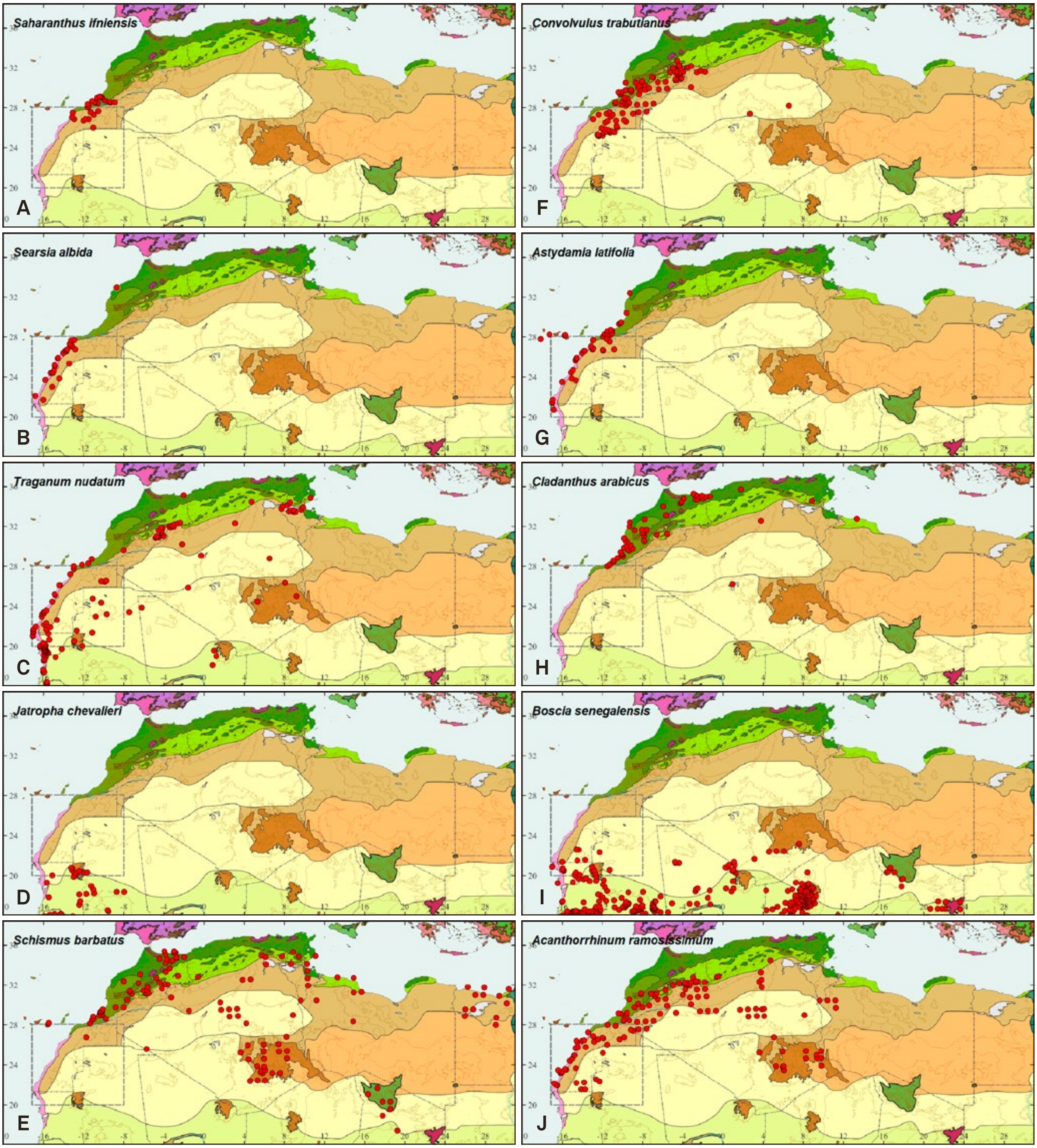

Fig. 7. – Some examples of species distributions present in the Atlantic Sahara. **A.** *Saharanthus ifniensis*: monospecific endemic genus of this area found in the northern limit of the study area and is associated with wadi (seasonally dry ravines); **B.** *Searsia albida*: small tree and strict endemic to the Atlantic Sahara coast, encountered in rock crevices at the tops of slopes; **C.** *Traganum nudatum*: Saharo-Sindian distribution occurring in Arabia, Syria, and Iran; **D.** *Jatropha chevalieri*: Afro-Tropical distribution endemic of western Africa; **E.** *Schismus barbatus*: Mediterranean distribution reaching the Sahara; **F.** *Convolvulus trabutianus*: endemic shrub found south-west of the High Atlas and in the Sahara limits; **G.** *Astydamia latifolia*: Canarian-Moroccan endemic found along the coast and occasionally inland; **H.** *Cladanthus arabicus*: Mediterranean distribution reaching the Sahara; **I.** *Boscia senegalensis*: Afro-tropical distribution; **J.** *Acanthorrhinum ramosissimum*: Saharo-Sindian and quite common.

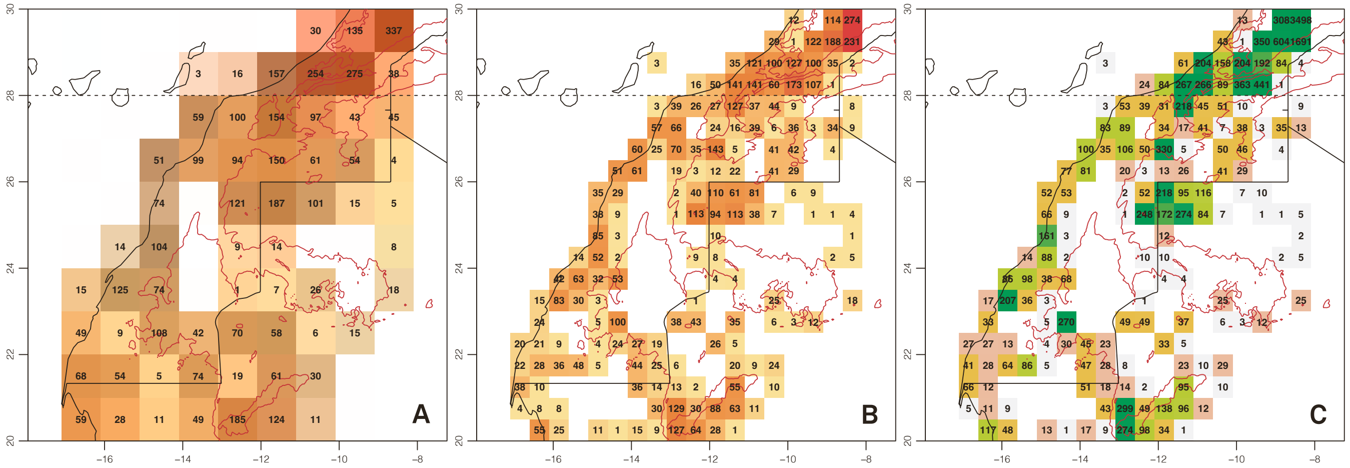

Fig. 8. – Vascular plant richness and number of collections in the Atlantic Sahara and neighboring areas. **A.** Number of plant species per 1° cell; **B.** Number of plant species per 0.5° cell; **C.** Number of observations per 0.5° cell.

Ranunculaceae and *Rutaceae*, which are uncommon south of 28°N.

In a subsequent analysis, we narrowed the geographical scale to include only areas south of the Draa valley, that is, the Atlantic Sahara s.str. We reduced the cell size to 0.5°, which yielded a total of 52 cells meeting our criteria (above) for cluster analysis. Here we identified a total of 578 species of vascular plants belonging to 352 genera and 80 families, many of these species being characteristic of arid and halomorphic environments (e.g. *Tetraena* and *Caroxylon* spp.). For 23% of the species (135 spp.) we have a single observation, for 43.5% (237 spp.) merely between 2 and 9 observations, for 34% (186 spp.) between 10 and 100 observations, and for only 0.5% (3 spp.) more than 100 observations (*Acacia tortilis* var. *raddiana, Nucularia perrinii*, and *Panicum turgidum*).

The variation in floristic richness between the 0.5° cells is considerable (Fig. 8B). The arid, sedimentary plains and *ergs* (e.g. in Oumm Drous Guébli) show the lowest values, with 4–10 species, compared with 50 to 149 species in the more diverse cells. The Guelta Zemmour and the Seguiet el Hamra are among the most diverse areas (116–119 spp./cell), as is the Atar region (150 spp.). In comparison, cells in the Mediterranean transition zone, above 28° north, show significantly greater richness (162–329 spp.). In the coastal area, the numbers of species per cell are relatively low (17–87 spp.).

Geographical distribution and endemism

According to Le Houérou (1995b), 32% of the overall Saharan flora are Afro-tropical in origin and 20% are Mediterranean. Our analysis (Table 2) for the Atlantic Sahara shows a somewhat lower percentage of species with Afro-tropical affinity (24%, n = 135 taxa). Cells in the northern part of the coast, not surprisingly, have lower numbers of Afro-tropical taxa (1–8 spp.), while this number progressively increases toward the south, reaching 60–70 spp. in the Adrar of Mauritania (Fig. 10C). Regarding strict Mediterranean (Me, n = 38) and Saharo-Mediterranean (Mes, n = 82) species, the percentage is 24%. In the north and along the coast, the cells have values of 18 to 37 spp., while in the south these values vary between 5 to 8 spp. (Fig. 10B). Saharan and Saharo-Sindian species are present in relatively low percentages in the Atlantic Sahara (n = 92, 16%), but with higher values naturally occurring inland (Table 2).

Overall, the Atlantic Sahara includes 78 endemic taxa (species and subspecies), of which 54 are strictly endemic. The rate of endemism s.l. is 13%, a significant rate for a desert area often considered to be species-poor and homogeneous. Some of these endemic taxa have their center of distribution in the northern Sahara, below the Atlas Mountains, in what Emberger (1971) had termed the Mauritanian-Atlantic domain. This group includes: *Ammodaucus maroccanus, Endopappus macrocarpus, Kleinia anteuphorbium*, and *Traganopsis glomerata* (Fig. 7; see Appendix 2), species which are also found in the Guelta Zemmour massif, contributing to the diversity of that region. The strictly coastal endemics include 54 taxa, many belonging to *Amaranthaceae* (e.g. *Suaeda ifniensis*), *Frankeniaceae* (e.g. *Frankenia* spp.), and *Plumbaginaceae* (e.g. *Limonium tuberculatum*). Those taxa are adapted to the halomorphic environments of the northern coast. Some species, such as *Polycarpaea nivea*, are widely distributed along the coast, while others, such as *Pentzia hesperidium* and *Hedysarum argenteum*, are known from just a few localities.

A correlation is evident between diversity and levels of endemism, but interpreting this pattern, as noted by Le Houérou (1997), is complex and there is much local variation. The Banc d'Arguin (in Mauritania, at the southern boundary of the Atlantic Sahara) is known for its unique biodiversity and importance as a refuge for fauna (Monod, 1988); nonetheless, it has few endemic plants (2 spp.).

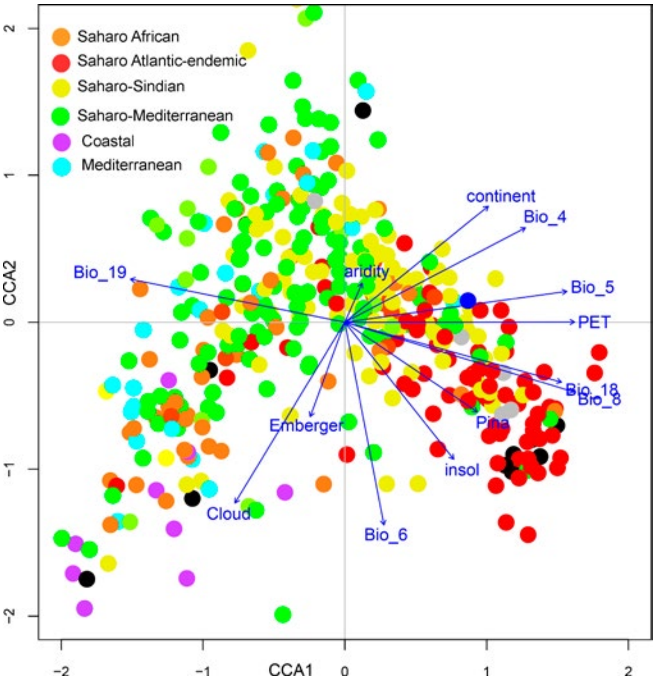

Fig. 9. – Scattergram of the Canonical Correspondence Analysis (CCA) performed between 13 bioclimatic variables (see Table 3) and the floristic data of the Atlantic Sahara. Dot colors correspond to domain affinities: Saharo-African species (orange), Saharo-Atlantic endemics (red), Saharo-Sindian species (yellow), Saharo-Mediterranean species (green), coastal species (purple), Mediterranean species (cyan), azonal and cultivated species (black).

The biogeographical affinities of the Atlantic-Sahara with Macaronesia are considerable: 21 % (121 spp.) of Atlantic-Saharan species are also found in the Canary Islands, and, of these, 15 species are Saharo-Macaronesian endemics (e.g. *Asteriscus schultzii*, *A. graveolens* subsp. *odorus*, *Limonium tuberculatum*, *Lotus arenarius*, *Ononis tournefortii*, and *Pulicaria burchardii*). Some of these endemic species characterize certain vegetation, for example the shrub *Euphorbia regis-jubae* and the vicariant taxa of the *E. balsamifera* group (Riina et al., 2021).

