



Pollen distribution in surface sediments of the northern Lower Medjerda valley (northeastern Tunisia)



E. Gaceur^{a,b,*}, S. Desprat^{b,c}, I. Rouis-Zargouni^{a,d}, V. Hanquiez^b, V. Lebreton^e, N. Combourieu Nebout^e, N. Kallel^a

^a GEOGLOB, Faculty of Sciences of Sfax, Sfax University, Route Soukra, BP. 802, 3038, Tunisia

^b Univ. Bordeaux, EPOC, UMR 5805, 33615 Pessac, France

^c EPHE, PSL Research University, 33615 Pessac, France

^d Faculty of Sciences of Gafsa, University of Gafsa, University Campus Sidi Ahmed Zarroug, 2112, Tunisia

^e Muséum National d'Histoire Naturelle, Département Homme et Environnement, HHNP, UMR 7194, F-75013 Paris, France

ARTICLE INFO

Article history:

Received 19 May 2017

Received in revised form 19 July 2017

Accepted 31 July 2017

Available online 03 August 2017

Keywords:

Surface pollen samples

Tunisian vegetation

Remotely sensed land cover data

Core-top pollen samples

Multivariate analyses

Ghar el Melh lagoon

ABSTRACT

Past Mediterranean vegetation dynamics are commonly reconstructed using fossil pollen records. However, the interpretation of pollen records in terms of vegetation, climate and land-use changes is often limited due to complex pollen–vegetation relationships. So far, such relationships have been poorly examined in the semi-arid regions of Northern Africa. This work aims to document the modern pollen assemblages that reflect the main vegetation types associated to different land-uses in the northeastern Tunisia. For that, we collected 29 modern terrestrial surface samples in the Lower Medjerda valley and compared the pollen spectra to remotely sensed vegetation data. This original approach, coupling pollen and remotely sensed land cover data, presents some limitations and errors affecting both datasets although it gives promising results. Multivariate analyses show that the composition of pollen samples collected within the Mediterranean maquis may be strongly influenced by adjacent land covers such as conifer woodland or open vegetation. In contrast, pollen spectra associated with land-uses corresponding to heterogeneous agricultural areas and open landscape, mainly irrigated lands, have a distinct signature. However, close to water bodies, pollen spectra reflect predominantly the characteristic halophytic vegetation whatever the surrounding land cover types. We also examined the pollen composition of sediment core-tops from the lagoon Sidi Ali Mekki, to evaluate the ability of pollen sequences to record past vegetation and land-use histories in the Ghar el Melh region. We found that core pollen signal is mainly imprinted by the predominant local vegetation of Sidi Ali Mekki shore although regional and extra-regional pollen inputs appear stronger than in modern surface samples.

© 2017 Published by Elsevier B.V.

1. Introduction

Fossil pollen is widely used for reconstructing past vegetation in order to study ecosystem, climate dynamics or land-use changes in relation to archeological problems. However, the image of the vegetation given by pollen assemblages is distorted by several factors relative for instance to differential pollen production and dispersal between taxa, the structure of the surrounding vegetation, the size and nature of the sampling site or the taxonomical pollen resolution and differential pollen preservation of different taxa (e.g. Havinga, 1984; Prentice, 1985; Sugita, 1994; Traverse, 2007; Broström et al., 2008; Bunting et al., 2013). The study of the pollen rain–vegetation relationship has a long history based on surface pollen samples usually taken in defined vegetation units characterizing an ecosystem or a bioclimate, the ultimate

goal being to improve the interpretation of the pollen signal from sedimentary records and to provide quantitative land cover and climate reconstructions (Davis et al., 2013; Parsons and Prentice, 1981). While modern pollen rain has been widely investigated in a wide variety of environments in Europe (Davis et al., 2013), the Mediterranean region of Northern Africa has been largely understudied. Most available data originates from Morocco (Cheddadi et al., 1998; Bell and Fletcher, 2016). For instance, the Tunisian vegetation pollen rain is poorly documented. A pioneer study from Daoud (1983) documented the overall Tunisian vegetation pollen rain using 48 dust samples. More locally, pollen composition of an oak forest in the northwestern humid Tunisia (Ben Tiba and Reille, 1982) and of the vegetation in sebkha environments of Central and Southern Tunisia (Jaouadi et al., 2015; Lebreton et al., 2015) was investigated using moss and soil surface samples. In Tunisia, like in most areas from the Mediterranean region, the landscape has been widely modified by human impact over the past centuries and millennia. Assessment of the pollen rain of degraded Mediterranean vegetation is a prerequisite for reconstructing vegetation and land-use histories. So

* Corresponding author at: GEOGLOB, Faculty of Sciences of Sfax, Sfax University, Route Soukra, BP. 802, 3038, Tunisia.

E-mail address: amna.gaceur@u-bordeaux.fr (E. Gaceur).

far, the impact of human activities on vegetation as reflected by the pollen rain has been mostly investigated in the Eastern Mediterranean (Bottema and Woldring, 1990).

When studying the pollen–vegetation relationship, pollen data are classically compared to vegetation data obtained from field survey. Remote sensing techniques are currently used to provide quantitative data of vegetation cover. Few works conjointly use pollen and remotely sensed vegetation data although they give encouraging results to reconstruct past vegetation (Williams and Jackson, 2003), landscape openness (McLauchlan et al., 2007), land-use changes (Anupama et al., 2014; Hansen et al., 2008) and to evaluate the pollen-derived reconstruction of vegetation cover using landscape reconstruction algorithm with the models REVEALS and LOVE (Hjelle et al., 2015) and pseudobiomization approach (Woodbridge et al., 2014).

This work aims at determining the composition of modern pollen assemblages associated with the Mediterranean vegetation of the north-eastern Tunisia, a region with semi-arid to subhumid climate favorable to thermophilous maquis and azonal vegetation close to water bodies consisting of halophyte plants (Bortoli et al., 1967). However, the natural vegetation of this area is strongly imprinted by human impact due to intensive agriculture expansion, pastoralism and afforestation programs over the past century. The study is based on the analysis of 29 surface samples taken in the Lower Medjerda valley, close to the lagoon Ghar El Melh. Pollen data were compared to remotely sensed vegetation data (Samaali, 2011) to assess the pollen composition associated to the main vegetation types and land-uses. In addition, in order to determine the nature of the pollen signal of sedimentary cores from the lagoon that will be used for reconstructing past vegetation and land-use changes, we compared the pollen data of two core-tops with the results obtained on the modern pollen rain.

2. Environmental setting

2.1. Geomorphology of the study area

The Lower Medjerda valley is located in northeastern Tunisia, on the northwestern edge of the Gulf of Tunis. The landscape of this area is marked by the past dynamics of the Medjerda River which is the largest water course of Tunisia. The lagoon Ghar el Melh (Fig. 1) which occupies the northernmost part of the deltaic plain is a vestige of the gulf of Utica that was filled up with fluvial deposits as a result of successive shifts of the river course over the past millennia (Paskoff and Trouset, 1992). This area corresponds to a complex lagoon system including a main water body and two evaporative annexes, namely Sidi Ali El Mekki and El Ouafi Lagoons. A coastal sand bar of up to 200 m-wide separates the lagoon from the Gulf of Tunis although a channel maintains the connection with the sea (Moussa et al., 2005). A series of hills delimit the northern and eastern side of the Lower Medjerda valley (Fig. 1). In particular, Djebel Edmina and Djebel Nadhour reaching elevations of 253 m and 324 m, respectively, form a steep relief bordering the northern side of the lagoon while Djebel Kechabta of 412 m a.s.l. is located further to the east (Khrystal Engineering, 2003; Samaali, 2011). South of the lagoon, the Medjerda delta displays numerous abandoned channels. The most recent paleochannel, exiting right south of the lagoon Ghar el Melh (Fig. 1), was abandoned consecutively to the major flood of 1973. Since then, the river occupies a man-made drainage channel which was connecting the Henchir Tobias to the sea, southward of Kalaât Landalous (Chelbi et al., 1995). This latest paleochannel is now used by a temporary stream (Samaali, 2011).

2.2. Climate

Northeastern Tunisia experiences a Mediterranean climate with warm and dry summers with a high evaporation rates and dry spells, and short mild and wet winters with heavy rainfall episodes and subsequent river flooding. The Lower Medjerda valley is located in the sub-

humid and semi-arid bioclimatic belts with mean annual precipitation between 600 and 450 mm·yr⁻¹ (INRF, 1976; Ouakad, 2007; Oueslati, 2004). Mean winter temperatures are ~11 °C and frosts are rare, in particular in the Ghar el Melh area. The highest temperatures are reached in August with mean values of ~27 °C, especially when the Sirocco wind is blowing. However, this warm and high-speed wind originating from the Saharan desert, rarely affects the Ghar el Melh region (Khrystal Engineering, 2003). The prevailing southerly winds (SE, SSE, S and SSW) during the summer season rarely exceed 10 m·s⁻¹. In winter, the so called “Chirch” which are dominant westerly to northwesterly winds, brings humidity to the study area (Ouakad, 2007).

2.3. Vegetation

While in northwestern Tunisia the humid to sub-humid climates allow the development of cork oak (*Quercus suber*) woodland with *Erica arborea* underbrush and deciduous forest with zeen oak (*Quercus canariensis*) at higher altitudes, in northeastern Tunisia, the prevailing semi-arid to subhumid bioclimates favor evergreen shrubs and trees (Boussaid et al., 1999; El Euch, 1995; Gounot et al., 1965; Fig. 1). However, Mediterranean shrublands and woodlands are actually quite limited in the region of the Lower Medjerda valley. Over the past century, the landscape has known important mutations due to programs of reforestation and intensification of the agriculture (dry and irrigated agriculture, arboriculture, market-gardening, fodder farming) (Kassab, 1981). Sheep farming has long been established in Tunisia although sheep livestock particularly declined consecutively to agricultural policy reform after the Tunisian independence (in 1956) which favored arboriculture expansion. In contrast, cattle livestock greatly increased for milk production but never compensated sheep farming decline (Kassab, 1981; Samaali, 2011). In addition, saline soils of the Medjerda deltaic plain promote widespread azonal vegetation with halophyte plants (Gounot et al., 1965).

In the vicinity of the Ghar el Melh lagoon, the oleo-lentiscus association with scattered *Ceratonia siliqua* is mainly found on the Djebel Edmina (Gounot et al., 1965). Native pine stands of Aleppo pine (*Pinus halepensis*) with brooms (*Genista* and *Calicotome*) and heath (*Erica multiflora*) are present (Khrystal Engineering, 2003; Posner, 1988). Kermes oak (*Quercus coccifera*) with *Ammophila arenaria* (Poaceae) and *Crucianella maritima* (Rubiaceae) is also found on Djebel Edmina but mainly on the active sand dune located on the north side of the hill, between Raf-Raf and Cape Ettarf. However, at the beginning of the century and after the Tunisian independency, stone pine (*Pinus pinea*) was largely planted from the Raf-Raf coastline to the Djebel Nadhour and up to Cape Ettarf (Ben Salem, 1996; Oueslati, 2004), restricting the oleo-lentiscus and kermes oak areas. *Eucalyptus* and *Acacia* were also locally planted (Khrystal Engineering, 2003). Market-gardening, mainly potato crops, takes place in a narrow band at the foothill of Djebel Edmina, close to the Ghar el Melh lagoon.

Oleo-lentisc shrubland is also found on Djebel Nadhour although agricultural activities are more expanded than on Djebel Edmina, in particular in the western part of the hill. In this area, heterogeneous agriculture dominates, including vegetables crops such as potatoes which are cultivated in terraces on the southern slopes of the hill although dry cultivations and diverse orchards are also present. Irrigated lands greatly expanded from the foot of the hill to the deltaic plain in the past decades at the expense of olive crops which are limited today to few small isolated areas. Those lands are essentially used for market-gardening (including tomatoes, potatoes, melons, watermelons) and arboriculture (mainly apple and pear trees) (Samaali, 2011). North of Djebel Nadhour, from Metline to Raf Raf, almond trees are cultivated, often associated with potato-growing (Ben Salem, 1996; Jaouani, 1976).

Even though sclerophyllous shrublands persist, Djebel Kechabta landscape is strongly anthropized. Dry farming, mainly wheat and barley, dominates (Samaali, 2011). An important wine estate, the Henchir El Houid, was located at the foot of Djebel Kechabta although its extent

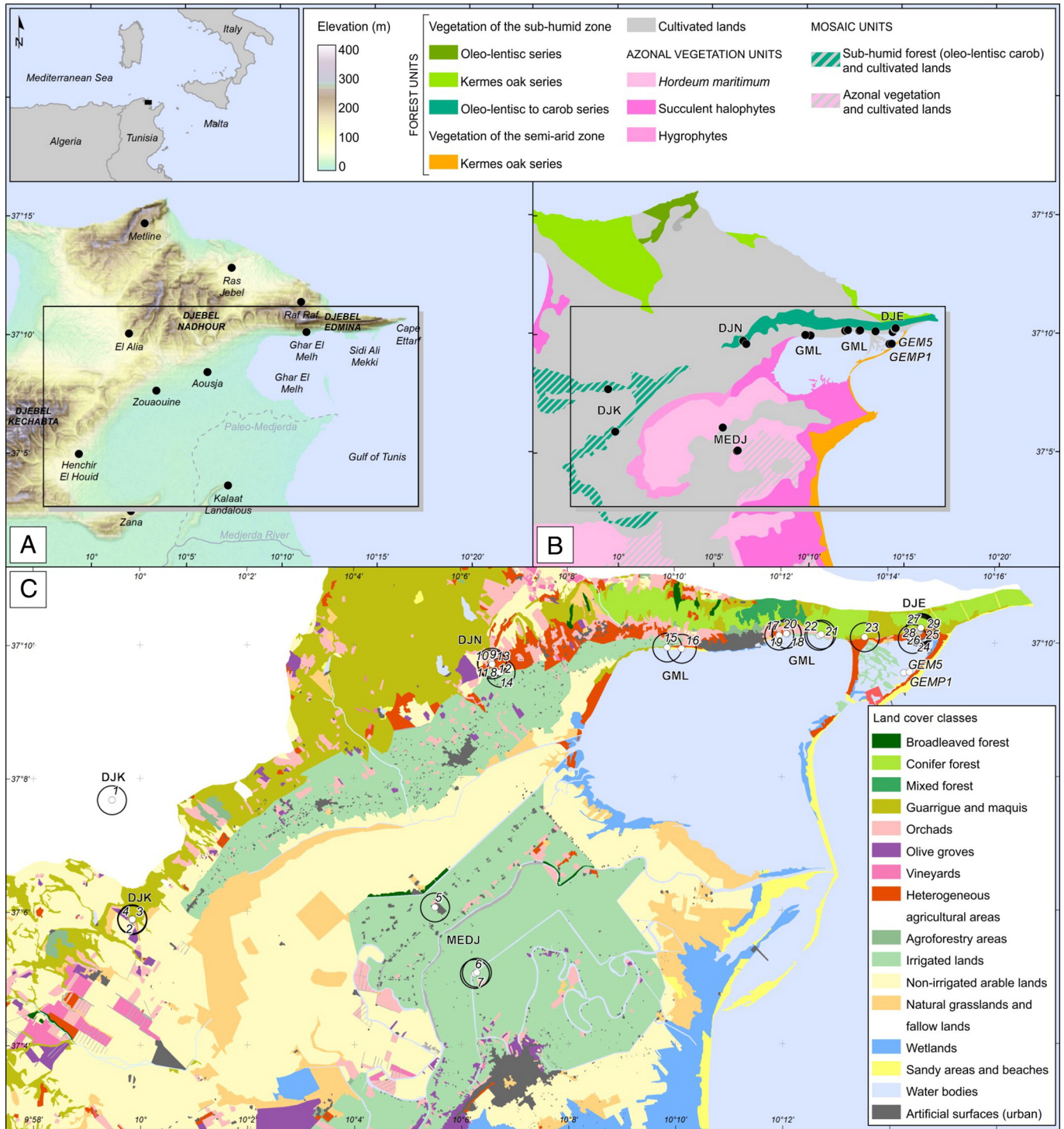


Fig. 1. Presentation of the study area and location of surface and core-top pollen samples: A) physical map, B) phyto-ecological map drawn after Gounot et al. (1965), C) land-cover map derived from remotely sensed vegetation data (Samaali, 2011). Black rectangle in insets A and B represented the area covered by the land cover map. In inset C, black circles around sites correspond to 400 m radius rings. Abbreviates are for samples located on Djebel Edmina (DJE), Djebel Nadhour (DJN) and Djebel Kechabta (DJK), close to the shore of the lagoon Ghar el Melh (GML) and nearby the Medjerda paleochannel (MEDJ).

substantially shrank after the Tunisian independency. Some small olive crops are also found in this area.

Succulent *Amaranthaceae* such as *Salicornia arabica* and *Halocnemum strobilaceum* dominate on the most saline soils of the deltaic plain, i.e. close to the lagoon and sea coastlines. *Phragmites communis* is also widespread along the Ghar El Melh shore. Kermes oaks with *Ammophila arenaria* and *Aristide pungers* (Poaceae) constitute the natural vegetation of the sand bar separating the lagoon from the

sea, although actually restricted. Diverse vegetable crops are found on polders built on the Sidi Ali El Mekki lagoon (Samaali, 2011). When soils become less saline as distance to the coast increases, succulent plants are naturally replaced by *Hordeum maritimum* (Poaceae). However, this area is marked by a strong land-use. A large area along the former natural position of the Medjerda River is devoted to irrigated cultivations mainly consisting in market-gardening and locally in fodder farming (Fig. 1). Otherwise, cereals are produced on non-irrigated lands

(Khrystal Engineering, 2003; Samaali, 2011). The largest olive fields of the study area are found near the cities of Kalaat Landalous and Zana (Fig. 1).

3. Materials and methods

Twenty-nine surface samples were collected in May 2013 and April 2015 in the Lower Medjerda valley, mainly around the Ghar El Melh lagoon (Fig. 1, Table 1). Surface soil samples were collected when moss pollsters were not available. Sample sites were chosen to represent the different vegetation types and land-cover uses:

- Samples 1- to 4-DJK are located at the foot of Djebel Kechabta, where the anthropogenic pressure is high. Samples 2 to 4-DJK have been collected in a small patch of evergreen maquis, nearby large non-irrigated arable lands, olive groves and small pastures. Sample 1-DJK has been taken on the side of a road bordered by dry cultivations.
- Another set of samples (5- to 7-MEDJ) was collected close to the most recent paleochannel of the Medjerda River between Kalaat Landalous and Aousja, an area dominated by irrigated lands used for diverse vegetable crops.
- Samples 8- to 14-DJN were collected on the western tip of the Djebel Nadhour. Excepting sample 14-DJN, they are located on lands dominated by the land cover type heterogeneous agricultural areas which consist of patches of shrublands and orchards, cereals, legumes and fodder crops on the same parcel or on small juxtaposed ones and significant area of natural vegetation. The land cover class associated to site 14-DJN is irrigated lands although it is located at the limit of heterogeneous agricultural zones.
- Samples 15- to 21-GML and 24-GML were taken along the shore of the Ghar el Melh lagoon which is dominated by halophytic vegetation. The nearby lands are mainly corresponding to heterogeneous agricultural areas.
- Samples were also collected on the southeastern side of Djebel

Edmina: at the foot of the hill within heterogeneous agricultural areas (mainly semi-open areas) and orchards for samples 22-, 23-, 25-DJE and more uphill in the evergreen maquis for samples 26- to 29-DJE.