Biogeographical delineation

The results identified eight well-supported and geographically coherent clusters (Fig. 11) which can be divided into two groups: one with Palearctic affinity (to the north), and one with Afro-tropical affinity (to the south). To find such a clear distinction in a region also described as a transition zone (White, 1986) may come as a surprise, but within these two groups the distinction is more subtle. The Palearctic group includes four clusters which can be divided into two entities. The first entity, compromising one cluster, is strictly coastal (light blue on Fig. 11). The second entity, with more steppic species, includes two groups, one more inland and arid (grey on Fig. 11), and the other more oceanic (green and dark blue on Fig. 11). The second group (with Afro-tropical affinity) includes four clusters with somewhat disjunct spatial distributions. These are all found in the south and include the Adrar of Mauritania.

Floristic assemblages and constituent species were identified for each of the eight clusters (see Appendix 1). Although species with only a single observation or which were found only in a single cluster were not included in the cluster analysis, they were nonetheless significant in characterizing the floristic groups and assessing endemism.

Bioclimatic approach

The canonical-correlation analysis (CCA) including bioclimatic (13 variables) and floristic data highlights a clear structuration of species. Mediterranean-aligned plants correlate closely with rainfall, and coastal plants closely with cloud cover. Endemic species, however, align simultaneously

Table 2. – Biogeographical spectrum and floristic richness for the eight clusters of the Atlantic Sahara obtained by the cluster analysis (UPGMA) (see Fig. 11). Pantropical, azonal and cultivated taxa have not been considered. Column titles: Mediterranean = Mes + Me; Afr.-Trop. = T + Tss; Saharan = SS + Sw + Swo (see Appendix 2 for further details).

Cluster /subregion	Mediterranean [%]	Afr.-Trop. [%]	Saharan [%]	Endemism [%]	Taxa [n°]
(1) Saharan Atlantic coastal desert, littoral	30.43	6.72	18.97	21.34	253
(2) Sub-Atlantic Sahara Desert	15.91	4.55	40.91	2.27	44
(3) Sub-Atlantic Xeric Steppe	21.05	8.27	36.84	10.53	133
(4) Sub-Atlantic Xeric Steppe	33.33	8.96	22.94	21.86	279
(5) Sub-Atlantic Sahara Desert	25.09	10.75	29.75	13.26	279
(6) Sub-Atlantic Sahara Desert	7.92	37.62	28.71	1.98	101
(7) Sub-Atlantic Sahara Desert	9.76	40.42	27.87	4.88	287
(8) Adrar Xeric Woodland	16.23	14.29	39.61	8.44	154
Total	**24 % (138 spp.)**	**24 % (135 spp.)**	**16 % (92 spp.)**	**13 % (78 spp.)**	**566**

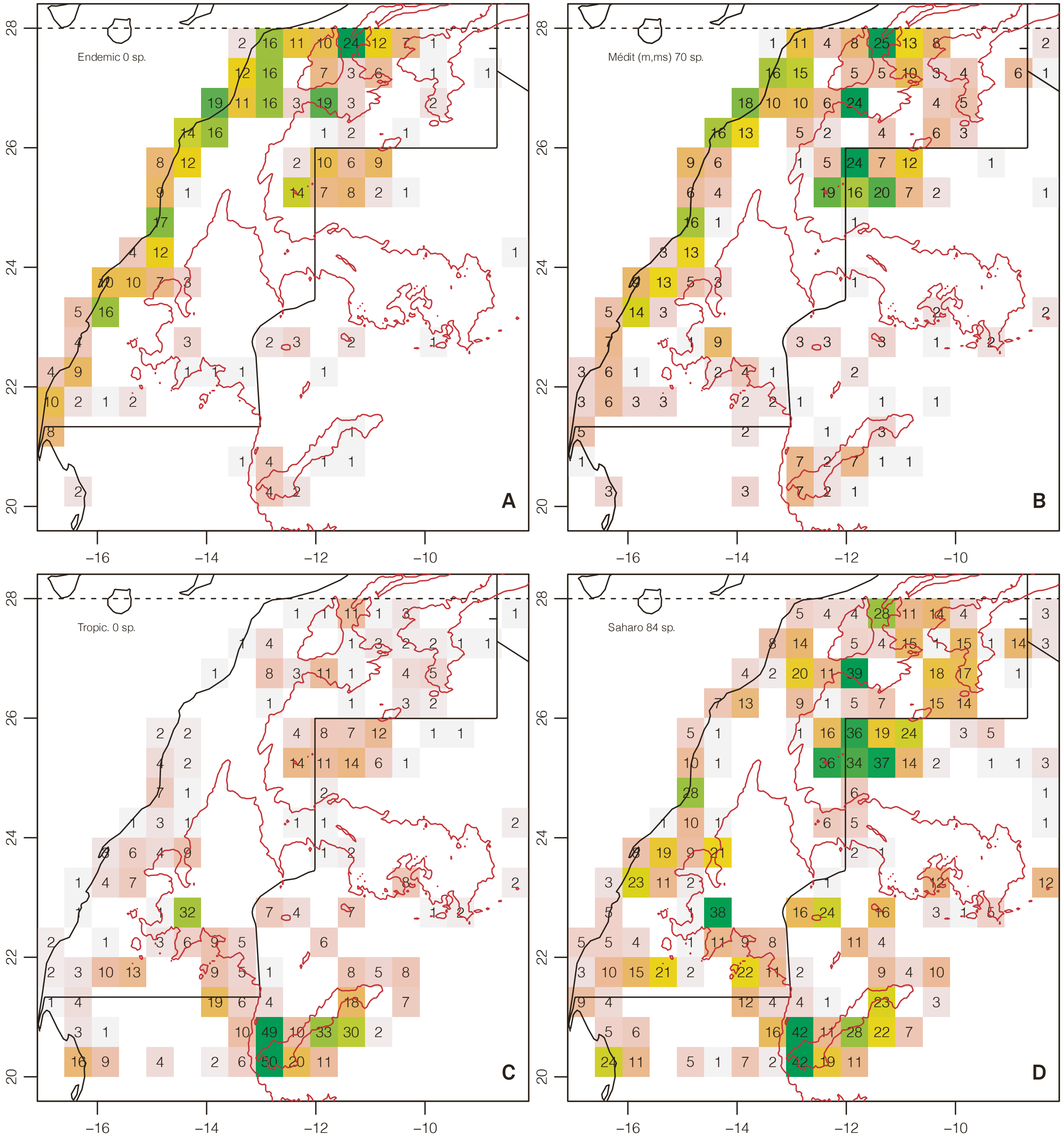

Fig. 10. – Number of plant species per cell according to their chorological status (cells with less than 3 species are not shown) of the Atlantic Sahara and neighboring areas. **A.** Endemic taxa; **B.** Mediterranean taxa; **C.** Tropical taxa; **D.** Saharan taxa.

with multiple parameters, most concerning degrees of aridity (Fig. 9). Species identified as Saharo-Sindian, on the other hand, are diffused along the two ordination CCA axes (eigen values 0.514 and 0.285). The other axes of the ordination (eigenvalues 0.243, 0.18) separate the different species affinities but they do not show strict groups, unlike the cluster analysis.

The variability on the first CCA axis can be explained by the maximum and average temperatures of the warmest season

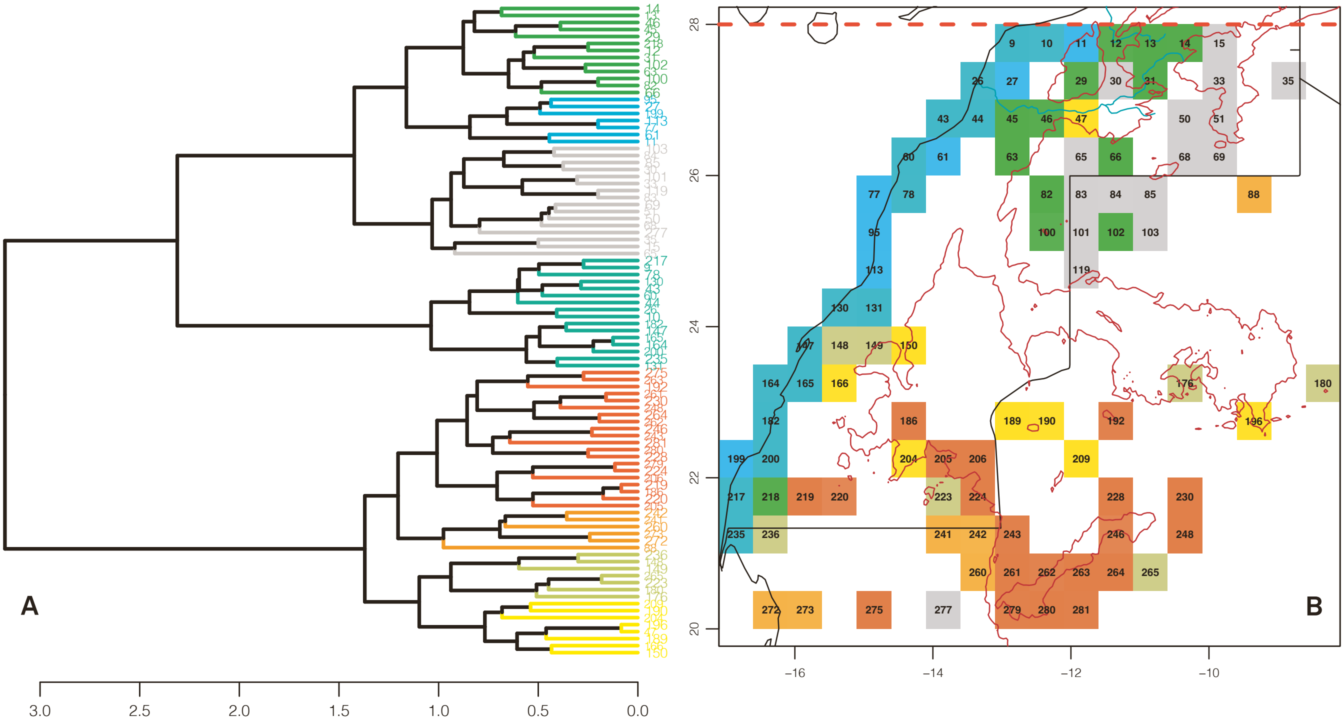

Fig. 11. – Cluster analysis of the vascular flora of the Atlantic Sahara and neighboring areas.
A–B. Cluster analysis (UPGMA) with a resolution of 0.5° cells. Numbers correspond to the cell identifier.

(Bio5, Bio8), the precipitation of the warmest season (Bio18), and the Potential Evapotranspiration (PET). These variables influence the distribution of Afro-tropical species while, conversely, the precipitation of the coldest season (Bio19) has an influence on the occurrence of Mediterranean species. The ordination of species on the second axis correlates with the minimum temperature of the coldest month (Bio6) and cloud cover. The positive relationship between cloud cover and the presence of coastal species is clear. The aridity and Emberger indices correlate with the third axis; the continentality and PINA indices, however, have weak correlations with species distributions.

A cluster analysis of the 13 climatic variables alone, without the floristic data, yields a map with delineations that correspond almost perfectly to those obtained from floristic data alone (Fig. 12, Table 3). Climate, should, of course, have a strong influence on the flora, but that the correlation is so explicit in the Atlantic Sahara is noteworthy. This could signify that the geology of the region and historical aspects of the flora have relatively little influence; though, in some cases, this seems unlikely, for example the ensembles of aquatic plants, or halophytes, or the azonal plants occurring only on certain *guelbs*. We did not have sufficient data to include the influence of wind, which is extremely important in the coastal zone, and can be even more so inland, depending on topography.

Discussion

Floristic richness of the Atlantic Sahara

Insufficient knowledge of plant species distributions in Africa has hindered a robust and much needed biogeographical delineation of the continent. Most modern floristic and biogeographical studies have concerned either the northern part of the Sahara, in the Mediterranean region (Meddour et al., 2019; Abdelaal et al., 2020), or sub-Saharan Africa (Linder, 2001; Linder et al., 2012), leaving the biodiversity of the Sahara Desert largely unexplored, despite being the largest desert in the world (Brito et al., 2014; Médail & Quézel, 2018). Our recent observations and collections (c. 12,000 plant occurrences), together with historical records of plant occurrences, have allowed us to begin to fill this gap for the Atlantic Sahara, a territory encompassing some 700,000 km^2.

We evaluate the floristic richness of the Atlantic and sub-Atlantic Sahara, s.str., at 578 plant species and subspecies (see Appendix 2). Lebrun (1998) estimated the floristic richness of the Atlantic Sahara to be 405 species, and Dobignard et al. (1992b) to be 430 species. This apparent increase derives from our more extensive surveys and a thorough review of published sources and herbarium specimens. Our figure includes the plants of the Adrar, as well as several new occurrences from the Banc d'Arguin (Mauritania), such as *Avicennia germinans, Suaeda arguinensis*, and *Tamarix senegalensis* (Attioui & Lemmel, 2020). Numerous new in situ observations, particularly those of Garcin (2016, 2019, 2022) and

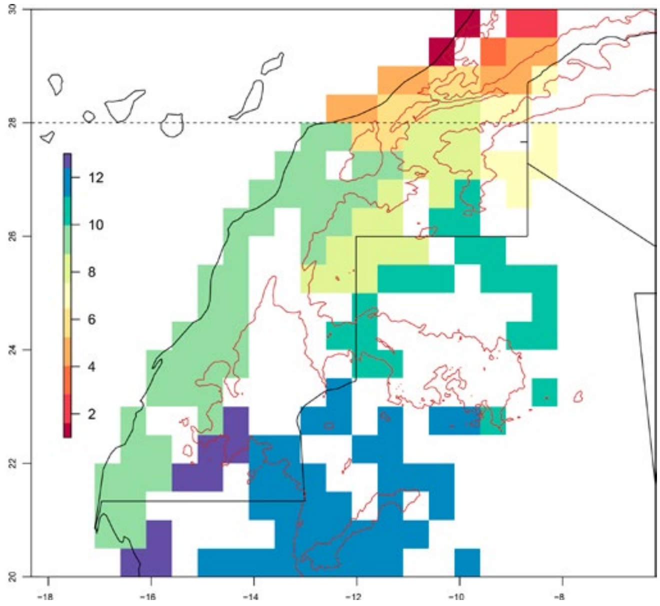

Fig. 12. – Spatial clustering of the Atlantic Sahara and neighboring areas based on the 13 bioclimatic variables.