In addition, we analyzed top samples (1 cm-thick) of two sediment cores collected using manual coring equipment (plastic liner tube of 8.5 cm diameter) on the northeastern edge of the lagoon, close to the Sidi Ali Mekki sand bar, namely cores GEM5 (37°09.39' N, 010°14.20' E) and GEMP1 (37°09.40' N, 010°14.31' E).

Surface and core-top pollen samples were prepared following standard procedure (described in detail at <http://ephe-paleoclimat.com/ephe/Pollen%20sample%20preparation.htm>). 5 cm³ samples were sieved through a 150 µm mesh screen. A tablet of exotic spores (*Lycopodium*) was added to each sample before treatments to calculate pollen concentrations. Successive acid attacks (cold HCl at 10%, 25% and 50% and cold at HF 40% and 70%) were performed to remove the carbonates, silica and silicates. Fluorosilicates were eliminated with a final treatment with cold HCl at 25%. For surface pollen samples only, acetolysis was additionally performed after the final stage of the procedure. The residues were sieved through a 10 µm nylon mesh screen and mounted in glycerol. Pollen counting was performed using a microscope Zeiss Axioscope at *400 and *1000 (immersion oil) magnifications. Pollen identification was based on pollen reference slides and palynological atlases (e.g. (Moore et al., 1991; Reille, 1992b)). At least 300 pollen grains and 20 morphotypes were counted for each sample. Pollen percentages were calculated using the pollen sum excluding spores, aquatic and indeterminate pollen grains. Spores, aquatic and indeterminate percentages were calculated using the total sum. Pollen data were plotted using psimpoll (Bennett, 2008).

Patterns in the pollen percentage data were extracted using multivariate techniques: hierarchical cluster analysis and correspondence

Table 1
Information on the surface and core-top pollen samples analyzed.

Sampling sites	Samples names	Altitude (m)	Latitude	Longitude	Sampling date	Land cover class at the sampling sites (Fig. 1)
Djebel Kechabta	1-DJK	119	37.12945	9.99175	April 2015	Undetermined
	2-DJK	74	37.09973	9.99795	April 2015	Garrigue and maquis
	3-DJK	70	37.09948	9.99801	April 2015	Garrigue and maquis
	4-DJK	62	37.09962	9.99813	April 2015	Garrigue and maquis
Medjerda River (between Aousja and Kalaat Landalous)	5-MEDJ	7	37.1025	10.09241	April 2015	Artificial surfaces (urban)
	6-MEDJ	6	37.0859	10.10482	April 2015	Irrigated lands
	7-MEDJ	7	37.0862	10.10539	April 2015	Irrigated lands
Djebel Nadhour (between Ras Jbel and Ghar el Melh)	8-DJN	52	37.16365	10.11025	April 2015	Heterogeneous agricultural areas
	9-DJN	42	37.16326	10.11043	April 2015	Heterogeneous agricultural areas
	10-DJN	0	37.16325	10.11044	April 2015	Heterogeneous agricultural areas
	11-DJN	38	37.10321	10.14658	April 2015	Heterogeneous agricultural areas
	12-DJN	38	37.10321	10.14658	April 2015	Heterogeneous agricultural areas
	13-DJN	38	37.10321	10.14658	April 2015	Heterogeneous agricultural areas
	14-DJN	30	37.16115	10.11303	April 2015	Irrigated lands
Shore of the lagoon Ghar el Melh	15-GEM	1	37.16735	10.16502	April 2015	Irrigated lands
	16-GEM	4	37.16702	10.16958	May 2013	Sandy areas and beaches
	17-GEM	3	37.17022	10.2	May 2013	Heterogeneous agricultural areas
	18-GEM	2	37.17067	10.20234	April 2015	Heterogeneous agricultural areas
	19-GEM	4	37.17068	10.20226	April 2015	Heterogeneous agricultural areas
	20-GEM	7	37.17069	10.20231	April 2015	Heterogeneous agricultural areas
	21-GEM	6	37.17017	10.21253	May 2013	Irrigated lands
Djebel Edmina	22-DJE	11	37.17048	10.2131	May 2013	Orchards
	23-DJE	21	37.16977	10.22672	May 2013	Garrigue and maquis
	24-DJE	2	37.16928	10.24167	May 2013	Heterogeneous agricultural areas
	25-DJE	16	37.17113	10.2439	May 2013	Heterogeneous agricultural areas
	26-DJE	21	37.17143	10.24398	May 2013	Heterogeneous agricultural areas
	27-DJE	28	37.17175	10.24403	May 2013	Garrigue and maquis
	28-DJE	35	37.1719	10.2443	May 2013	Garrigue and maquis
	29-DJE	38	37.17202	10.2443	May 2013	Garrigue and maquis
	GEM 5	–	37.161	10.239	2012	Water bodies
	GEMP 1	–	37.161	10.241	2012	Water bodies

analysis (CA). Before any analysis, in particular because CA ordination shows sensitivity to low frequency taxa, the pollen percentage dataset was reduced based on filter for a 3% minimum taxa presence in at least two samples. Data filtering was performed in the R environment v. 3.1.1 (R Core Team, 2016) using the function “filter.p()” from the R package “paleoMAS” (Correa-Metrio et al., 2011). Hierarchical cluster analysis was applied to the filtered pollen percentage dataset based on the Ward’s agglomerative procedure using the function “hclust()” from the R package “Rioja” (Juggins, 2009). Since core-top pollen samples may represent different spatial and temporal scales, CA ordination was performed on the filtered dataset including only modern surface samples using the function “cca()” from the R package “vegan” (Oksanen et al., 2016). Core-top sample scores were estimated using the function “predict()” of the R package “vegan”.

To assess the pollen representation of the vegetation around the lagoon, we compared the surface pollen data to the modern land cover. We used the land-use map of the Medjerda delta established from remote sensing data for the year 2007 which has a decameter resolution (Samaali, 2011; Fig. 1). Land cover was validated using ground-truth data (Samaali, 2011). To allow comparison with pollen data, the original land cover classes were merged into seven categories which appear more meaningful for pollen data in our study area: A) open landscape which groups the classes “irrigated and dry cultivated lands”, “fallow” and “grasslands”, B) heterogeneous landscape made of “Heterogeneous agricultural areas”, “agroforestry areas”, “olive groves”, “vineyards” and other “orchards”, C) “conifer woodlands”, D) other woodlands consisting of “broadleaved forest” and “mixed forest”, D) “garrigue and maquis”, E) wetlands, F) undetermined.

We assigned a single land cover class to each modern pollen site (Table 1) and extracted surfaces of the different land cover classes within rings of 400 and 800 m radius around each site using ArcGIS for Desktop (Esri) software. Rings intend to represent potential relevant source areas of pollen (RSAP). Although previous works tend to provide RSAP estimates, they remain difficult to define since they vary between less than 10 m and 400 m for moss samples and up to 1000 m for small lake samples depending on the nature of the surface sample and the size of the basin for lake samples as well as the type, composition and structure of the surrounding vegetation (Bunting et al., 2013; Bunting et al., 2004; Gaillard et al., 1994; Sugita et al., 1999). No information is available in the literature on the RSAP of soil samples. Surface percentages were calculated for amalgamated land cover types within each ring in excluding areas with artificial covers and water bodies. We add a category named “undetermined” for areas with no land-use information. They are only found within few 800 m radius rings although site 1 which is located outside the land-use map is entirely allocated to this class. The “balloonplot()” function from the R package “gplots” (Warnes et al., 2016) was used for land-use data representation. To describe the relationship between pollen spectra and vegetation, we fitted smoothed surfaces of the main land cover type areas within 400 m ring based on Generalized Additive Models (GAM) into the CA ordination using the “ordisurf()” function of the R package “vegan” (Oksanen et al., 2016).

4. Results

4.1. Main features of the pollen spectra

Pollen results are presented in Fig. 2 that shows the percentages of the main relevant taxa for characterizing the vegetation in our study area. Among the 29 surface samples analyzed, two of them (samples 24- and 26-DJE) were pollen-barren. We identified 66 distinct pollen taxa from the surface and core-top samples.

Arboreal pollen (AP) taxa, mainly *Pinus* and *Pistacia* and *Olea*, show high values in the samples from Djebel Edmina (DJE) and Djebel Nadhour (DJN) and some of the Ghar el Melh lagoon shore (18- to 21-GML). The highest abundances of *Pinus* (up to 46%) are recorded in

the DJE samples which are located more uphill (27, 28 and 29-DJE). *Pinus* also presents relatively high values in some DJN and GML samples (8- and 11-DJN and 18-, 19- and 21-GML).

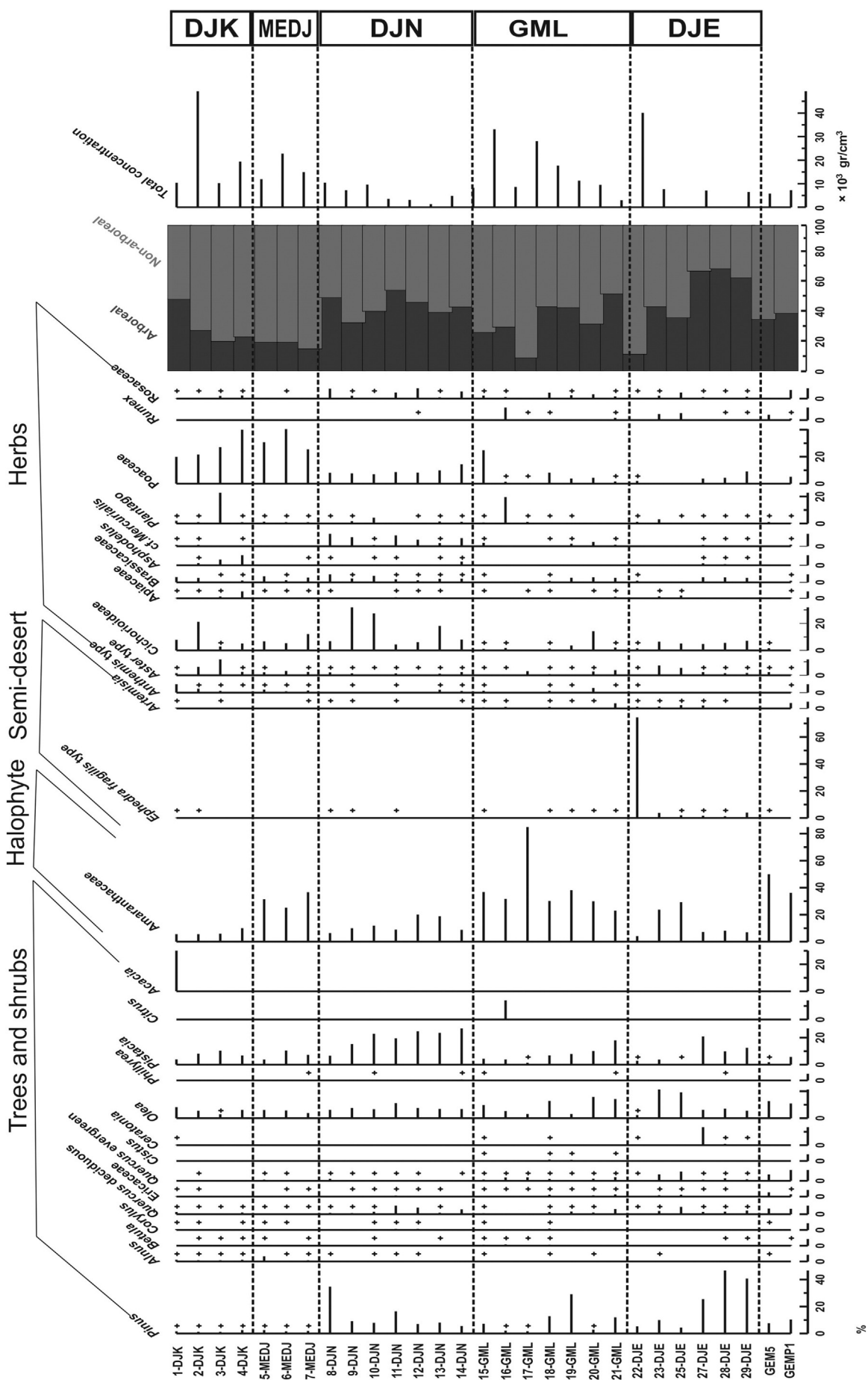
Olea and *Pistacia* are recorded in all samples. *Pistacia* is well-represented in DJN samples (except 8-DJN) reaching 25% and in 27- to 29-DJE, while *Olea* appears as the main sclerophyllous taxa in 23 and 25-DJE and in the core-top samples. Both taxa are also well represented in some GML samples (18 to 21-GML). *Ceratonia* pollen is sporadically present in DJK and GML spectra but it is mainly recorded in the group of DJE samples located more uphill (maximum abundance of 13% in 27-DJE). Evergreen *Quercus* pollen occurs in almost all samples but is better represented in DJE and GML spectra and in particular in 23- and 25-DJE (~5 and 7%, respectively). Abundances of deciduous tree morphotypes and Ericaceae (Fig. 2) remain low in all samples although they are more frequently observed in DJE and DJN samples and in the core-top samples (up to 6% for deciduous *Quercus*). Some arboreal taxa are specifically related to a particular site, such as *Acacia* (30%) only recorded in sample 1-DJK and *Citrus* (14%) in sample 16-GML.

The herbaceous pollen sum displays the highest values in samples located in the deltaic plain close to the Medjerda abandoned arm (MEDJ), at the foot of the Djebel Kechabta (DJK), in part of the samples from the Ghar El Melh lagoon shore (15- to 17-GML) and in 22-DJE. Abundances of Amaranthaceae are high in all GML and MEDJ samples (between ~25 and 40%, excepting in 17-GML where abundance reaches 84%). This morphotype is also well represented in 23- and 25-DJE (~20%) and in the core-top samples. Poaceae displays the highest values in MEDJ, DJK spectra and in one of the GML samples (15-GML). All DJN spectra present low but steady abundances of Poaceae. The main other herbaceous taxa are Asteraceae morphotypes (Cichorioideae, *Aster*-type), *Asphodelus*, *Mercurialis*, Brassicaceae and *Plantago* although their abundances are highly variable from one sample to another. Highest values of Cichorioideae are observed in 9-, 10-, 13-DJN and 2-DJK, and of *Plantago* in 16-GML and 3-DJK. *Asphodelus* is well represented in DJK spectra and occurs in DJN and DJE spectra. *Mercurialis* is best represented in DJN spectra. Rosaceae pollen occurs in almost of all samples but higher values are displayed in some DJN spectra. Abundances of the semi-desert taxa *Artemisia* and *Ephedra fragilis*-type remains low in all samples, excluding in 22-DJE where *Ephedra fragilis*-type reaches 74%.

4.2. Discrimination between the pollen spectra using statistical analysis

We used multivariate analyses to summarize the relationships between the samples based on their pollen abundances. The hierarchical cluster analysis separates the surface samples in four distinct groups (Fig. 3). The sample 22-DJE which presents large dissimilarity with other pollen spectra, likely due to particularly high percentages of *Ephedra fragilis*-type, is not included in the defined clusters. Cluster A groups most of DJN samples marked by high abundances of *Pistacia* and low *Pinus* values. Cluster B includes the DJE and DJN samples which display high values of AP taxa, mainly associated with *Pinus*. The herbaceous-dominated pollen spectra from DJK and MEDJ, all presenting high values of Poaceae, are grouped in cluster C. Sample 15-GML which has high values of Poaceae is also included in this cluster. Cluster D groups samples with low to intermediate NAP values mainly associated with Amaranthaceae, including almost all GML samples and 23 and 25-DJE. Both core-top pollen spectra (GEM5 and GEMP1) present low dissimilarity with the surface samples from cluster D.

In the initial run of the CA ordination, sample 22-DJE appears unsurprisingly as an outlier making all the other points tight together, impeding the interpretation of the CA biplot. We excluded this sample from the final analysis presented in Fig. 4 that shows the distribution of samples and taxa scores on the first and second CA axes. The combined axes account for 48% of the variance (Axis 1, eigenvalue = 0.25447, Axis 2, eigenvalue = 0.22694). Axis 1 mainly discriminates samples on the basis of the AP and NAP values. Sample scores on Axis 1 are positively



correlated with AP percentages ($R = 0.8812$, $p < 0.0001$). The main taxa having a strong contribution to this axis are *Pinus* and *Pistacia* (37 and 5%, respectively) and *Amaranthaceae*, *Plantago* and *Poaceae* (14%, 20% and 6%, respectively). The DJN and DJE samples characterized by highest abundances of tree and shrub pollen, mainly *Pinus* and *Pistacia*, are clearly distinguished from DJK and MEDJ samples which are dominated by herbaceous taxa, mainly *Poaceae* and *Amaranthaceae*. This axis only separates the GML samples which are largely dominated by herbaceous taxa, i.e. 16- and 17-GML. Axis 2 mainly discriminates between clusters C and D, i.e. between MEDJ and DJK samples presenting high values of *Poaceae* and GML samples marked by high abundances of *Amaranthaceae*. Both taxa are the major contributors to this axis (20% and 35%, respectively). Although MEDJ and DJK are not clearly separated by the CA and both included in cluster C, scores of MEDJ samples are higher due to the co-dominance of *Poaceae* and *Amaranthaceae*. 15-GML which displays a pollen spectrum close to MEDJ samples present lower scores than the other GML samples and also belongs to cluster C. In contrast, 23 and 25-DJE which display high *Amaranthaceae* values are grouped with GML samples by the CA and cluster analyses. DJE and DJN samples are less clearly distinguished on this axis, although samples from cluster B have more positive values than spectra included in cluster A. Estimated scores of the core-top pollen spectra are negative on Axis 1 and markedly high on Axis 2, likely related to the low values of *Pinus* and *Pistacia* and to the high contribution of *Amaranthaceae*, respectively. Both CA and cluster analyses show that these pollen spectra display similarities with GML and 23- and 25-DJE samples.