Chambouleyron et al. (2022), have added or confirmed the presence of some ten species (e.g. *Boscia senegalensis, Corchorus depressus*, and *Euploca rariflora*). The final number of species for this vast area is likely to grow in the future. As just one example, there are no floristic observations, to our knowledge, for the *guelb* of Oum Dreyga, which rises in a central zone at the interface of two floristic regions. The Atlantic Sahara merits and needs much further study and surveying, despite genuine logistical challenges and geopolitical obstacles.

If we had included the zone to the north of the Draa valley (28°N to 30°N) as also part of the Atlantic Sahara, this expanded area would then harbor approximately 922 species. This northern zone stands out for its high diversity, floristic transitions, and strong Mediterranean affinity.

Compared to the floristic diversity of the Hoggar, which is approximately 350 species for 150,000 km^2 (Quézel, 1954), or that of southern Tunisia, with 300 species for 30,000 km^2 (Le Houérou, 1995b), the Atlantic Sahara has greater floristic diversity overall, though it also constitutes a much greater area. Weighting areal richness, however, though widely used, may be of less relevance in desert areas, where small and restricted areas (e.g. some inselbergs or small perennial pools) may concentrate great diversity. This richness of the desert area of the Atlantic Sahara is explained, in part, by humidity from the Atlantic Ocean. The Atlantic Sahara's limited extension latitudinally (c. 1,000 km from the Anti-Atlas to the Mauritanian Adrar) also allows the penetration of both Mediterranean elements from the north and Afro-tropical elements from the south. If the vegetation of the coast (the strict Atlantic zone) contributes significantly to the total floristic diversity, with several cells having over 60 species (and in one case, 80 spp.), this diversity is nonetheless exceeded in some more internal desert zones, such as the region of Azefal, and even more so in the hilly part of Zemmour (up to 119 spp.).

The significant plant diversity of the sub-Atlantic area is at first glance counter-intuitive, given that the internal desert environments are particularly harsh and rather monotonous on a large scale. The observed richness could be explained by two phenomena. First, the interpenetration of various floristic assemblages, in that the southern cells, in contact with the Afro-tropical or Sudano-Sahelian areas, and the northern cells, in contact with the arid Mediterranean area, both at the coast and inland, are relatively more diverse than inland or central areas. This leads us to consider that the Atlantic Sahara indeed represents a biogeographical transition zone, as suggested by White (1986), joining the Palearctic and the Afro-tropical realms. Second, the presence of small mountain ranges (*guelbs*), which serve as refuges for certain Afro-tropical plants (Médail & Quézel, 2018), contribute importantly to the region's biodiversity. Our recent explorations found 16 new occurrences of Afro-tropical species in these rocky massifs, which encompass at least 105 species (Garcin, 2016, 2022). New missions will likely add further discoveries.

Plant endemism

As reported above, we identified 78 endemic plant taxa, of which 51 are strict endemics for the Atlantic Sahara. There is only one endemic genus, *Saharanthus* (*Plumbaginaceae*; Fig. 7), with a center of distribution near the boundary of the Sahara and Mediterranean areas. We identify 34 endemics restricted to the Atlantic coast, including *Traganum moquinii*, a species pertaining to the "Oceanic" cluster, and one quarter of these are also found in the Canary Islands. Indeed, the arid and semi-arid Macaronesian flora is roughly similar to that of the Atlantic-Sahara, and 24 endemic taxa are shared by the two areas. Some of these species, such as *Astydamia latifolia* (Fig. 7) and *Euphorbia balsamifera* subsp. *balsamifera*, can be encountered more than 100 km inland, on a number of rocky outcrops. While the majority of endemic species are found in the coastal zone (Fig. 10A), the presence of endemic taxa further inland is not negligible. For example, for Zemmour there are 10 to 16 endemic spp./cell, and most of these have Mediterranean affinity, with distributions extending somewhat to the north of the Atlantic Sahara: *Anethum theurkauffii*, *Cladanthus eriolepis, Coris monspeliensis* subsp. *maroccana* (new presence according to Garcin, 2022), *Endopappus macrocarpus, Euphorbia officinarum* subsp. *echinus, Kleinia anteuphorbium, Perralderia coronopifolia*, and *Thymelaea antiatlantica*. These endemic species also characterize the floristic gradient marking the transition zone. When considering the Atlantic Sahara broadly and including the edge of the Sahel (for example the Mauritanian Adrar and the Banc d'Arguin) several endemic species can be added, including: *Barleria lancifolia* subsp. *charlesii*, with a small distribution at the boundary of Adrar; *Jatropha chevalieri*, for which the Atlantic Sahara forms a northern limit (Fig. 7); and *Suaeda arguinensis*, which is found only in the Banc d'Arguin.

While figures for regional endemism and country endemism are not commensurate, comparing these can nonetheless provide a rough indication of the significance of the biodiversity of the Atlantic Sahara, with an endemism level of about 13 %. Endemism rates for individual countries dominated by Saharan environments are considerably lower, from the relatively high level for Algeria at 6.3 % (Meddour et al., 2023) to the much lower levels for other predominantly arid African countries, such as Egypt at 2.3 % (Abdelaal et al., 2018) and Chad at 1 % (César & Chatelain, 2019). The percentage of endemism for the broader Sahara is uncertain, since there is no recent, critical checklist for the desert as a whole. It was estimated, however, to be 12 % (190 taxa) by Quézel (1978) and 15.4 % (250 taxa) more recently by Médail & Quézel (2018). The number of endemics will certainly grow, as illustrated by the recent descriptions of two new endemic plants for the Central Sahara (Chatelain et al., 2022; Vázquez-Pardo et al., 2022) and another endemic for the Atlantic Sahara (Chatelain et al., 2020). For the Canary Islands, Beierkuhnlein et al. (2021) calculate an endemism rate of between 25 % and 32 % (499 to 608 spp.), varying according to the different taxonomic conceptions of the investigators.

An important refuge area for the Sudano-Sahelian flora

The plant diversity of the Atlantic Sahara can be explained in part by its biogeographical history, particularly in providing refuge areas during paleoclimatic fluctuations since the end of the Cenozoic and the formation of the Sahara some 7 million years ago (Médail & Quézel, 2018). Population contractions or expansions, responding to the dry or wet conditions of each climatic cycle, led to the current disjointed distribution of many tropical species, for example the Guinean tilapia (*Coptodon guineensis*) isolated in the small ponds of *sebkha* of Imlili, near Dakhla (Qninba et al., 2020). The Atlantic Sahara could also serve as a dispersal corridor, especially along the coast, which may experience greater climatic stability (Velo-Antón et al., 2018).

Floristically, the Sudano-Sahelian element, and sub-Saharan African species (known also as "Tropical-Sahelian" or simply "Afro-tropical"), survive in certain suitable, relatively humid habitats, such as at the margins of *guelbs*, along seeps, at the bottom of canyons and valleys, and surrounding *guelta* (small perennial pools), which constitute true biodiversity hotspots (Vale et al., 2015). In our field expeditions we found eleven Afro-tropical plant species which had not previously been recorded for the Sahara: *Corchorus depressus, Crotalaria arenaria*, *Euploca rariflora* subsp. *rariflora*, *Geigeria alata, Grewia villosa, Helichrysum glumaceum, Indigofera argentea,*

Table 3. – Climatic values for each cluster of the climatic analysis (20°N to 30°N) (see Fig. 2) Abbreviations: **Aridity:** aridity index; **ETP**: evapo transpiration; **Emb_Q**: Emberger Q index; **Contin_i**: Continentality index; **Pina6**: Pina index; **Cloud**: average of days with cloud cover in 2020, by MODAL2; **INSOl**: insolation radiation by CERS; **Tmin Bio_6**: min. temperature of coldest month; **Tmax Bio_5**: max. temperature of warmest month; **Prec W Bio_18**: precipitation of warmest quarter; **Seas Bio_4**: temperature seasonality (standard deviation ×100); **TMean Bio_8**: mean temperature of wettest quarter; **Prec Bio_19**: precipitation of coldest quarter.

Localities	id	Aridity	ETP	Emb_Q	Contin_i	Pina6	Cloud	INSOl	Tmin Bio_6	Tmax Bio_5	PrecW Bio_18	Seas Bio_4	Tmean Bio_8	Prec Bio_19
Taliouine Souss	1	75.7	1080.2	56.1	7.0	4.9	60.1	120.6	8.0	25.2	5.0	244.5	13.6	132.0
Agadir	2	74.5	1323.2	55.0	18.9	15.8	67.6	122.8	0.2	35.5	11.0	692.8	8.8	148.0
Guelmin	3	81.5	1307.2	31.2	13.5	3.7	59.7	124.1	6.0	29.9	6.5	435.6	13.8	110.0
Djebel Bani	4	76.4	1438.9	35.8	18.2	8.7	56.4	124.3	1.1	32.6	8.4	624.4	9.2	119.6
Draa valley	5	92.8	1678.2	10.5	18.7	2.4	33.5	124.7	6.1	38.1	2.9	664.7	17.4	41.9
Sidi Ifni	6	88.2	1168.6	28.0	7.4	2.6	113.4	117.9	9.6	28.1	3.3	293.3	16.1	67.7
Oum el assel	7	83.5	1686.8	27.9	18.7	7.9	34.9	124.9	6.4	39.6	2.0	651.6	15.4	60.0
Oum el Driss Guebli	8	98.6	2013.2	2.5	20.0	0.6	34.8	122.4	8.0	43.1	7.3	698.1	28.9	7.4
Tarfaya-Goulimine	9	93.9	1331.9	14.8	9.0	1.2	51.0	119.3	9.3	29.7	4.0	319.8	16.3	42.5
Littoral-Nouadhibou	10	97.5	1420.3	6.5	7.5	0.8	115.9	120.6	12.6	30.8	9.7	257.1	22.0	15.3
Hawza-Zemmour	11	97.2	1607.4	6.0	13.7	0.8	36.9	120.1	9.2	34.7	7.8	473.7	19.8	16.7
Littoral Boujdour	12	97.5	1444.0	6.2	8.7	0.8	41.5	124.2	12.2	31.6	10.6	301.6	22.4	13.3
Adrar-Azefal	13	97.5	1964.3	5.9	13.7	1.0	42.2	125.4	12.0	40.1	26.0	518.0	32.0	4.9
Mean		96.2	1736.8	7.6	14.3	1.3	44.4	123.1	9.8	37.2	12.2	509.2	24.8	18.8

I. sessiliflora, *Pegolettia senegalensis, Polygala irregularis,* and *Tephrosia uniflora*. Many new occurrences have been added for several species previously known from just a few localities, including: *Boscia senegalensis, Chrozophora brocchiana, Combretum aculeatum, Cullen plicatum, Gisekia pharnaceoïdes, Seddera latifolia, Senna italica,* and *Sesuvium hydaspicum* (Garcin, 2022). Most of these taxa were in the Djebel Derraman, a granitic massif which constitutes a singular refuge deserving protection; a significant portion (35 spp., 33 %) of its total flora of 105 species is of Afro-tropical origin. Several regions within the Atlantic Sahara have been identified as refugia, reflecting its environmental conditions and complex historical biogeography (Médail & Quézel, 2018).

A new biogeographical delineation supported by bioclimatic data

We propose a new biogeographical delineation of the Atlantic Sahara based on a quantitative method categorizing regular geographical units based on their plant composition and bioclimatic data. This represents the first such large-scale quantitative and geostatistical approach for the Sahara, the largest desert of the world. The only similar study in arid North Africa concerned just one country, Egypt (Abdelaal et al., 2020), an administrative entity. Here, we consider a vast area of some 560,000 km^2 transcending geopolitical boundaries. Our analysis lends support to some earlier hypotheses and proposed delineations, while refining certain points.

First, our results show a clear north-south biogeographical separation, and in this sense, they align relatively closely with the delineation proposed by Guinea (1945; Fig. 5C), who had anticipated a rise in Sudano-Sahelian species to the south, though without quantifying it. This separation is clearly not a line, but rather a transition zone, which had already been suspected for the Sahara as a whole by Monod (1944). Frankenberg (1978), however, was probably the first to offer a robust argument for a large biogeographical transition at the scale of the Sahara, noting that "we can see a floristic continuity from Holarctic to Paleotropical species" and that "it seems difficult to set the true limits of floral realms in such continuity" (Frankenberg, 1978). This interpretation was retained by White (1986) in his phytogeographical study of the African continent, as well as by Médail & Quézel (2018) in their synthesis of the phytogeography of the Sahara. Our results further support Frankenberg's position.

One of the fundamental questions for the biogeographical delineation of the Atlantic Sahara has been the influence of the Atlantic Ocean and how far this this climatic driver extends inland. Ideally, to assess this question we would inventory regularly spaced plots moving inland from the ocean. But theory is far from reality, especially in a region where constraints on fieldwork are great, and access is difficult, at times nearly impossible. Despite our determination to collect data widely, our information is heavily weighted toward localities along the 850 km of coastline and remains far scarcer inland. Nevertheless, the results of the factorial analysis (CCA) for climatic variables confirm the prominent roles of both winter rainfall, a characteristic of the Mediterranean climate, and rainfall during the warmer months, a more tropical influence. Though some authors have emphasized broad biogeographical patterns, rather than climate, in explaining the observed distributions and diversity of plants in the Atlantic Sahara (Barry, 1990; Lamarche, 2002), our results suggest that climatic holds great influence (Fig. 12). The results of the CCA analysis of climate data alone coincide almost perfectly with the results of the cluster analyses based on plant distributions (Fig. 11B). This strong congruence between the biogeographical and bioclimatic approaches, we believe, adds to the robustness of the new delineation.