4.3. Land cover data at sampled sites

Since surface samples recruit pollen from vegetation surrounding the sampled sites, we determined the land-cover types within a ring of 400 m radius from the land cover data derived from remote sensing (Figs. 1 and 5). Forest and shrubland mostly of conifers and sclerophylls, are the main land cover types around DJE sites while open vegetation type (irrigated lands mainly) dominates the area around MEDJ sites. The 400 m rings around DJK sites mainly include shrublands and open lands (grasslands and non-irrigated lands). Finally, land cover around DJN and GML sites is mainly characterized by heterogeneous agricultural areas and arboriculture, excepting at 15-GML and 14-DJN where open vegetation (mainly irrigated lands) occupies a larger area. Since RSAP is difficult to precisely define, we also analyzed the land cover within rings of 800 m radius. This analysis displays similar results although surface of woodland and shrubland appear larger around GML sites (Fig. 5). In addition, the 800 m rings around DJE sites include up to 15% of undetermined surfaces since rings stretch into the northern side of the Djebel Edmina for which land cover data are not available (white areas in Fig. 1C). Therefore, the relationships between the pollen spectra of the different studied sites and the main representation of the vegetation were examined using land cover data within 400 m radius rings around the sites. For that, fitted smoothed surface of the different land cover types around the sites into the ordination space was used (Figs. 4 and 6). Areas with more than the largest values of open land cover are associated with sites from cluster C (MEDJ and DJK) which have pollen spectra dominated by the herbaceous taxa *Poaceae* and *Amaranthaceae* while lowest values are found with DJE sites which present the highest AP percentages (Fig. 6c). Highest conifer woodland and garrigue and maquis areas are associated with DJE sites (Fig. 6a and b) while increased values of shrubland surfaces are also associated with DJK sites despite low AP values. DJN site scores are mainly correlated with highest surfaces of heterogeneous agriculture and arboriculture (>50%), while MEDJ and DJK site scores are clearly associated with lowest areas (<20%) (Fig. 6d). GML site scores are not clearly explained by the four land cover type variables.

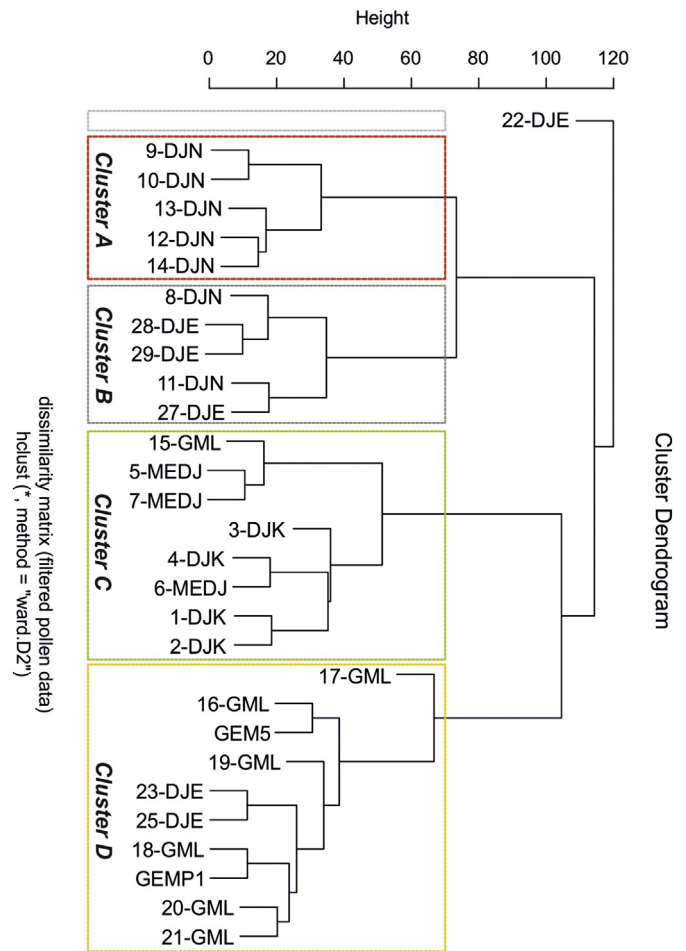


Fig. 3. Cluster dendrogram established from unconstrained hierarchical cluster analysis of the surface and core-top pollen data.

5. Discussion

5.1. Characterization of the vegetation in the Lower Medjerda valley by pollen assemblages

The multivariate analyses of the surface sample pollen data and the comparison with land cover data enable to distinguish the modern pollen rain of different land cover types in the Lower Medjerda valley. In particular it allowed characterizing the pollen spectra of the Mediterranean shrubland which is the typical vegetation of the hills bordering the Lower Medjerda valley and the vegetation of the deltaic plain and lagoon shore with different degree of human disturbance.

Pollen samples collected within the Mediterranean shrubland of Djebel Edmina are dominated by arboreal pollen. Typical sclerophyllous taxa, namely *Pistacia*, *Olea* and *Ceratonia* are represented although *Pinus* appears as the major AP taxa. These sites are likely influenced by the pollen rain of pine stands growing close by as shown by the presence of conifer woodlands within the 400 m ring. These woodlands mainly consist of stone pines which have been largely planted during the past century, replacing wide areas formerly occupied by thermophilous maquis (Khrystal Engineering, 2003; Samaali, 2011). Few native Aleppo pine stands are also present in this area (Bortoli et al., 1967). *Pinus* pollen are however likely over-represented in these pollen spectra since pines are well-known high producers of pollen that are largely dispersed (Traverse, 2007). In surface samples from Beliche floodplain

Fig. 2. Pollen diagram displaying the percentages of the main pollen taxa. Sum of arboreal and non-arboreal pollen percentages and total concentrations are also shown. Crosses indicate values below 3%.

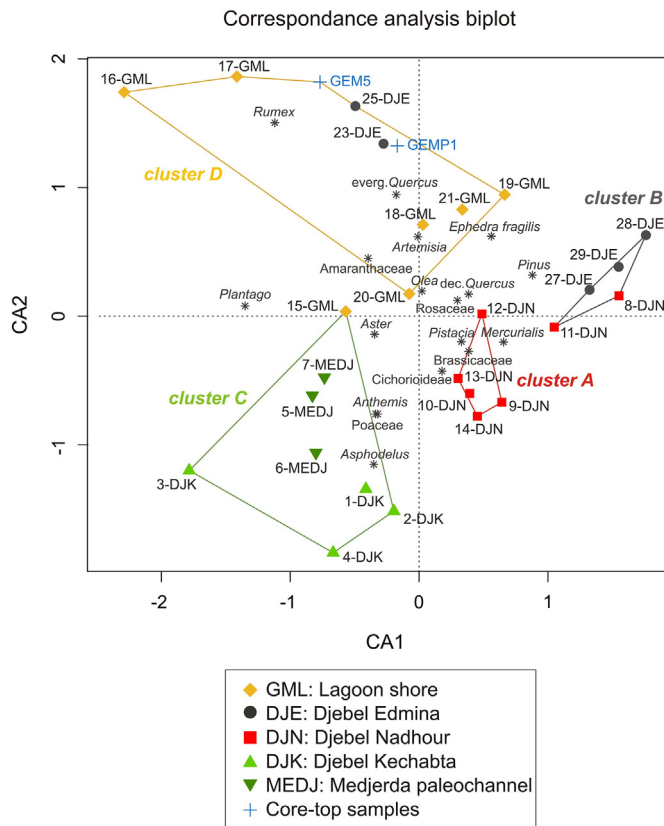


Fig. 4. Correspondence analysis biplot based on surface pollen samples; scores of core-top samples were predicted.

(southern Portugal), *Pinus* is also well represented in hill-slope samples taken from areas with Mediterranean scrubs and olive groves although it is likely associated with extralocal to regional sources. In contrast, *Calycotome villosa* which is the main component associated with pines on Djebel Edmina is not recorded. The study of pollen–vegetation relationships in Cyprus shows that *Calycotome* is among the taxa displaying lowest fidelity (Fall, 2012) because this legume shrub is an entomophilous low pollen producer (Arroyo, 1981). Although also mainly associated with woodland and shrubland within the 400 m ring, pollen spectra 23- and 25-DJE display a different composition than the other samples from Djebel Edmina. Slight increase in agricultural areas may explain the lower contribution of *Pistacia* and *Pinus*. Increased *Olea* abundances are recorded although they remain largely below values generally found within and around olive fields (Díaz Fernández, 1994; Fletcher, 2005; Lebreton et al., 2015). Remotely sensed vegetation data do not show nearby olive groves. *Olea* contribution at those sites is likely associated with scattered olive trees commonly found in fields for familial olive production or used in private gardens as ornamental plants.

Samples collected within the thermophilous maquis from Djebel Kechabta display high NAP values and are hardly differentiated from MEDJ samples which are associated with irrigated lands. The surprising pollen signature of the maquis in this area can be explained by its small extent and sparseness. As shown by the land cover data (Figs. 4, 5 and 6), these sites are related to large surrounding areas of open landscape mainly consisting of non-irrigated arable lands and pastures. Even though wheat and barley cultivation is the main use for non-irrigated arable lands in this area, the pollen spectra do not record these cereals. It has been observed that wheat and barley pollen abundances drastically decrease with distance to the field because both cereals are almost exclusively self-pollinating plants and produce large pollen which are weakly wind-dispersed, mostly remaining enclosed in the spikelets. Cereal pollen spreading is mainly man-made during the harvesting and crop transport (Vuorela, 1973). Since surface sample collection was

done before harvesting, it can explain the recorded virtual absence of cereals. Pollen assemblage composition is, in turn, dominated by Poaceae with diverse Asteraceae taxa which can be related to farming activity (Bottema and Woldring, 1990). In addition, *Asphodelus* pollen grains in DJK samples can be related to asphodel species favored by overgrazing and man-made fires (Djamali et al., 2013). This suggests that in areas where the maquis is highly degraded, pollen composition hardly distinguishes it and reflects instead graminoid steppes that can be related to the steppisation of the landscape subsequent to human activities.

In the western part of Djebel Nadhour, most of the maquis has been cleared for agricultural purpose. Pollen spectra from this zone are strongly related to the land cover type of heterogeneous agricultural areas (Figs. 4 and 6). This type refers to lands mainly occupied by agriculture, i.e. orchards, vegetable and fodder crops on the same parcel or on small juxtaposed ones, that can be interspersed with significant natural areas occupied here by thermophilous maquis. The CA and cluster analyses separate most of the DJN samples within a cluster marked by *Pistacia* as the major AP taxa although two samples presenting higher values of *Pinus* are grouped with pollen spectra representing the Djebel Edmina shrubland. *Pistacia* values can be representative of the residual patches of thermophilous maquis or partly associated to long-distance transport since pistachios are wind-pollinated (Petanidou and Vokou, 1990). However, *Pistacia* is also considered as a shrub that can be promoted by vegetation clearing (Behre, 1990) and therefore its representation in pollen spectra from heterogeneous agricultural areas could be related to human disturbances. In addition, all samples from Djebel Nadhour are particularly marked by diverse NAP taxa such as Cichorioideae, Brassicaceae, *Mercurialis*, *Rumex* which are considered as secondary anthropogenic indicators, i.e. favored by human activities (Bottema and Woldring, 1990). These taxa are associated with *Asphodelus*. Additionally, Rosaceae which is consistently recorded in DJN samples, may be associated with pear or apricot orchards present in this area although it is a large family including a large number of wild and cultivated species. Because arborescent Rosaceae such as *Prunus* and *Pyrus* are insect pollinated, this taxon is likely under-represented in our record as found in pollen samples from semi-arid regions such as Iran and Turkey (Bottema and Woldring, 1990; Djamali et al., 2009).

The statistical analyses show that pollen spectra close to the Medjerda paleochannel are strongly related to open landscape area. In this zone, land-use is almost exclusively market gardening on irrigated lands. However, Poaceae and Amaranthaceae dominate instead of taxa associated with the diverse crops (artichokes, cabbage, watermelon etc.). These cultivated plants are generally insect-pollinated and their pollen grains are difficult to separate from wild species in pollen spectra. Most importantly, MEDJ samples have not been collected in the middle of cultivated fields but along road side or close to irrigation canal where halophyte Poaceae (*Hordeum maritimum*) and Amaranthaceae species naturally develop (Novikoff, 1965) likely explaining why both taxa dominates. One sample from the lagoon shore, GML-15 which is associated to irrigated lands, presents a similar pollen spectra than the MEDJ samples. However, the high representation of Poaceae in this spectrum may also be associated to *Phragmites* developing close the nearby lagoon shore.

The multivariate analyses separated the other pollen spectra characterized by high values of Amaranthaceae that were collected close to the lagoon shore and are mainly associated with heterogeneous agricultural areas. Amaranthaceae is a large family including species associated to a large variety of habitat. However, this taxon is commonly found in pollen spectra from semi-arid areas (Brun, 1985; El-Moslimany, 1987) and it is highly represented in saline environments such as delta, sea coast, sebkas or lagoon shore (Ayyad et al., 1992; Bottema and Woldring, 1990; Cambon et al., 1997) due to the prevalence of halophyte species. Therefore, the GML pollen spectra primarily reflect the local halophytic vegetation developed on the shore of the lagoon Ghar El Melh despite large agricultural areas close to the sites.

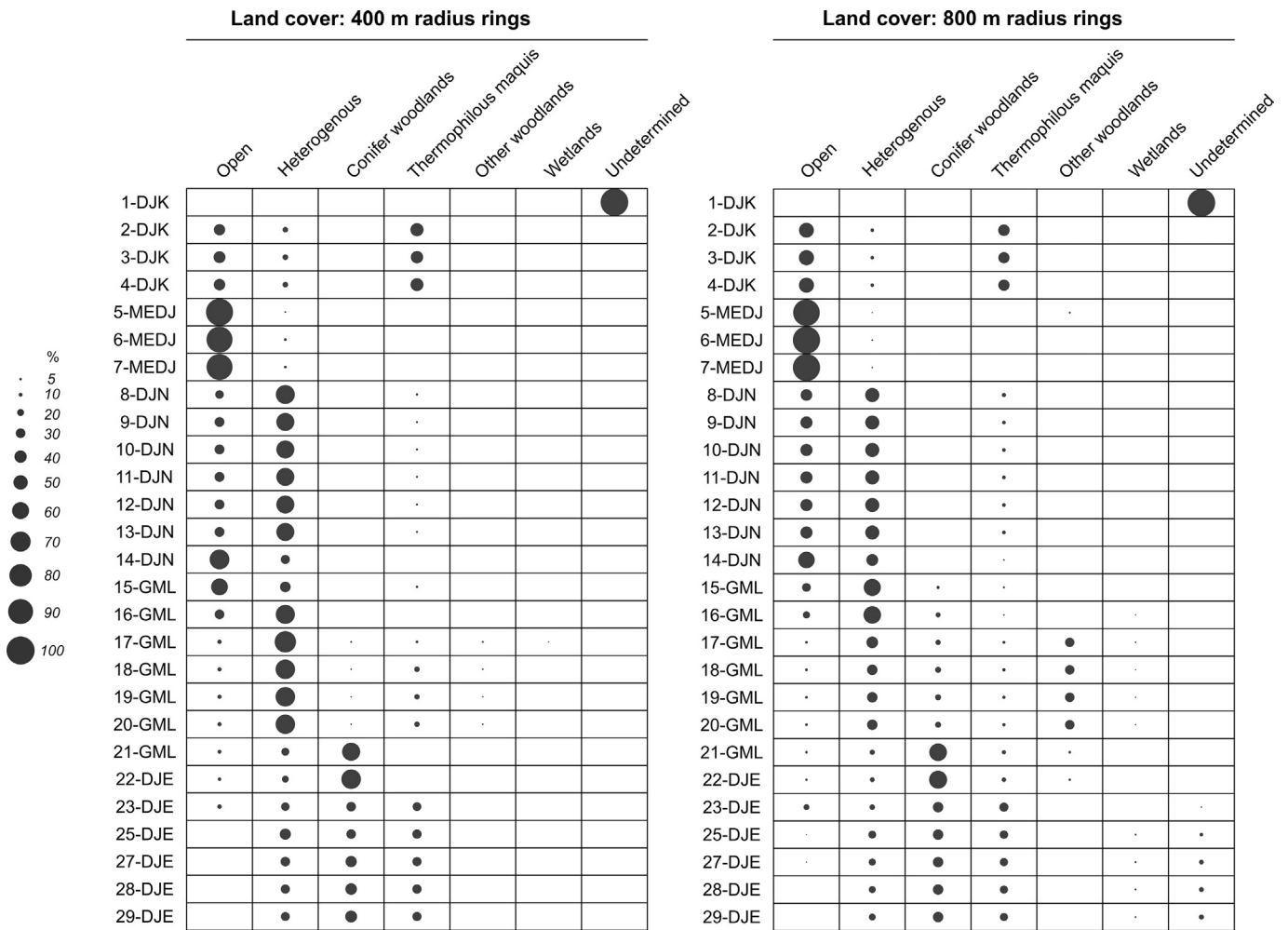


Fig. 5. Surfaces of the different amalgamated land cover types found within 400 m and 800 m radius ring for each sampled site based on remotely sensed data presented in Fig. 1: A) open landscape which groups the classes "irrigated and dry cultivated lands", "fallow" and "grasslands", B) heterogeneous landscape made of "Heterogeneous agricultural areas", "agroforestry areas", "olive groves", "vineyards" and other "orchards", C) "conifer woodlands", D) other woodlands consisting of "broadleaved forest" and "mixed forest", E) "garrigue and maquis" (mainly consisting of maquis as shown in Samaali, 2011, F) undetermined.

5.2. Uncertainties in the comparison of pollen spectra and land cover data

We used an original approach coupling quantified land cover data derived from remote sensing and pollen data from surface samples to evaluate the relationship between vegetation and pollen spectra. We showed that the pollen rain associated with heterogeneous agricultural areas and open landscape (irrigated lands) have a distinctive pollen signature while the Mediterranean maquis pollen composition may be strongly overprinted by adjacent land covers such as conifer woodland or open vegetation. However, different sources of error that are inherent to pollen data and remotely sensed land cover data (Woodbridge et al., 2014) can affect their comparison.

At site-specific scale, land cover types are more poorly estimated using remote sensing techniques than at a regional scale (Hjelle et al., 2015; Woodbridge et al., 2014). Remotely sensed land cover data fail to represent the vegetation mosaic since assigned class to one pixel correspond to the dominant class detected, may contain errors on land cover determination (vegetation identification using remote sensing data is never 100% successful) and are limited by the resolution of the spatial images. These inaccuracies may explain why while pollen spectra located close to the lagoon shore present a strong imprint of the local halophyte vegetation, the remotely sensed land cover data failed to detect small areas of wetland on the northern lagoon shore. In addition, georeferencing errors affect both pollen and land cover datasets

(Woodbridge et al., 2014). For instance, in our data, the allocation to artificial surfaces of sample 5-MEDJ which has been collected within irrigated lands is clearly due to uncertainties in georeferencing. Uncertainties may also derive from discrepancies between pollen sample collection date, time period represented by the sample (for instance, moss samples may include several years of pollen rain (Bunting et al., 2013; Lisitsyna et al., 2012) and dates of remotely sensed data, in particular in areas with intense human activities (Woodbridge et al., 2014). In our work, pollen samples have been collected in 2015 and 2013 while the land use map is based on remotely sensed data from 2007. Google Earth images covering the period between 2006 and 2017 shows that large changes in land use did not occur around the studied sites over the last ten years although cultivated fields slightly expand over the maquis at Djebel Kechabta between 2007 and 2013, suggesting that shrubland surface in land cover data is over-estimated. However, the over-estimation is probably weak and do not entirely explain the under-representation of the Mediterranean maquis by pollen data at Djebel Kechabta. This discrepancy may also be related to the difficulty of determining the RSAP which varies depending on diverse local factors (Broström et al., 2008).