The delineation of Dobignard et al. (1992a), for the Moroccan Sahara (Fig. 1A), presented a good synthesis of the pioneering work done a half-century earlier. Our current analysis based on more recent data, however, indicates that the boundaries of the sub-sector ("XIXd"), which includes the Guelta Zemmour should probably be reduced towards the south. Our results show that the latter is floristically closer to the Seguiet el Hamra than to the Hamada sedimentary region circumscribed by Dobignard et al. (1992a). The "Hammada XIXc" sub-sector thus could be larger, encompassing the Zemmour, Smara and Hawsa areas. The separation of a Bir Moghrein region also seems justified, due to its distinct geology (Reguiba belt) and flora. For the coastal zone, Dobignard et al. (1992a) proposed a north-south separation around 27°N. Based on our results, however, a separation further south, around 24.5°N, has more support. This is consistent with the delineation proposed earlier by Guinea (1945). We have grouped Adrar Souttouf with the Azifal-Tijirit, as they have few floristic differences.

The maps of the first biogeographers of the Atlantic Sahara (Murat, 1944; Monod, 1944; Guinea, 1945; Dobignard, 1992a, b; Frankenberg, 1978; White, 1986) used the classic categories of the discipline, such as regions, domains, subdomains, and sectors. Current conventions for biogeographical maps, however, have shifted toward the ecoregion concept, with the Ecoregion2017 map (Dinerstein et al., 2017) representing an aggregation of such efforts at a large scale. This latter endeavor also envisions protecting half of all the land on Earth to save the living terrestrial biosphere. Although we do not address the conservation status of the Atlantic Sahara extensively here, we believe that the delineation proposed in this work will also provide a stronger basis for managing and conserving its biodiversity (Ladle & Whittaker, 2011), and with these shared concerns, we similarly adopt the ecoregion framework.

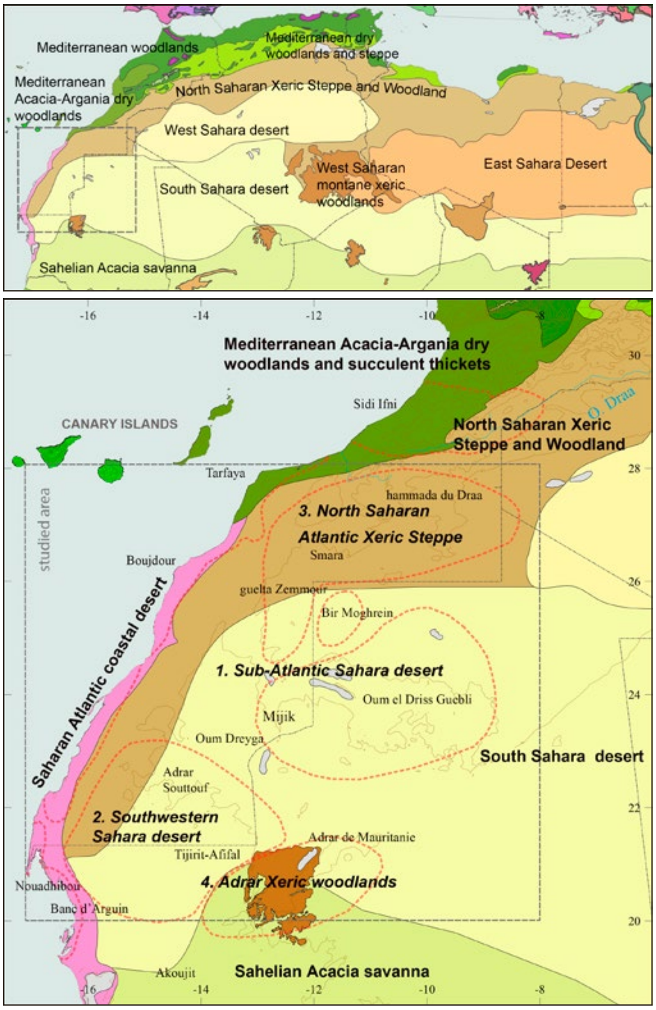

Fig. 13. – Ecoregion 2017 map of the Atlantic Sahara and neighboring areas (Dinerstein et. al., 2017) with our newly proposed subregions indicated with red dashes.

Based on our data, particularly from lesser-known areas such as Azifal and northern Mauritania, we propose refining the Ecoregion2017 map by modifying some boundaries and recognizing four new subregions (Fig. 13). For the South Sahara Desert ecoregion, we identify two subregions which we have tentatively named "Sub-Atlantic Sahara Desert" [1] and "Southwestern Sahara Desert" [2]. For the North Saharan Xeric Steppe and Woodland ecoregion, we propose a new subregion named "North Saharan Atlantic Xeric Steppe" [3]. For the West Saharan Mountain Xeric Woodlands ecoregion, we also propose a new subregion named "Adrar Xeric Woodland" [4], covering the Adrar of Mauritania and the Atar region. The main justification for this new subregion is that it is distinct from the high mountains of the Central Sahara and the Aïr, with which this area was previously grouped, differing significantly in terms of climate (cloud cover from the ocean vs. summer rainfall), geology, plant species composition, and endemism (Table 2). The four new proposed subregions are described briefly as follows (further characterizations are provided in Appendix 1):

1. "Sub-Atlantic Sahara Desert". This new subregion is distinct for its climate, large *sebkha* (dry, alkaline basins; Fig. 4G), and flora adapted to halomorphic soils. The western elements of the "Saharan Halophytics" ecoregion group of the Ecoregions2017 map could be included here, as they form part of the same landscape.
2. "Southwestern Sahara Desert". This is distinct from the main South Sahara Desert in that its flora benefits from summer monsoon rainfall and shows a greater affinity with the Afro-tropical biome.
3. "North Saharan Atlantic Xeric Steppe". This corresponds to the western extremity of the current "North Saharan Xeric Steppe" ecoregion of Dinerstein et al. (2017), which extends westward from Egypt, across Libya, and reaching Nouadibhou in Mauritania. This is not warranted climatically or floristically, and the sub-Atlantic portion should be separated. The oceanic influence there, reflected both in cloud densities and temperatures, distinguishes it from the Egyptian and Libyan portions, but even more important, plant species compositions and endemics are significantly different. This distinction was already recognized by Maire & Wilczek (1935) and Emberger (1939), and in all subsequent biogeographical studies.
4. "Adrar Xeric Woodland". This proposed subregion had been joined with the Hoggar massif and the Tibesti mountains of the central Sahara by Dinerstein et. al. (2017). These latter two ranges, however, with their high elevations (2500–3000 m), have floras with significant numbers of species of Mediterranean affinity (Médail & Quézel, 2018). The Adrar mountains of Mauritania, in contrast, are of much lower elevation (c. 350 m; see photo, Fig. 4J) and harbor many Afro-tropical species. Although Monod (1944) was uncertain whether the Adrar of Mauritania should be considered part of the Atlantic Sahara or instead as an independent sector of the Sudanian Domain, our results confirm a floristic affinity with the Atlantic Sahara, despite many distinctive features, including more than 32 exclusive species.

Our proposal here regarding subregions are limited to the Atlantic Sahara, though additional modifications to the Ecoregion2017 map for North Africa should be considered. The position of the Paleo-tropical limit, for example, probably should be moved north, and the area of the Mediterranean *Acacia-Argania* dry woodland ecoregion should likely be reduced. Additionally, in the Appendix 1 we provide a comprehensive characterization of the ecoregions "Saharan Atlantic coastal desert" and "Sahelian Acacia savanna", which were proposed by Dinerstein et al. (2017). This Appendix presents floristic data while framing each entity in relation to the earlier subdomains, sectors and districts that have been proposed for the Atlantic Sahara. Although the data supporting these new subregions appears strong, we do not advocate, at this stage, definitive boundaries or necessarily final names. Rather, we propose this delineation as a first step toward a more in-depth revision and standardization of the biogeographical regionalization of the world, as advocated by Morrone (2018), and as a complement to other recent work focused on North Africa, such as by Meddour et al. (2019) and Abdelaal et al. (2020).

The boundary between the Palearctic (Mediterranean) and the Afrotropic (tropical) realms has often been placed at the Sahara, though its precise delineation is complex and remains unclear, in part because the Sahara may best be understood as a transition zone. Our geostatistical analysis of the Atlantic Sahara focusing on vascular plant distributions and endemism suggests that the point at which Afrotropic representation exceeds Mediterranean representation lays further north than the current Palearctic limit depicted on the Ecorregions2017 map. Further confirmation by extending the boundaries of the area studied and increasing the size of the cells for cluster analyses will be helpful. For the Atlantic Sahara, the southern portion is characterized by a flora largely of Paleotropical affinity (37–40 %), whereas in the northern the flora is largely of Mediterranean affinity (30–33 %). Further such approaches for the rest of the Sahara, North Africa, and the Mediterranean will shed more light on this long-standing biogeographical question.

As argued above, the Atlantic Sahara is a strong example of a wide transition zone, in the sense of White (1986). Also referred to as ecotones, such areas have often been neglected in biogeography and conservation (Van Rensburg et al., 2009; Pálinkás, 2018), and their importance underestimated. For example, the coastal part of the Atlantic Sahara, with all the characteristics of a transition zone, is believed to have been an important biogeographic corridor during the Pleistocene (Velo-Antón et al., 2018); populations there could contract or expand in response to climatic oscillations leading to drier or more humid environments.

Our recent observations, beyond supporting the view that the Atlantic Sahara is a transition zone, have also identified many new occurrences for Afro-tropical species further toward the east, and we thus propose extending this biogeographic corridor inland, even though it is true that plant richness falls, overall, when moving away from the coast. There are exceptions, however, and our data also confirm the important role of isolated small mountain ranges and rocky outcrops as islands of biodiversity, and likely refugia, in desert environments (Danin, 1999). The refuge zones with the greatest climatic stability, however, appear to be those located along the Atlantic coast (Médail & Quézel, 2018; Velo-Antón et al., 2018).

Conclusion

Nearly all recent studies of the arid environments of North Africa lament the dearth of robust scientific knowledge (Brito et al., 2014; Médail & Quézel, 2018; Brito & Pleguezuelos, 2020). Saharan biodiversity clearly needs much further study in the fields of ecology, biogeography, conservation biology, and climate-change science.

Relying on vascular plant biodiversity and endemism, this study presents a more precise biogeographical assessment of the Atlantic Sahara We propose four new subregions and adjustments to the existing regions for the Ecoregions of the World map. The earlier delineations for the western part of the Sahara are uncertain and imprecise (e.g., the Adrar of Mauritania is entirely distinct from the Hoggar; Sebkha cannot be an ecoregion). Our contribution is only a first step toward a revision of the biogeographical delimitation of the Sahara, which may ultimately lead to a reconsideration of the currently assigned regions and ecoregions for North Africa.

Further botanical inventories and investigations using cells along latitudinal and longitudinal transects will be needed to fill remaining gaps and to standardize datasets for a more robust analysis. Ideally, plant occurrences would be recorded for cells along latitudinal transects from the Mediterranean to the beginning of the Sahel. This type of transect, using 5 km^2 cells, was performed for the northern edge of the Moroccan Sahara, in Tata province, by the Emirates Center for Wildlife Propagation (ECWP). Extending such a project across the Atlantic Sahara, even at a lower resolution, would require a dedicated program and considerable funding, and the endeavor would have to overcome many obstacles. Many annual plants, for example, appear and bloom briefly, and only during favorable (but infrequent) rainy years, and it is precisely at these times that plant surveys must occur. Field work must be highly focused at the time of these ephemeral blooms, and collecting data along a lengthy transect would require dozens of botanists to be available on relatively short notice. Beyond these issues of timing and human resources, many other logistical and geopolitical challenges remain.

The Sahara, the largest desert in the world, is much more complicated and heterogeneous than might appear from species numbers alone, and better understanding its biogeographic history and structure remains a priority for better apprehending the region. We hope that this study will spark further research toward a comprehensive biogeographical delineation of the Sahara based on vascular flora, which remains the most discriminating basis for biodiversity regionalization.

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Appendix 1. – Floristical data for the proposed subregions and additions to Dinerstein's ecoregions

Proposed subregions

1. "Sub-Atlantic Sahara Desert"

This subregion corresponds, in part, to the large sub-oceanic and meridional sectors "10" and "12" from Monod (1945). It is floristically poor yet heterogeneous due to the mosaic of soils, which range from halomorphic to sandy. Two areas are salient:

The Bir Moghrein area, bordering the southern part of the Zemmour, is a sandy landscape marked by granitic *guelbs*, and has some 150 identified species, many found growing among the rocks along the bases of the *guelbs*, including *Convolvulus trabutianus, Launaea arborescens, Limonium* spp., *Periploca angustifolia, Perralderia coronopifolia,* as well as several *Amaranthaceae* such as *Hammada articulata* (characteristic of steppes, according to Barry, 1990), *Anabasis articulata, Salsola glomerata, Searsia tripartita and Traganopsis glomerata*. Here one can observe species which have not been mentioned for Gueltat Zemmour (to the west), such as *Salsola glomerata, Hamada scoparia, Phagnalon purpurescens,* and *Plantago amplexicaulis*. These are absent from the xeric steppes of the Black Zemmour (Oudeiat el Kiam, to the northwest). In the Bir Moghrein area, species such as *Aeluropus lagopodiodes* and *Cressa cretica* are encountered in depressions at the edges of *sebkha*, particularly on strongly sedimentary soils, and on sands one finds *Pergularia tomentosa* and *Stipagrostis plumosa*.