We compared pollen percentages to surfaces of land-cover even if relationship between abundances of pollen and plants is known to be non-linear. Distance-weighted plant abundances within RSAP are generally used for modeling pollen-dispersal and deposition in order to

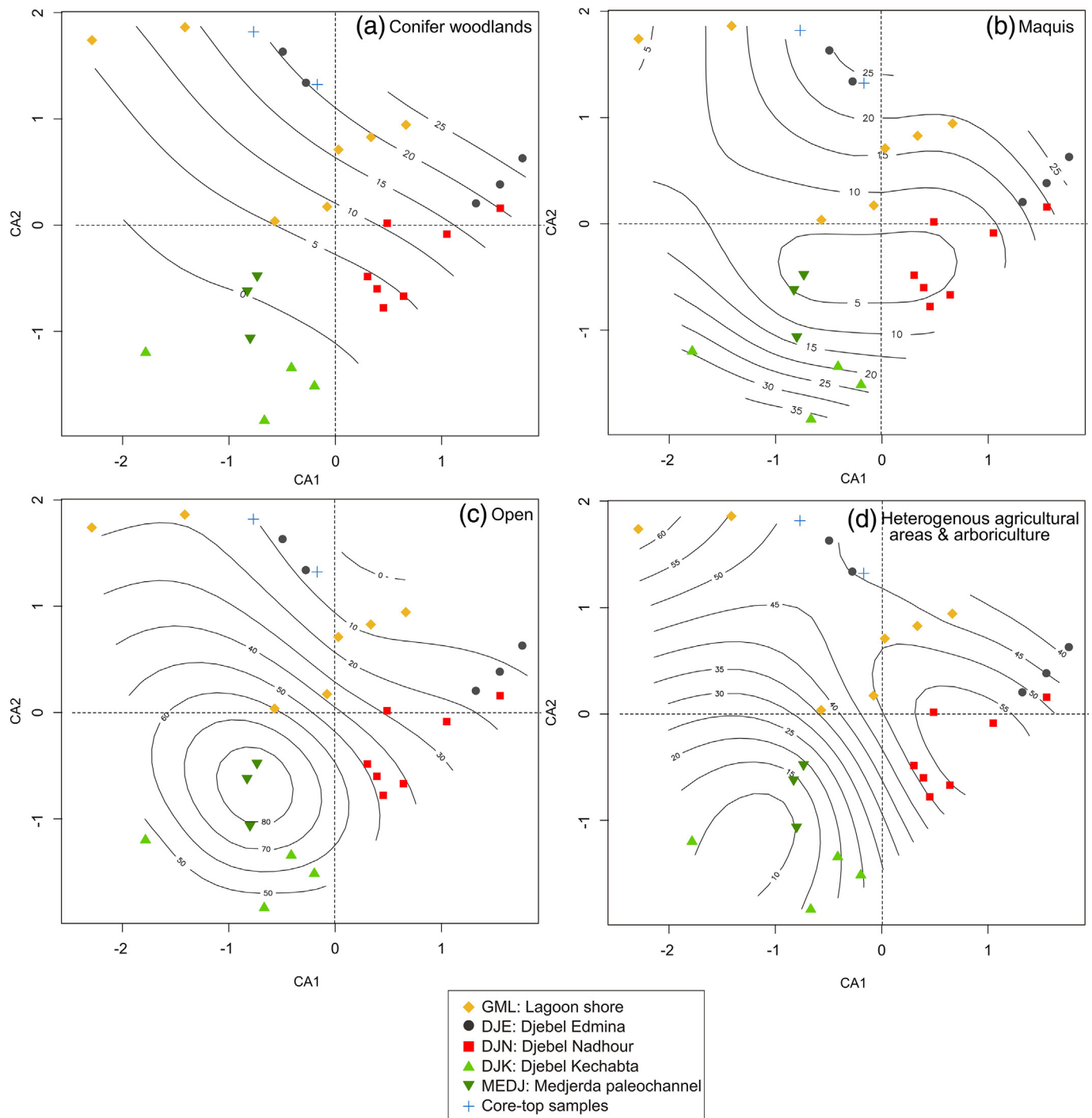


Fig. 6. GAM fitted smoothed surfaces into the CA ordination biplot of the main land cover type areas present within the 400 m radius ring around each sampled site: (a) conifer woodlands, (b) thermophilous maquis and guarigue, (c) open vegetation mainly consisting of irrigated lands, dry cultivated lands, grasslands and fallows, (d) heterogeneous agricultural areas and orchards.

reflect the varying pollen contribution as a function of the source distance (Calcote, 1995; Prentice, 1985; Sugita, 1994). However, the pollen-loading distance and RSAP are taxon-specific and can be site-specific depending on the structure and composition of the vegetation (Broström et al., 2008; Broström et al., 2004; Bunting et al., 2004). Pollen rain in open landscape such as in semi-arid environments may be prone to increased contribution of pollen originating from far-distant vegetation (Bunting et al., 2004; Carrión, 2002). Despite prevailing local character of the pollen rain, long-distance transport of anemophilous taxa is a common factor biasing the depiction of the local vegetation by pollen assemblages (e.g. Traverse, 2007). *Pinus* pollen over-representation is

the most widely known example. However, we showed that most pollen spectra displaying high contribution of *Pinus* are from sites closely located to the conifer woodlands. Sites from GML and DJE located downhill show weak *Pinus* representation even if conifer woodlands are present within a 400 m radius ring. Other studies from the Mediterranean region have shown that *Pinus* is not over-represented in surface samples resulting from the higher abundances of other AP taxa in areas with mixed vegetation forests (Bell and Fletcher, 2016; Reille, 1992a). However, in our study area, vegetation being mostly open or semi-open, relief and wind pattern are reasonably the main factors unfavorable to pine pollen dispersion to the sampled sites.

Background signal of long-distance transport is also evidenced for *Pistacia* and in particular *Olea* which are both wind-pollinated. Both pollen taxa are present in all samples even though thermophilous maquis, olive and pistachio crops are not recorded in the surrounding areas. The MEDJ pollen spectra taken from lands are used for market gardening are clear examples. While most *Pistacia* pollen grains likely come from the maquis located on the djebels which includes the wild species *Pistacia lentiscus*, some may also originate from central or southern Tunisia where *Pistacia vera* cultivations are widespread (Ghorbel et al., 1998). *Olea* is never highly represented in the collected samples particularly because olive crops are confined to small groves in northeastern Tunisia, the most important being located close to Kaalat Landalous and Zana (Fig. 1). Olive trees have long been grown in Tunisia since the Carthaginian epoch (Stuijts, 1991) and in the mid-20s century, large olive plantations flourished in northeastern Tunisia, like near Aousja but they dramatically shrank since the seventies as cities and agricultural activities such as market-gardening expanded (Ben Salem, 1996; Samaali, 2011). Except for sample 22-DJE, in which the high *Ephedra fragilis*-type abundances reaching 75% is likely due to an anther fall (Bunting et al., 2013), the extremely low values of the semi-desert taxa recorded suggest an airborne regional transport. *Ephedra fragilis* has moderate pollen production but high dispersal (Djamali et al., 2009). Pollen traps in the Alps record *Ephedra fragilis*-type pollen coming from North Africa, attesting that this taxon is prone to extremely long transport (Markgraf, 1980). *Artemisia*, another semi-desert taxa represented in the surface samples, is a great anemophilous pollen producer that can also be transported over long-distance (El-Moslimany, 1990). In contrast, *Acacia* which also belongs to the Central and southern Tunisian vegetation, produces large and hardly dispersible pollen. Although individual pollen grains have been found 250 to 300 km to the source area (Daoud, 1983), high *Acacia* values (~30%) in DJK-1 cannot be attributed to long-distance transportation. Such abundances are likely due to planted trees nearby the sampling site. *Acacia* species, in particular *A. cyanophylla*, are commonly cultivated in northern Tunisia for livestock breeding or used as ornamental plants (El Euch, 2000; Hadj Hamda et al., 2017). While some pollen grains from taxa characteristic of the central southern semi-arid to arid region may be transported by southerly winds, others such as deciduous *Quercus*, *Alnus* and *Betula* pollen likely originate from southern Europe or the humid northwestern Tunisia. Extra-regional long distance transport of these tree taxa was also documented from pollen traps (Daoud, 1983).

5.3. Pollen signal of sedimentary cores from the Sidi Ali Mekki lagoon

The comparison between the core-top and surface sample pollen spectra may be hampered by the discrepancy in time interval represented in the samples. However, core-top samples which are of 1-cm depth only likely cover the last decade as shown by nearby dated cores from Sidi Ali Mekki lagoon (Dezileau, personal communication). Both GEM 5 and GEMP1 cores are located on the southeastern edge of the small lagoon of Sidi Ali Mekki far away from large vegetated areas (Fig. 1). The most represented pollen taxon is *Amaranthaceae* reflecting the predominant influence of the local halophyte vegetation developing on the coastal dunes and marshy areas bordering the lagoon like for GML samples. The multivariate analyses confirm that both core-tops have a similar pollen signature than the surface samples from the Ghar El Melh lagoon shore. Similarly, the herbaceous “anthropogenic indicators” characterizing the pollen samples associated with heterogeneous cultivated lands are not well represented despite their proximity. In pollen spectra from lagoon environments, the dominance of halophytes may mask important component of the surrounding vegetation. Therefore excluding *Amaranthaceae* from the pollen sum would avoid over-representation of the local vegetation in lagoon records, as recommended for records from inland playas, saline lake and estuarine environments (Fletcher, 2005; Djamali et al., 2008). Pollen rain of *Pinus* woodland from Djebel Edmina also weakly contributes due to unfavorable

dominant wind direction. In contrast, both sites appear slightly more affected by long-distance aeolian pollen transport of evergreen *Quercus* and deciduous trees. Regional and extra-regional pollen inputs to the core sites appear higher than in the GML surface samples likely because of the openness of the environment although it does not mask the predominant local vegetation signal of Sidi Ali Mekki shore.