The Mijik area, made up of very arid sedimentary plains which extend from the large *sebkha* of Idjil and Oum el Driss Guebli of Mauritania toward the Atlantic coast, supports only a very impoverished vegetation; we were only able to record four species: *Astragalus vogelii, Fagonia glutinosa, Tetraena gaetula* cf. subsp. *waterlotii* and *Tetraena simplex*, in part due to the extremely dry conditions at the time of our visit. But even in better conditions the number of species is low, for example Barry (1990) found just 27 species in this same region. The area corresponds approximately to the longitudinal limit between Tropical Africa and the Paleartic realm and is depicted on the maps of Dubief (1963) as having the region's lowest rainfall (although these are extrapolations, as no actual measurements exist for the area). The whole area to the northeast of this region is unknown to us, but it appears to be desert with numerous *sebkhas*. The Hank region forms the southern limit.

Notes. – At the eastern edge of this subregion, Monod (1945) defined a Saharo-tropical sector ("13") no longer under sub-Atlantic influence. We were only able to partially analyze this area in our study, and only on the basis of observations and collections by Barry on the Hank and by Sougy on the Iguidi and Yetti (Vernet & Chatelain, 2022). The heterogeneity of the cells, the presence or absence of springs (as in Chegga), and the small number of species left our statistical analyses inconclusive. One must recognize that this is an area of harsh desert zones, whereas all our other analyzed areas correspond to steppe-deserts. Monod (1945; Fig. 5B) placed the Tiris, Yetti and Hank in a "Saharo-Mediterranean sector", but he acknowledged that he was uncertain about this choice. He suggested that the presence of *Nucularia perrinii* was indicative; we argue, however, that the presence of *Maerua crassifolia*, *Schouwia purpurea* and many other Afro-tropical elements justify a Saharan-African affinity.

2. "Southwestern Sahara Desert"

This subregion corresponds, in part, to Monod's very large sector 12, encompassing several districts, such as Tijirit ("12a"), for which he had no data. It includes the following areas:

The Azifal-Tijirit area, corresponding to the Tiris district (Monod's "12b"), an area dominated by sandy terrain interrupted by granitic *guelbs*. The vegetation is typical of *ergs*, with *Acacia tortilis* var. *raddiana* and *Panicum turgidum*. The greatest diversity can be seen around the many granitic *guelbs*. Of the 74 species inventoried, 45 % are typically Saharo-Sindian, while 33 % have Africo-tropical affinity, confirming the biogeographical affinity of this region with the Adrar of Mauritania and the Saharo-African subdomain.

The Adrar Souttouf area, located in the sedimentary zone bordering Monod's sectors "12" and "10", is made up of low-lying areas with large stands of *Acacia ehrenbergiana* and *A. tortilis* var. *raddiana*. Most of the Sudano-Sahelian species likely reflect a refuge situation; these include *Boscia senegalensis*, *Pegolettia senegalensis*, *Polygala irregularis*, *Senna italica* among others (Médail, pers. comm.). In our inventory we found 56 species.

3. "North Saharan Atlantic Xeric Steppe"

This subregion corresponds to the districts of black Zemmour, Guelta Zemmour, Hawza-Abeth, Hammada (Monod, 1944; Murat, 1994), and our cluster 3 and 4. Located mainly on the *hammada* of the Draa, according to the observations by Dubuis et al. (1960); we have not been to these sites. The subregion also includes the Zemmour, but excludes the Bir Moghrein area, which is entirely granitic with many *guelbs* (Sougy, 1964; Villeneuve et al., 2015). The number of species is estimated at 149, with 12 endemics, including *Abutilon albidum, Anethum foeniculoides, A. theurkauffii, Deverra triradiata* subsp. *intermedia*, and *Thymelaea antiatlantica*. Species with high importance values include *Ammodaucus leucotrichus, Catananche arenaria, Cenchrus divisus, Echiochilon simonneaui, Hammada scoparia, Helianthemum canariense, Matthiola maroccana, Paronychia arabica* subsp. *cossoniana, Ziziphus lotus* subsp. *lotus, Pteranthus dichotomus, Silene vivianii,* etc. Affinity with Mediterranean flora is evident, representing 41 % of spp. on average in the cells of this subregion.

Notes. – The flora of the wetland around Gueltat Zemmour (600 m^2 ?) remains unknown to us, as it is located within an inaccessible military zone. Rungs & Sauvage (1945) report some species for the area, noting especially the presence of *Faidherbia albida*, which is extremely rare in this region. We visited the rocky slopes in the vicinity of the wetlands (outside the military zone), and there we were able to inventory at least 51 species.

4. "Adrar Xeric Woodland"

This subregion corresponds to the "Saharo-African" domain and "Adrar" sector of Monod (1945) and was included in the "West Saharan Mountain Xeric Woodlands ecoregion" of Dinerstein et. al. (2017).

The Adrar of Mauritania, a long sedimentary plateau dating from the Cambrian-Carboniferous period, is essentially comprised of *regs* (rocky desert) dominated by *Pergularia tomentosa,* with ephemeral watercourses, where *Acacia ehrenbergiana, Cymbopogon schoenanthus, Grewia tenax, Ziziphus lotus* subsp. *saharae* are found. The slopes are carved by large canyons sheltering *gueltats*, and some oases are found beneath the cliffs, as in Ouadane. The northern part (from El Beyedh to el Halleluiah) is bordered by large savannas with *Acacia tortilis* and *Panicum turgidum* and valleys where large stands of *Balanites aegyptica* flourish. This species is found much further north, in Morocco on the Jebel Bani, and characterizes the continental Saharan boundary.

We were able to inventory 187 species for the Adrar, and 32 of these are only rarely found further north, and 11 are entirely absent in the Atlantic Sahara s.str.: *Abutilon pannosum* (found in Gueltat of the Adrar and Banc d'Arguin), *Barleria lancifolia* subsp. *charlesii* (endemic to Ez Zerga), *Corchorus tridens, Cyperus laevigatus* (Gueltat), *Eclipta prostrata* (Gueltat in the Adrar), *Euphorbia scordifolia, Glinus lotoides* (also found in Akjouit), *Gymnosporia senegalensis* (Gueltat in the Adrar, the Banc d'Arguin and probably more widespread), *Jatropha chevalieri* (coastal and inland Mauritania), *Limeum obovatum, Microcharis disjunctata, Rhynchosia minima*, and *Scoparia dulcis*. Trees as *Acacia nilotica* and *Phoenix dactylifera* are only present in the oases, and *Marsilea* cf. *aegyptiaca* and *Potamogeton crispum* are encountered in *gueltats* (here new for Mauritania).

In the surrounding Akjouit region (south-west), The percentage of Sudano-Sahelian species reaches 52–80 %, which clearly demonstrates its Afro-tropical affinity.

Notes. – Monod (1952) published an inventory for the Adrar, counting 227 species of vascular plants and noting that this sector, "strongly infiltrated with Sudanese-Deccanian elements", could not be included in the Sahel and that it was clearly separate from the Zemmour. Our analysis supports his position, as our cells covering the Adrar show a strong affinity with those of the Azifal-Tijirit. For this reason, it seems quite clear to us that the Adrar of Mauritania pertains to the Saharan transition zone, as does Azifal-Tijirit.

Additions to Dinerstein's ecoregions

Saharan Atlantic coastal desert

This ecoregion includes our clusters 1 and 2 and corresponds to the "Oceanic subdomain" of Monod (1945) and four sectors on Murat's maps (Fig. 5A): the estuary of the Draa, Cape Juby-Bojador, Aguerguer, and Imraguen. It is located along the coast, over a width of 10 to 50 km. Inland, the oceanic influence is identifiable by the presence of lichens of the genus *Ramelina* and the abundance of *Frankeniaceae* and *Plumbaginaceae* (over salt deposits).

Some species are restricted to the northern part, including *Asteriscus graveolens* subsp. *odorus* (endemic), *Asteriscus schultzii* (endemic), *Astydamia latifolia* (rare in the south), *Erodium crassifolium* subsp. *maroccanum, Euphorbia balsamifera* subsp. *balsamifera, Halocnemum cruciatum, Limonium chrysopotamicum, L. tuberculatum, Pentzia hesperidium* (endemic, on sands), *Suaeda ifniensis*. Some others are found throughout the coast, such as *Arthrocaulon macrostachyum, Echiochilon chazaliei* and *Frankenia corymbosa* (all endemics), and *Ononis tournefortii*; others, such as *Frankenia chevalieri*, are found only in the south. The south coastal zone (Cabo Blanco region) is distinguished by the absence of most of the species found in the north, with exceptions as *Limonium tuberculatum, Polycarpaea nivea*. Naegelé (1960) counted 50 species in the Cabo Blanco area. *Anabasis articulata* is present in the coastal desert, while also being found on the steppes of Zemmour and the Draa but being totally absent from the sandy Azifal-Adrar-Tiris area. We identify 184 species, including at least 33 exclusively coastal species, but our inventory is not exhaustive. We distinguish between: (1) species linked to highly saline coastal soils or run-off, such as *Cyperus capitatus, Frankenia corymbosa, Halocnemum cruciatum, Limbarda crithmoides* subsp. *longifolia, Sarcocornia fruticosa, Suaeda ifniensis, Tamarix amplexicaulis, and T. boveana;* (2) species found in breaks in the rocky margins at the top of slopes and cliffs overlooking the ocean, such as *Asteriscus graveolens* subsp. *odorus, Lotus halophilus*, *L. assakensis, Nitraria retusa* and *Searsia albida;* (3) species located on sandy soils on plateaus, such as *Atriplex glauca* subsp. *ifnensis*, *Echiochilon chazaliei*, *Kickxia monodiana*, *K. aegyptiaca* subsp. *frruticosa,, Limonium chrysopotamicum, L. tuberculatum, Mesembryanthemum nodiflorum and Ononis serrata;* (4) species characteristic of seashores (dunes), such as *Euphorbia chamaesyce, Polycarpaea nivea, Sporobolus pungens,* etc.

Notes. – The Banc d'Arguin, a coastal region overlaying a sedimentary substrate, and corresponding to sector "11" on the Monod map (Fig. 5A, B), is made up of a narrow barrier beach with *Avicennia* and *Tamarix*; a low littoral zone with *Arthrocnemum* sp., *Nitraria retusa, Sesuvium* sp., *Traganum* *moquini* etc., interspersed with shallow, clayey estuaries with *Arthrocnemum macrostachyum*; and an inland sedimentary plateau dominated by *Cornulaca monacantha* and *Stipagrostis pungens*. In his inventory for the Banc d'Arguin, Monod (1988) cited 110 especies. During an expedition of several weeks in 2019, Lemmel in Attioui & Lemmel (2020) made 378 observations, indentifying 87 species, 55 of which are also found in Azifal-Tijirit. Eight species do not extend north of the Banc d'Arguin: *Avicennia germinans, Corchorus trilocularis, Euphorbia forsskalii, Salsola glomerata* (= *S. sieberi*, noted by Monod)*, Sesuvium portulacastrum* (= *S. sesuvioides* noted by Monod), *Suaeda arguinensis, Tamarix senegalensis,* and *Trianthema triquetra*. *Polygonum argyrocoleum* extends north only slightly.

Among the biogeographical questions posed by Monod (1945), one concerned whether the Banc d'Arguin should be included in his sector 12. Comparison of floristic data shows a similarity between the Adrar, the Azifal and the Banc d'Arguin, showing a "continental" affinity similar to the Azifal-Tijirit and expressed by the presence of species such as *Aerva javanica, Astragalus vogelii, Crotalaria saharae*, *Indigofera sessiliflora,* and *Maerua crassifolia*.

The cells covering the Banc d'Arguin are distinguished by the presence of some Sudano-Sahelian species on the coast, such as *Avicennia germinans* and *Suaeda arguinensis*; halophilic species such as *Lycium intricatum, Nitraria retusa, Suaeda vermiculata, Tetraena gaetula* subsp. *waterlotii, Tetraena simplex*; and the lack of coastal genera or species characteristic of the region north of Cap Blanc (Ras Nouadhibou) such as *Frankenia, Limonium*, and *Anvillea,* as well as*, Euphorbia regis-jubae, Gymnocarpos sclerocephalus, Lotus arenarius, L. assakensis, Salsola* spp., and *Searsia albida*. According to Monod (1988), one of the plants exclusive to the Banc d'Arguin was *Salsola sieberi*, but observations (Attioui & Lemmel, 2020) of fruiting individuals, and comparison with numerous recent collections in the suboceanic sector, lead us to confirm that it is *S. glomerata*, a taxon with a wider distribution.

Sahelian Acacia savanna

This ecoregion corresponds to the Sudano-Decanian region and the Sudanian Domain (Monod, 1957); or for White (1986), part of the Sahelian Transition zone. We mention it here because it is the ecoregion that borders our study area to the south, forming a strip from Senegal to Sudan with grassy to shrubby steppes and characteristic annual *Poaceae*, such as *Cenchrus biflorus*, and perennials such as *Andropogon gayanus*, clearly within the Afro-Tropical realm.

Appendix 2. – List of the 570 taxa of the Atlantic-Sahara between 20°N and 28N° to 8°W including Adrar and Banc d'Arguin

Abbreviations: **T** = Sudano-Sahelan; **Tss** = Sudano-Sahelan+Saharo-Sindian; **Me** = Mediterranean; **Mes** = Mediterranean-steppic; **Mess** = Mediterranean+Saharo-Sindien, **SS** = Saharo-Sindien; **Mesw** = Mediterraneo-steppic-Western; **Sw** = Saharo Atlantic; **Swo** = Saharo Oceanic; **Lit** = Littoral azonal; **P** = Pantropical-cosmopolite; **Saf** = Southern-Africa; **Can** = Canary Islands; **az** = azonal (guelta); **cult** = cultivated; **end** = endemic; **nv** = data from literature, not seen, in need of verification; **Mau** = exclusives species from Mauritania, as sudano-sahelian, or from Adrar or from banc d'Arguin as **Adrar** or **Arguin** respectively.

Acanthaceae

Barleria hochstetteri Nees ex DC. .... [T-Adrar]
Barleria lancifolia subsp. *charlesii* (Benoist) J.-P. Lebrun et al. .... [Swo-end-Mau]
Barleria schmittii Benoist .... [Swo-end]
Blepharis edulis (Forssk.) Pers. .... [SS]
Blepharis linariifolia Pers. [nv] .... [T-Adrar]

Aizoaceae

Aizoon canariense L. .... [SS-Can]
Mesembryanthemum cryptanthum Hook. f. .... [Mesw-Can]
Mesembryanthemum nodiflorum L. .... [Mess-saf-Can]
Sesuvium hydaspicum (Edgew.) Gonç. .... [T]
[= *S. sesuvioides* auct.]
Sesuvium portulacastrum (L.) L. .... [cult-Can]
Trianthema portulacastrum L. .... [T-Mau]
Trianthema sedifolia Vis. .... [T-Mau]
Zaleya pentandra (L.) C. Jeffrey .... [T-Mau]

Alismataceae

Damasonium alisma subsp. *bourgaei* (Coss.) Maire .... [Me]

Amaranthaceae

Aerva javanica (Burm. f.) Juss. ex Schult. .... [Tss]
Amaranthus blitoides S. Watson .... [Me-Can]
Amaranthus graecizans L. .... [P-Can]
Anabasis articulata (Forssk.) Moq. .... [SS]
Anabasis oropediorum Maire .... [Mes]
Arthrocaulon macrostachyum (Moric.) Piirainen & G. Kadereit .... [cult-Can]
Atriplex glauca subsp. *ifniensis* (Caball.) Rivas Mart. et al. .... [Lit]
Atriplex halimus L. .... [P-Can]
Bassia muricata (L.) Asch. .... [SS]
Bassia tomentosa (Lowe) Maire & Weiller .... [Sw-Can]
Caroxylon gaetulum (Maire) Akhani & Roalson .... [S]
[= *Salsola imbricata* subsp. *gaetula* (Maire) Boulos]
Caroxylon imbricatum (Forssk.) Akhani & Roalson .... [Tss]
Caroxylon tetragonum (Delile) Moq. .... [Mes]
[= *Salsola tetragona* Delile]
Caroxylon tetrandrum (Forssk.) Akhani & Roalson .... [Mess-Can]
[= *Salsola* tetrandra Forssk.]
Caroxylon vermiculatum (L.) Akhani & Roalson .... [Mess-Can]
[= *Salsola vermiculata* L.]
Cornulaca monacantha Delile .... [SS]
Halocnemum cruciatum (Forssk.) Tod. .... [Lit]
Hammada articulata (Moq.) O. Bolòs & Vigo .... [Mess]
[= *Hammada scoparia* (Pomel) Iljin]
Nucularia perrinii Batt. .... [Mesw]
Patellifolia procumbens (C. Sm.) A.J. Scott et al. .... [Mes-Can]
[= *Patellifolia patellaris* auct.]
Salsola glomerata (Maire) Brullo .... [Swo-end]
[= *Salsola sieberii, S. monodiana*]
Salsola gymnomaschala Maire .... [Swo-end]
Salsola longifolia Forssk. .... [SS-Mau]
Sarcocornia fruticosa (L.) A.J. Scott .... [Lit-Can]
Sarcocornia perennis (Mill.) A.J. Scott .... [Lit-Can]
Suaeda arguinensis Maire .... [Swo-end-Arguin]
Suaeda ifniensis Caball. ex Maire .... [Swo-end-Can]
Suaeda maritima (L.) Dumort. [nv] .... [Swo-end-Can]
Suaeda vera Forssk. ex J.F. Gmel. .... [Me-Can]
Suaeda vermiculata Forssk. ex J.F. Gmel. .... [Mess-saf-Can]
Traganopsis glomerata Maire & Wilczek .... [Swo-end]
Traganum moquinii Webb ex Moq. .... [Swo-end-Can]
Traganum nudatum Delile .... [SS]

Amaryllidaceae

Pancratium trianthum Herb. .... [SS]

Anacardiaceae

Pistacia atlantica Desf. .... [Me-Can]
Searsia albida (Schousb.) Moffett .... [Swo-end-Can]
Searsia tripartita (Ucria) Moffett .... [Mess-Can]

Apiaceae

Ammodaucus leucotrichus Coss. & Durieu .... [Mess]
Ammodaucus maroccanus (P.H. Davis et al.) C. Chatel. & Chambouleyron .... [Mesw-Can]
Anethum foeniculoides Maire & Wilczek .... [Swo-end]
Anethum theurkauffii Maire .... [Swo-end]
Astydamia latifolia (L. f.) Kuntze .... [Swo-end]
Bupleurum semicompositum L. .... [Me]
Crithmum maritimum L. .... [Lit-Can]
Deverra battandieri (Maire) Podlech .... [Mesw]
Deverra denudata (Viv.) Pfisterer & Podlech .... [Mesw]
Deverra scoparia Coss. & Durieu .... [Mess]
Deverra triradiata subsp. *intermedia* (L. Chevall.) Pfisterer & Podlech .... [Sw-end]
Eryngium ilicifolium Lam. .... [Mesw]
Pseudorlaya biseriata (Murb.) Sáenz de Rivas .... [Mesw]
Sclerosciadium nodiflorum (Schousb.) Ball .... [Swo-end]

Apocynaceae

Apteranthes europaea (Guss.) Murb. .... [Mes]
Calotropis procera (Aiton) W.T. Aiton .... [P]
Cynanchum boveanum Decne. .... [SS]
Desmidorchis retrospiciens Ehrenb. .... [T]
Leptadenia pyrotechnica (Forssk.) Decne. .... [Tss Mau]
Orbea decaisneana subsp. *hesperidum* (Maire) Jonkers .... [Mes]
Pergularia tomentosa L. .... [SS]
Periploca angustifolia Labill. .... [SS]

Arecaceae

Borassus aethiopum Mart. .... [T-Mau]
Phoenix dactylifera L. .... [S]

Asparagaceae

Asparagus altissimus Munby .... [Swo-end]
Asparagus pastorianus Webb & Berthel. .... [Swo-end-Can]
Autonoë latifolia (Willd. ex Schult. f.) Speta .... [Swo-end-Can]
Battandiera amoena (Batt.) Maire .... [Mesw-end]
Dipcadi panousei Sauvage & Veilex .... [Mesw-end]
Dipcadi serotinum (L.) Medik. .... [Mess-Can]
Dipcadi viride (L.) Moench .... [T-Adrar-nv]
Vera-duthiea noctiflora (Batt. & Trab.) Speta .... [Mesw]

Asphodelaceae

Asphodelus refractus Boiss. .... [Mes]
Asphodelus tenuifolius Cav. .... [Mess-Can]

Asteraceae

Anacyclus homogamos (Maire) Humphries .... [Mes]
Anvillea garcinii subsp. *radiata* (Coss. & Durieu) Anderb. .... [SS]
Anvillea platycarpa (Maire) Anderb. .... [Mesw-end-Can]
Artemisia reptans Buch .... [Swo-end]
Asteriscus graveolens subsp. *odorus* (Schousb.) Greuter .... [Swo-end]

Asteriscus graveolens (Forssk.) Less. ... [SS]
Asteriscus schultzii (Bolle) Pit. & Proust ... [Swo-end]
Atractylis aristata Batt. ... [Mess]
Atractylis babelii Hochr. ... [Mesw]
Atractylis delicatula Batt. ex L. Chevall. ... [Mes]
Brocchia cinerea (Delile) Vis. ... [Mess]
Catananche arenaria Coss. & Durieu ... [Mess]
Centaurea bimorpha Viv. ... [Me-Can]
Centaurea eriophora L. ... [Me]
Centaurea pungens subsp. *austromaroccana* Förther & Podlech ... [Swo-end]
Centaurea pungens Pomel ... [SS]
Chrysanthellum indicum DC. [nv] ... [T]
Cladanthus arabicus (L.) Cass. ... [Mess]
Cladanthus eriolepis (Maire) Oberpr. & Vogt ... [Sw-end]
Cotula anthemoides L. ... [Tss, Adrar]
Echinops spinosissimus subsp. *spinosus* Greuter ... [Mes]
Eclipta prostrata (L.) L. ... [cult-Mau]
Endopappus macrocarpus (Coss. & Kralik) Sch. Bip. ... [Swo-end]
Filago desertorum Pomel ... [Mes]
Geigeria alata (DC.) Oliv. & Hiern ... [T]
Glebionis coronaria (L.) Spach ... [Me]
Helichrysum glumaceum DC. ... [T]
Ifloga spicata (Forssk.) Sch. Bip. ... [Mess]
Kleinia anteuphorbium (L.) Haw. ... [Mesw-end]
Launaea amal-aminiae N. Kilian ... [Swo-end]
Launaea arborescens (Batt.) Murb. ... [Mess]
Launaea capitata (Spreng.) Dandy ... [Mess-Can]
Launaea fragilis (Asso) Pau ... [Mes]
Launaea intybacea (Jacq.) Beauverd ... [T-Adrar]
Launaea mucronata (Forssk.) Muschl. ... [Mess]
Launaea nudicaulis (L.) Hook. f. ... [Mess-Can]
Lifago dielsii Schweinf. & Muschl. ... [S]
Limbarda crithmoides subsp. *longifolia* (Arcang.) Greuter ... [Lit]
Nolletia chrysocomoides (Desf.) Cass. ... [Mess]
Otoglyphis maroccana (Ball) Dobignard ... [Mesw-end]
Otoglyphis pubescens (Desf.) Pomel ... [Mes]
Pallenis hierichuntica (Michon) Greuter ... [Mesw]
Pegolettia senegalensis Cass. ... [Tss]
Pentzia hesperidum Maire & Wilczek ... [Swo-end]
Perralderia coronopifolia Coss. ... [Mesw]
Phagnalon purpurascens Sch. Bip. ... [Swo-end]
Picris albida Ball ... [SS]
Pluchea ovalis (Pers.) DC. ... [T-Mau]
Pulicaria alveolosa Batt. & Trab. ... [S]
Pulicaria arabica (L.) Cass. ... [Mes]
Pulicaria burchardii Hutch. ... [Swo-end]
Pulicaria incisa (Lam.) DC. (incl. subsp. *candolleana*) ... [SS-Adrar]
Pulicaria inuloides (Poir.) DC. ... [S]
Pulicaria mauritanica Batt. ... [Mesw-end]
Pulicaria undulata (L.) C. A. Mey. ... [SS]
Reichardia tingitana (L.) Roth [?] ... [Me]
Scorzoneroides muelleri subsp. *austromaroccana* (Maire) Greuter ... [Sw-end]
Senecio flavus (Decne.) Sch. Bip. ... [Mess-Saf]
Senecio glaucus subsp. *coronopifolius* (Maire) C. Alexander ... [SS]
Silybum marianum (L.) Gaertn. ... [Mess-Saf]
Sonchus oleraceus L. ... [Mes-Adrar]
Sonchus tenerrimus L. subsp. *tenerrimus* ... [Mes]
Tourneuxia variifolia Coss. ... [S]
Verbesina encelioides (Cav.) A. Gray ... [Nat]
Volutaria crupinoides (Desf.) Maire ... [Mes]
Volutaria lippii (L.) Cass. ex Maire (incl. subsp. *medians*) ... [Mes]
Volutaria sinaica (DC.) Wagenitz ... [S]
Warionia saharae Benth. & Coss. ... [Mesw-end]

Avicenniaceae
Avicennia germinans (L.) L. ... [T-Arguin]

Boraginaceae
Cordia sinensis Lam. ... [Tss-Adrar]
Echiochilon chazaliei (H. Boissieu) I.M. Johnst. ... [Swo-end]
Echiochilon simonneaui Faurel & Dubuis ... [Swo-end]
Echium horridum Batt. ... [Mess]
Echium trygorrhizum Pomel ... [SS]
Euploca rariflora (Stocks) Diane & Hilger ... [Tss]
Euploca strigosa (Willd.) Diane & Hilger ... [T]
Heliotropium bacciferum Forssk. ... [Tss]
Heliotropium erosum Lehm. ... [SS]
Heliotropium ramosissimum (Lehm.) DC. ... [SS]
Moltkiopsis ciliata (Forssk.) I.M. Johnst. ... [SS]
Nonea calycina (Roem. & Schult.) Selvi et al. ... [Me]
Nonea vesicaria (L.) Rchb. ... [Me]
Ogastemma pusillum (Bonnet & Barratte) Brummitt ... [Mess-Can]
Trichodesma africanum (L.) R. Br. ... [Tss]
Trichodesma calcaratum Coss. ex Batt. ... [Mesw]

Brassicaceae
Anastatica hierochuntica L. ... [Mess-Can]
Diplotaxis harra (Forssk.) Boiss. ... [Mes]
Diplotaxis pitardiana Maire ... [Swo-end]
Diplotaxis virgata (Cav.) DC. ... [Mesw]
Eremobium aegyptiacum (Spreng.) Boiss. (incl. subsp. *longisilicosum*) ... [SS]
Eruca aurea Batt. ... [Me]
Farsetia aegyptiaca Turra ... [Mess]
Farsetia occidentalis B.L. Burtt ... [Mesw]
Farsetia stylosa R. Br. ... [SS]
Kakile maritima subsp. *integrifolia* (Hornem.) Greuter & Burdet ... [Lit]
Lobularia canariensis subsp. *marginata* (Coss.) L. Borgen ... [Sw-Can]
Matthiola longipetala subsp. *livida* (Delile) Maire ... [Mess-Can]
Matthiola maroccana Coss. ... [Mes]
Morettia canescens Boiss. ... [SS]
Notoceras bicorne (Aiton) Amo ... [Mes]
Schouwia purpurea (Forssk.) Schweinf. ... [S]
Sinapis alba L. ... [cult]
Sisymbrium irio L. ... [Mes-Adrar]
Zilla spinosa subsp. *costata* Maire & Weiller ... [Me]
Zilla spinosa subsp. *macroptera* (Coss.) Maire & Weiller ... [Me]

Campanulaceae
Wahlenbergia silenoides Hochst. ex A. Rich. ... [T-Adrar]

Capparaceae
Boscia senegalensis (Pers.) Lam. ex Poir. ... [T]
Cadaba farinosa Forssk. ... [T]
Capparis decidua (Forssk.) Edgew. ... [Tss]
Capparis sepiaria L. ... [T-Mau]
Cleome gynandra L. ... [T]
Cleome viscosa L. ... [T]
Cleome amblyocarpa Barratte & Murb. subsp. *amblyocarpa* ... [SS]
Cleome amlyocarpa subsp. *glandulosa* (Forssk.) Botsch. ... [Mess-Mau]
[= *Cleome africana* auct.]
Crateva adansonii DC. ... [T-Adrar]
Gilgella scaposa (DC.) Roalson & J.C. Hall ... [T]
Maerua crassifolia Forssk. ... [Tss]
Stylidocleome brachycarpa (Vahl ex DC.) Roalson & J.C. Hall ... [Tss]
[= *Cleome brachycarpa* DC.]

Caryophyllaceae
Dianthus crinitus Sm. ... [Mesw]
Gymnocarpos decandrus Forssk. ... [Mess]
Gymnocarpos sclerocephalus (Decne.) Ahlgren & Thulin ... [SS]
Herniaria cinerea DC. ... [Me]
Herniaria fontanesii J. Gay ... [Mesw]

Loeflingia hispanica subsp. *baetica* (Lag.) Maire .... [Me]
Paronychia arabica (L.) DC. subsp. *arabica* .... [Mess]
Paronychia arabica subsp. *breviseta* (Asch. & Schweinf.) Chaudhri .... [Mes]
Paronychia arabica subsp. *cossoniana* (J. Gay ex Batt.) Batt. .... [Mes]
Paronychia arabica subsp. *longiseta* (Batt.) Batt. .... [Mes]
Polycarpaea akkensis Coss. ex Maire .... [Swo-end]
Polycarpaea nivea (Aiton) Webb .... [Swo-end]
Polycarpaea repens (Forssk.) Asch. & Schweinf. .... [Tss]
Polycarpaea robbairea (Kuntze) Greuter & Burdet .... [SS]
Polycarpon tetraphyllum (L.) L. .... [Mes]
Pteranthus dichotomus Forssk. .... [Mess]
Silene villosa Forssk. .... [Mes]
Silene vivianii Steud. .... [Mesw]
Spergula diandra (Guss.) Boiss. .... [Mes]
Spergula marina (L.) Bartl. & H.L. Wendl. .... [Mes]
Spergularia flaccida (Madden) I.M. Turner .... [Mes]
Spergularia media subsp. *intermedia* (Maire) Lambinon & Dobignard .... [Mes]

Celastraceae
Gymnosporia senegalensis (Lam.) Loes. .... [T]

Cistaceae
Helianthemum canariense (Jacq.) Pers. .... [Swo-end]
Helianthemum confertum Dunal .... [S]
Helianthemum lippii (L.) Dum. Cours. .... [Mess]

Colchicaceae
Androcymbium gramineum (Cav.) J.F. Macbr. .... [SS]

Combretaceae
Combretum aculeatum Vent. .... [T]

Commelinaceae
Commelina rupicola Font Quer .... [Swo-end]

Convolvulaceae
Camonea umbellata (L.) A.R. Simões & Staples .... [T-Mau]
Convolvulus althaeoides L. .... [Me]
Convolvulus caput-medusae Lowe .... [Sw-Can]
Convolvulus fatmensis Kunze .... [Mes]
Convolvulus prostratus Forssk. .... [Tss-Mau]
Convolvulus siculus subsp. *elongatus* Batt. .... [Mess]
Convolvulus supinus Coss. & Kralik .... [Mess]
Convolvulus trabutianus Schweinf. & Muschl. .... [Mesw]
Cressa cretica L. .... [Mess-ica-Mau]
Cuscuta planiflora Ten. .... [Me]
Ipomoea asarifolia (Desr.) Roem. & Schult. .... [T]
Seddera latifolia Hochst. & Steud. .... [Tss]

Crassulaceae
Kalanchoe faustii Font Quer .... [Swo-end]

Cucurbitaceae
Citrullus colocynthis (L.) Schrad. .... [P]
Citrullus lanatus (Thunb.) Matsum. & Nakai .... [cult]
Cucumis melo L. .... [cult]
Cucumis prophetarum L. .... [T]
[= ? *Cucumis ficifolius* A. Rich.]
Momordica balsamina L. .... [T-Mau]

Cynomoriaceae
Cynomorium coccineum L. .... [az]

Cyperaceae
Bolboschoenus glaucus (Lam.) S.G. Sm. .... [az]
Bolboschoenus maritimus (L.) Palla .... [Mes]
Cyperus capitatus Vand. .... [Me]
Cyperus conglomeratus Rottb. .... [SS]
Cyperus laevigatus L. .... [Tss-Mau]
Cyperus laevigatus subsp. *distachyos* (All.) K. Richt. .... [P]
Cyperus rotundus L. .... [az]
Fimbristylis ferruginea (L.) Vahl .... [T]
Mariscus dubius (Rottb.) C.E.C. Fisch. .... [T]

Ephedraceae
Ephedra alata Decne. .... [Mess]
Ephedra altissima Desf. .... [Me]
Ephedra foliata Boiss. ex C.A. Mey. .... [SS]
[= ? *E. rowlandii Maire]*
Ephedra fragilis subsp. *cossonii* (Stapf) Maire .... [Mesw-end]

Euphorbiaceae
Chrozophora brocchiana (Vis.) Schweinf. .... [Tss]
Chrozophora senegalensis (Lam.) A. Juss. ex Spreng. .... [T-Mau]
Euphorbia balsamifera Aiton subsp. *balsamifera* .... [Sw-Can]
Euphorbia balsamifera subsp. *sepium* (N.E. Br.) Maire .... [Swo-end]
Euphorbia calyptrata Coss. & Kralik .... [Mess-Can]
Euphorbia chamaesyce L. .... [Swo-end]
Euphorbia dracunculoides subsp. *flamandii* (Batt.) Maire .... [Mess]
Euphorbia dracunculoides subsp. *inconspicua* (Ball) Maire .... [Mesw]
Euphorbia forsskaolii J. Gay .... [T]
Euphorbia granulata Forssk. .... [SS]
Euphorbia inaequilatera Sond. .... [T]
Euphorbia officinarum L. (incl. subsp. *echinus* & *officinarum*) .... [Mesw-end]
Euphorbia paralias L. .... [cult]
Euphorbia regis-jubae J. Gay .... [Sw-end-Can]
Euphorbia retusa Forssk. .... [Mess]
Euphorbia scordifolia Jacq. .... [Tss]
Euphorbia segetalis L. .... [M]
Euphorbia terracina L. .... [M]
Jatropha chevalieri Beille .... [Swo-end-Mau]
Ricinus communis L. .... [P]

Fabaceae
Argyrolobium arabicum (Decne.) Jaub. & Spach .... [Tss]
Argyrolobium microphyllum Ball .... [Mesw-end]
Astragalus akkensis Coss. .... [SS]
Astragalus arpilobus subsp. *hauarensis* (Boiss.) Podlech .... [S]
Astragalus boeticus L. .... [Me]
Astragalus crenatus Schult. .... [SS]
Astragalus eremophilus Boiss. .... [SS]
Astragalus gombo subsp. *gomboeformis* (Pomel) Eug. Ott .... [Mes]
Astragalus mareoticus Delile .... [SS]
Astragalus maurorum Murb. .... [Me]
Astragalus saharae Pomel .... [Mes]
Astragalus solandri Lowe .... [Mess-Can]
Astragalus tribuloides Delile .... [Mes]
Astragalus trigonus DC. .... [SS-Mau]
Astragalus vogelii (Webb) Bornm. .... [S]
Chamaecrista mimosoides (L.) Greene .... [T-Mau]
Crotalaria arenaria Benth. .... [T]
Crotalaria saharae Coss. .... [S-3]
Cullen plicatum (Delile) C.H. Stirt. .... [Tss]
Hedysarum argyreum Greuter & Burdet .... [Swo-end]
Hippocrepis constricta Kunze .... [SS]
Hippocrepis multisiliquosa L. .... [Mess-Can]
Indigofera argentea Burm. f. .... [Tss]
Indigofera colutea (Burm. f.) Merr. .... [T-Mau]
Indigofera hochstetteri Baker .... [T-Mau]
Indigofera oblongifolia Forssk. .... [T-Mau]
Indigofera semitrijuga Forssk. .... [Tss-Mau]
Indigofera senegalensis Lam. .... [T]
Indigofera sessiliflora DC. .... [T]
Kebirita roudairei (Bonnet) Kramina & D.D. Sokoloff .... [Mesw-end]
Leobordea platycarpa (Viv.) B.E. van Wyk & Boatwr. .... [S]
Lotus arenarius Brot. .... [Mesw-end]

Lotus assakensis Coss. ex Brand .... [Mesw-end]
Lotus chazaliei H. Boissieu .... [Mesw-end]
Lotus corniculatus subsp. *preslii* (Ten.) P. Fourn. .... [Me]
Lotus glinoides Delile .... [Mess-Can]
Lotus halophilus Boiss. & Spruner .... [M]
Lotus jolyi Batt. .... [Mes]
Lotus zemmouriensis C. Chatel. & al. .... [Swo- end]
Lupinus tassilicus Maire .... [Mess]
Medicago laciniata (L.) Mill. .... [Mes]
Microcharis disjuncta (J.B. Gillett) Schrire .... [T-Mau]
Ononis angustissima subsp. *paralias* (Förther & Podlech) Dobignard [Sw-end]
Ononis natrix subsp. *hesperia* Maire .... [Mesw-end]
Ononis serrata Forssk. .... [Mes]
Ononis sicula Guss. .... [Me-Can]
Ononis tournefortii Coss. .... [Swo-end]
Prosopis juliflora .... [T-nat]
Retama sphaerocarpa (L.) Boiss. .... [Mes]
Rhynchosia minima (L.) DC. .... [T-Mau]
Senna italica Mill. .... [T]
Senna obtusifolia (L.) H.S. Irwin & Barneby .... [T]
Tamarindus indica L. .... [T]
Tephrosia purpurea subsp. *leptostachya* (DC.) Brummitt .... [Tss]
Tephrosia purpurea (L.) Pers. subsp. *purpurea* .... [T]
Tephrosia uniflora Pers. .... [Tss]
Trigonella anguina Delile .... [Mess-Saf]

Frankeniaceae
Frankenia chevalieri Maire .... [Swo-end]
Frankenia corymbosa Desf. .... [Mess]
Frankenia laevis L. subsp. *laevis* .... [Me]
Frankenia laevis subsp. *velutina* (DC.) Maire .... [Swo-end]
Frankenia thymifolia Desf. .... [Swo-end]

Gentianaceae
Centaurium erythraea Rafn. .... [Mes]
Centaurium pulchellum (Sw.) Druce .... [Tss-Mau]
Centaurium tenuiflorum (Hoffmanns. & Link) Fritsch .... [Me-Can]

Geraniaceae
Erodium crassifolium subsp. *maroccanum* (Maire) Greuter .. [Swo-end]
Erodium glaucophyllum (L.) L'Hér. .... [Mes]
Erodium meynieri Maire .... [Mes]
Erodium pulverulentum (Cav.) Willd. .... [Mes]
Erodium stellatum Delile .... [Mesw]
Erodium touchyanum Delile .... [Mess]
Monsonia heliotropioides (Cav.) Boiss. .... [SS]
Monsonia nivea (Decne.) Webb .... [SS]

Globulariaceae
Globularia arabica Jaub. & Spach .... [Mes]

Juncaceae
Juncus acutus L. .... [Mes]
Juncus bufonius L. .... [az]
Juncus rigidus Desf. .... [az]
Scirpoides holoschoenus (L.) Soják .... [Mes]

Lamiaceae
Ajuga iva (L.) Schreb. .... [Me]
Lavandula coronopifolia Poir. .... [S]
Lavandula multifida L. .... [Mes]
Marrubium deserti (de Noé) Coss. .... [S]
Salvia aegyptiaca L. .... [SS]
Teucrium aureo-candidum Andr. .... [Mesw]
Teucrium chardonianum Maire & Wilczek .... [Swo-end]
Teucrium helichrysoides (Diels) Greuter & Burdet [nv] .... [S]
Teucrium jolyi Mathez & Sauvage .... [Swo-end]
Teucrium polium L. .... [Me]

Lophiocarpaceae
Corbichonia decumbens (Forssk.) Exell .... [T]

Lythraceae
Lawsonia inermis L. .... [cult]

Malvaceae
Abutilon albidum (Willd.) Sweet .... [Swo-end]
Abutilon fruticosum Guill. & Perr. .... [T]
Abutilon pannosum (G. Forst.) Schltdl. .... [T-Mau]
Althaea ludwigii L. .... [Mess-Saf]
Corchorus depressus (L.) Stocks .... [Tss]
Corchorus tridens L. .... [Tss]
Corchorus trilocularis L. .... [Tss]
Grewia tenax (Forssk.) Fiori .... [Tss]
Grewia villosa Willd. .... [T]
Hibiscus micranthus L. f. .... [T]
Malva aegyptia L. .... [Mess]
Malva parviflora L. .... [Mes]
Melhania ovata (Cav.) Spreng. .... [T-Mau]

Marsileaceae
Marsilea aegyptiaca Willd. .... [az]

Menispermaceae
Cocculus pendulus (J.R. Forst. & G. Forst.) Diels .... [SS]

Mimosaceae
Acacia ehrenbergiana Hayne .... [SS]
Acacia gummifera Willd. .... [Mes-end]
Acacia nilotica (L.) Willd. ex Delile .... [cult]
Acacia senegal (L.) Willd. .... [cult]
Acacia seyal Delile .... [SS]
Acacia tortilis var. *raddiana* (Savi) Brenan .... [S]
Faidherbia albida (Delile) A. Chev. .... [Tss]

Molluginaceae
Gisekia pharnaceoides L. .... [Tss]
Glinus lotoides L. .... [T]
Limeum obovatum Vicary .... [Tss]
Limeum viscosum (J. Gay) Fenzl .... [T]

Moraceae
Ficus abutilifolia (Miq.) Miq. .... [T-Mau]
Ficus cordata subsp. *lecardii* (Warb.) C.C. Berg .... [T-Mau]
Ficus sycomorus L. .... [T-Mau]

Neuradaceae
Neurada procumbens L. .... [SS]

Nitrariaceae
Nitraria retusa (Forssk.) Asch. .... [S]
Peganum harmala L. .... [Mes-az]

Nyctaginaceae
Boerhavia repens subsp. *viscosa* (Choisy) Maire .... [T]
Commicarpus helenae (Schult.) Meikle .... [Tss]

Ophioglossaceae
Ophioglossum polyphyllum A. Braun .... [az]

Orobanchaceae
Cistanche phelypaea (L.) Cout. .... [SS]
[= *Cistanche lutea* (Desf.) Hoffmanns. & Link]
Cistanche tinctoria (Forssk.) Deflers .... [Mes]
Cistanche violacea (Desf.) Hoffmanns. & Link .... [SS]
Phelipanche aegyptiaca (Pers.) Pomel (subsp. ined.) .... [Sw-end]
Phelipanche ramosa (L.) Pomel .... [Mes Adrar]
Phelipanche reuteriana (Rchb. f.) Carlón et al. .... [SS]
Striga barthlottii Eb. Fisch. et al. .... [Mesw-end]

Pedaliaceae
Rogeria adenophylla J. Gay .... [T]

Phyllanthaceae

Andrachne telephioides L.	[SS]
Phyllanthus reticulatus Poir.	[T-Mau]
Phyllanthus rotundifolius Klein ex Willd.	[T-Mau]

Plantaginaceae

Acanthorrhinum ramosissimum (Coss. & Durieu) Rothm.	[SS]
Kickxia aegyptiaca (L.) Nábelek subsp. *aegyptiaca*	[Mess]
Kickxia aegyptiaca subsp. *battandieri* (Maire) Wickens	[SS]
Kickxia aegyptiaca subsp. *fruticosa* (Desf.) Wickens	[SS]
Kickxia heterophylla (Schousb.) Dandy	[Mes]
Kickxia monodiana (Maire) D.A. Sutton	[Swo-end]
Plantago afra L.	[Mes]
Plantago akkensis Coss. ex Murb.	[Swo-end]
Plantago akkensis subsp. *ounifensis* (Batt.) Maire	[Sw-end]
Plantago amplexicaulis Cav.	[Mess]
Plantago ciliata Desf.	[Mess-Can]
Plantago coronopus L.	[P]
Plantago lagopus L.	[Me-Can]
Plantago ovata Forssk.	[Mes]
Striga barthlottii Eb. Fisch. et al.	[Mesw]

Plumbaginaceae

Limonium asperrimum Maire	[Mesw-end]
Limonium chazaliei (Boissieu) Maire	[Swo-end]
Limonium chrysopotamicum Maire	[Swo-end]
Limonium fallax (Wangerin) Maire	[Swo-end]
Limonium sinuatum (L.) Mill. subsp. *sinuatum*	[Me]
Limonium sinuatum subsp. *beaumierianum* (Maire) Sauvage & Vindt	[Swo-end]
Limonium tuberculatum (Boiss.) Kuntze (incl. *L. alleizettei*)	[Swo-end]
Saharanthus ifniensis (Caball.) M.B. Crespo & Lledó	[Swo-end]

Poaceae

Aeluropus lagopoides (L.) Trin. ex Thwaites	[Mes]
Aeluropus littoralis (Gouan) Parl.	[Mes]
Ammochloa palaestina Boiss.	[Me]
Aristida adscensionis L.	[Mess-Saf]
Aristida funiculata Trin. & Rupr.	[T]
Aristida mutabilis Trin. & Rupr.	[Tss]
Aristida stipoides Lam.	[T]
Arundo donax L.	[az]
Bothriochloa ischaemum (L.) Keng	[Mess]
Brachypodium distachyon (L.) P. Beauv.	[Me-Can]
Bromus lanceolatus Roth	[Me]
Cenchrus americanus subsp. *monodii* (Maire) Sosef	[T]
Cenchrus biflorus Roxb.	[T-Mau]
Cenchrus ciliaris L.	[P]
Cenchrus divisus (J.F. Gmel.) Verloove et al.	[SS]
Cenchrus pennisetiformis Hochst. & Steud.	[T-Mau]
Centropodia forsskalii (Vahl) Cope	[SS]
Centropodia fragilis (Guinet & Sauvage) Cope	[Tss]
Chloris virgata Sw.	[P]
Chrysopogon aucheri (Boiss.) Stapf	[Mes]
Cutandia memphitica (Spreng.) Benth.	[Mess]
Cymbopogon schoenanthus (L.) Spreng.	[Tss]
Cynodon dactylon (L.) Pers.	[P]
Dichanthium annulatum (Forssk.) Stapf	[SS]
Dichanthium foveolatum (Delile) Roberty	[T]
Digitaria nodosa Parl.	[S]
Elionurus royleanus Nees ex A. Rich.	[T]
Enneapogon desvauxii P. Beauv.	[Tss]
Enneapogon lophotrichus H. Scholz & P. König	[Tss]
Enneapogon scaber Lehm.	[Mess-Saf]
Enteropogon prieurii (Kunth) Clayton	[T-Mau]
Eragrostis aegyptiaca (Willd.) Delile	[Tss]
Eragrostis barrelieri Daveau	[Mess-Saf]
Eragrostis cilianensis (All.) Janch.	[T]
Eragrostis ciliaris (L.) R. Br.	[T-Mau]
Eragrostis domingensis (Pers.) Steud.	[T-Mau]
Eragrostis japonica (Thunb.) Trin.	[T-Mau]
Eragrostis papposa (Roem. & Schult.) Steud.	[T-Mau]
Eragrostis pilosa (L.) P. Beauv.	[T-Mau]
Heteropogon contortus (L.) Roem. & Schult.	[T-Can]
Hyparrhenia hirta (L.) Stapf	[Mess-Saf]
Lasiurus scindicus Henrard	[SS]
Leptothrium senegalense (Kunth) Clayton	[T-Mau]
Lolium rigidum subsp. *lepturoides* (Boiss.) Sennen & Mauricio	[Mes-Can]
Lygeum spartum L.	[Me]
Panicum turgidum Forssk.	[Tss]
Paspalum vaginatum Sw.	[T]
Phalaris minor Retz.	[Mess]
Phragmites australis (Cav.) Trin. ex Steud.	[Mes]
Polypogon monspeliensis (L.) Desf.	[Mess-Saf]
Rostraria pumila (Desf.) Tzvelev	[Mes]
Schismus barbatus (Loefl. ex L.) Thell.	[Mess-Saf]
Schoenefeldia gracilis Kunth	[T-Mau]
Setaria adhaerens (Forssk.) Chiov.	[P]
Setaria verticillata (L.) P. Beauv.	[P]
Spartina maritima (Curtis) Fernald	[Lit]
Sporobolus pungens (Schreb.) Kunth	[Lit]
Sporobolus robustus Kunth	[Tss]
Sporobolus spicatus (Vahl) Kunth	[Mess-Saf]
Stapfochloa lamproparia (Stapf) H. Scholz	[T-Mau]
Stipagrostis acutiflora (Trin. & Rupr.) De Winter	[S]
Stipagrostis ciliata (Desf.) De Winter	[Mess-Saf]
Stipagrostis foexiana (Maire & Wilczek) De Winter	[Mesw]
Stipagrostis hirtigluma (Trin. & Rupr.) De Winter	[Tss]
Stipagrostis obtusa (Delile) Nees	[Mess-Saf]
Stipagrostis plumosa (L.) Munro ex T. Anderson	[SS]
Stipagrostis pungens (Desf.) De Winter	[Mess]
Stipagrostis uniplumis (Roem. & Schult.) De Winter	[T-Mau]
Stipagrostis vulnerans (Trin. & Rupr.) De Winter	[T-Mau]
Stipellula capensis (Thunb.) Röser & Hamasha	[Mess-Saf]
Tetrapogon villosus Desf.	[P]
Tragus racemosus (L.) All.	[SS]
Tricholaena teneriffae (L. f.) Link	[Sw-Can]
Tripidium ravennae (L.) H. Scholz	[Mes]
Triraphis pumilio R. Br.	[Tss]

Polygalaceae

Polygala arenaria Willd.	[T-Imlili]
Polygala erioptera DC.	[T]
Polygala irregularis Boiss.	[T]

Polygonaceae

Calligonum polygonoides subsp. *comosum* (L'Hér.) Soskov	[S]
Emex spinosa (L.) Campd.	[Mess-Can]
Polygonum argyrocoleum Steud. ex Kuntze	[SS]
Polygonum equisetiforme Sibth. & Sm.	[Mess]
Rumex bipinnatus L. f.	[Mes]
Rumex simpliciflorus Murb.	[SS]
Rumex vesicarius L.	[SS]

Portulacaceae

Portulaca grandiflora Hook.	[T-Mau]
Portulaca oleracea L.	[Tss]
Portulaca quadrifida L.	[T-Mau]

Potamogetonaceae

Potamogeton crispus L.	[az]
Stuckenia pectinata (L.) Börner [= *Potamogeton pectinatus* L.]	[az]

Primulaceae
Coris monspeliensis subsp. *maroccana* (Murb.)
Greuter & Burdet .... [Mesw-end]
Lysimachia arvensis f. *latifolia* (L.) B. Bock .... [Me]
Samolus valerandi L. .... [az]

Pteridaceae
Adiantum capillus-veneris L. .... [az]

Resedaceae
Caylusea hexagyna (Forssk.) M. L. Green .... [SS]
Oligomeris linifolia (Vahl ex Hornem.) J.F. Macbr. .... [SS]
Randonia africana Coss. .... [SS]
Reseda arabica Boiss. .... [SS]
Reseda arabica subsp. *moroccana* Abdallah & de Wit .... [Mes-end]
Reseda lutea subsp. *neglecta* (Müll. Arg.) Ball .... [Mesw]
Reseda villosa Coss. .... [SS]

Rhamnaceae
Rhamnus lycioides subsp. *oleoides* (L.) Jahand. & Maire .... [Me]
Ziziphus lotus subsp. *saharae* (Batt. & Trab.) Maire .... [SS]
Ziziphus lotus (Batt. & Trab.) Maire .... [SS]
Ziziphus mauritiana Lam. .... [T]

Rubiaceae
Plocama reboudiana (Coss. & Durieu) M. Backlund & Thulin .... [SS]

Ruppiaceae
Ruppia maritima L. .... [az-Imlili]

Rutaceae
Haplophyllum broussonetianum Coss. .... [Mesw]

Salvadoraceae
Salvadora persica L. .... [Tss]

Santalaceae
Osyris lanceolata Hochst. & Steud. .... [Tss]

Sapindaceae
Lepisanthes senegalensis (Juss. ex Poir.) Leenh. .... [T-Mau]

Sapotaceae
Argania spinosa (L.) Skeels .... [Mesw-end]

Scrophulariaceae
Scoparia dulcis L. .... [T]
Verbascum longirostre (Murb.) Hub.-Mor. .... [SS]

Solanaceae
Hyoscyamus muticus subsp. *falezlez* (Coss.) Maire .... [SS]
Lycium intricatum Boiss. .... [Me]
Lycopersicon esculentum Mill. .... [cult]
Nicotiana glauca Graham .... [nat]
Physalis angulata L. .... [P]
Solanum nigrum L. .... [P]

Tamaricaceae
Tamarix africana Poir. .... [Mes]
Tamarix amplexicaulis Ehrenb. .... [Mes]
Tamarix aphylla (L.) H. Karst. .... [SS]
Tamarix boveana Bunge .... [Mes]
Tamarix gallica L. .... [Me]
Tamarix senegalensis DC. .... [Tss]

Thymelaeaceae
Thymelaea antiatlantica Maire .... [Meswo-end]

Typhaceae
Typha domingensis Pers. .... [az]

Urticaceae
Forsskaolea tenacissima L. .... [Mess]

Verbenaceae
Verbena supina L. .... [P]

Zannichelliaceae
Zannichellia palustris L. .... [az]

Zygophyllaceae
Balanites aegyptiaca (L.) Delile .... [Tss]
Fagonia arabica L. .... [SS]
Fagonia bruguieri DC. .... [SS]
Fagonia glutinosa Delile .... [Mess]
Fagonia harpago Emb. & Maire .... [Mesw-end]
Fagonia indica Burm. f. (auct.) .... [SS]
Fagonia jolyi Batt. (incl. *Fagonia indica* auct.) .... [SS]
Fagonia latifolia Delile .... [SS]
Fagonia longispina Batt. .... [Mes]
Fagonia zilloides Humbert .... [Swo-end]
Seetzenia lanata (Willd.) Bullock .... [SS]
Tetraena fontanesii (Webb & Berthel.) Beier & Thulin .... [Mesw-Can]
Tetraena gaetula subsp. *waterlotii* (Maire) Beier & Thulin .... [Mes]
Tetraena gaetula (Emb. & Maire) Beier & Thulin .... [SS]
Tetraena simplex (L.) Beier & Thulin .... [Tss]
Tribulus bimucronatus Viv. .... [SS]
Tribulus macropterus Boiss. .... [Tss]
Tribulus pentandrus Forssk. .... [SS]
Tribulus terrestris L. .... [P]