6. Conclusions

Effort is most often done to provide information on modern surface pollen assemblages of vegetation as natural as possible, in particular in southern Europe. However, since Mediterranean vegetation in sub-humid to semi-arid environments has been strongly disturbed by human activities for millennia, it is essential to examine the pollen assemblages associated to degraded vegetation. We used terrestrial surface samples compared to remotely sensed land cover data to document the modern pollen rain in northeastern Tunisia that reflects the main vegetation types associated to different land-uses. We found that the Mediterranean maquis pollen composition may be strongly influenced by adjacent land covers such as conifer woodland or open vegetation. In contrast, the pollen assemblages mainly associated with land-uses corresponding to heterogeneous agricultural areas and open landscape, mainly irrigated lands, have a distinctive signature; the former areas are characterized by *Pistacia*, *Rosaceae* and diverse NAP taxa such as *Cichorioideae*, *Brassicaceae*, *Mercurialis*, *Rumex* while the latter are dominated by *Amaranthaceae* and *Poaceae*. However, close to water bodies, pollen spectra reflect predominantly the characteristic halophytic vegetation whatever the surrounding land cover types. The recent pollen signal of two lagoon cores was also compared with the modern pollen spectra in order to determine the representativeness of fossil pollen in sediment cores from this area and their ability to record past vegetation and land-use histories in the Ghar el Melh region. We found that pollen signal of both cores mainly represents the predominant local vegetation of Sidi Ali Mekki shore although regional and extra-regional pollen inputs to the core sites appear stronger than in surface samples. The original approach used here, coupling pollen data and remotely sensed land cover data, give substantial results although further investigations are required because of limitations and errors affecting both datasets.

Acknowledgements

This work is part of the French–Tunisian Joint Project PHC-Utique (Partenariats Hubert Curien: No. 14G1002 – Campus France No. 30587QH). The CMCU (14G1002) program and Labex COTE (2017) provided financial support. We thank Marie-Hélène Castéra and Muriel Georget for sample preparation. We are grateful to Samaali Hamouda for kindly providing land use data of the Medjerda deltaic plain and Amina Daoud for her help. We thank Emna Medhyoub for providing the physical maps and data of the study area. Finally we are grateful to the referees for their constructive comments.

References

- Anupama, K., Prasad, S., Reddy, C.S., 2014. Vegetation, land cover and land use changes of the last 200 years in the Eastern Ghats (southern India) inferred from pollen analysis of sediments from a rain-fed tank and remote sensing. *Quat. Int.* 325, 93–104.
- Arroyo, M., 1981. Breeding systems and pollination biology in leguminosae. In: Polhill, R., Raven, P. (Eds.), *Advances in legume systematics*, part 2. Royal Botanic Gardens, Kew, pp. 723–769.
- Ayyad, S.M., Moore, P.D., Zahran, M.A., 1992. Modern pollen rain studies of the Nile Delta, Egypt. *New Phytol.* 121, 663–675.
- Behre, K.-E., 1990. Some reflections on anthropogenic indicators and prehistoric occupation phases in the Near East. In: Bottema, S., Entjes-Nieborg, G., van Zeist, W. (Eds.), *Man's Role in the Shaping of the Eastern Mediterranean Landscape*. Balkema, Rotterdam, pp. 219–230.
- Bell, B.A., Fletcher, W.J., 2016. Modern surface pollen assemblages from the Middle and High Atlas, Morocco: insights into pollen representation and transport. *Grana* 55, 286–301.

- Ben Salem, M., 1996. Le Sahel de Bizerte: Cartographie de l'occupation du sol et de sa Dynamique. 238. Faculté des Sciences Humaines et Sociales de Tunis, Tunis.
- Ben Tiba, B., Reille, M., 1982. Recherches pollénanalytiques dans les montagnes de Kroumirie (Tunisie septentrionale): Premiers résultats. *Ecol. Mediterr.* 8, 75–86.
- Bennett, K., 2008. psimpoll and pscmb. Unknown Publisher <http://chrono.qub.ac.uk>.
- Bortoli, L., Cointepas, J.P., Dimanche, P., Dumont, H., Floret, C., Gounot, M., Guyot, L., Jacquinet, J.C., Mori, A., Schoenberger, A., Soler, A., 1967. Carte Phyto-écologique de la Tunisie Septentrionale: Echelle 1:200.000. Bizerte, Tunis; Tabarka, Souk El Arabe. Notice Détaillée. Centre d'études Phytosociologiques et Ecologiques, Montpellier.
- Bottema, S., Woldring, H., 1990. Anthropogenic indicators in the pollen record of the Eastern Mediterranean. In: Bottema, S., Entjes-Nieborg, G., van Zeist, G. (Eds.), *Man's Role in the Shaping of the Eastern Mediterranean Landscape*. Balkema, Rotterdam, pp. 231–265.
- Boussaid, M., Ben Fadhel, N., Chemli, R., Ben M'hamed, M., 1999. Structure of vegetation in Northern and Central Tunisia and protective measures. In: Heywood, V.H., Skoula, M. (Eds.), *Wild Food and Non-food Plants: Information Networking. Cahiers Options Méditerranéennes No. 38*. CIHEAM, Chania, pp. 295–302.
- Broström, A., Sugita, S., Gaillard, M.J., 2004. Pollen productivity estimates for the reconstruction of past vegetation cover in the cultural landscape of southern Sweden. *The Holocene* 14, 368–381.
- Broström, A., Nielsen, A.B., Gaillard, M.J., Hjelle, K., Mazier, F., Binney, H., Bunting, J., Fyfe, R., Meltsov, V., Poska, A., Räsänen, S., Soepboer, W., Von Steding, H., Suutari, H., Sugita, S., 2008. Pollen productivity estimates of key European plant taxa for quantitative reconstruction of past vegetation: a review. *Veg. Hist. Archaeobotany* 17, 461–478.
- Brun, A., 1985. La couverture steppique en Tunisie au Quaternaire supérieur. *C. R. Acad Sci II* 14, 1085–1090.
- Bunting, M.J., Gaillard, M.J., Sugita, S., Middleton, R., Broström, A., 2004. Vegetation structure and pollen source area. *The Holocene* 14, 651–660.
- Bunting, M.J., Farrell, M., Broström, A., Hjelle, K.L., Mazier, F., Middleton, R., Nielsen, A.B., Rushton, E., Shaw, H., Twiddle, C.L., 2013. Palynological perspectives on vegetation survey: a critical step for model-based reconstruction of Quaternary land cover. *Quat. Sci. Rev.* 82, 41–55.
- Calcote, R., 1995. Pollen source area and pollen productivity: Evidence from Forest Hollows. *J. Ecol.* 83, 591–602.
- Cambron, G., Suc, J.-P., Aloisi, J.-C., Giresse, P., Monaco, A., Touzani, A., Duzer, D., Ferrier, J., 1997. Modern pollen deposition in the Rhône delta area (lagoonal and marine sediments). *France. Grana* 36, 105–113.
- Carrión, J.S., 2002. A taphonomic study of modern pollen assemblages from dung and surface sediments in arid environments of Spain. *Rev. Palaeobot. Palynol.* 120, 217–232.
- Cheddadi, R., Lamb, H.F., Guiot, J., Van de Kaars, S., 1998. Holocene climatic change in Morocco: a quantitative reconstruction from pollen data. *Clim. Dyn.* 14, 883–890.
- Chelbi, F., Paskoff, R., Troussset, P., 1995. La baie d'Utique et son évolution depuis l'Antiquité: une réévaluation géoarchéologique. *Antiq. Afr.* 31, 7–51.
- Correa-Metrio, A., Urrego, D.H., Cabrera, K., Bush, M., 2011. paleoMAS: Paleoeocological Analysis. R Package Version 2.0. The Comprehensive R Archive Network.
- Daoud, A., 1983. Spectres Polliniques de l'atmosphère et d'échantillons de Surface en Tunisie: Relations avec la Végétation. 94. Université des Sciences et Techniques du Langueod, Montpellier.
- Davis, B.A.S., Zanon, M., Collins, P., Mauri, A., Bakker, J., Barboni, D., Barthelmes, A., Beaudouin, C., Bjune, A.E., Bozilova, E., Bradshaw, R.H.W., Brayshay, B.A., Brewer, S., Brugiapaglia, E., Bunting, J., Connor, S.E., Beaulieu, J.-L., Edwards, K., Ejarque, A., Fall, P., Florenzano, A., Fyfe, R., Galop, D., Giardini, M., Giesecke, T., Grant, M.J., Guiot, J., Jahns, S., Jankovská, V., Juggins, S., Kahrmann, M., Karpińska-Kolaczek, M., Kolaczek, P., Kühl, N., Kuneš, P., Lapteva, E.G., Leroy, S.A.G., Leydet, M., Guiot, J., López Sáez, J.A., Masi, A., Matthias, I., Mazier, F., Meltsov, V., Mercuri, A.M., Miras, Y., Mitchell, F.J.G., Morris, J.L., Naughton, F., Nielsen, A.B., Novenko, E., Odgaard, B., Ortu, E., Overballe-Petersen, M.V., Pardoe, H.S., Peglar, S.M., Pidek, I.A., Sadori, L., Seppä, H., Severova, E., Shaw, H., Świąta-Musznicka, J., Theuerkauf, M., Tonkov, S., Veski, S., Knaap, W.O., Leeuwen, J.F.N., Woodbridge, J., Zimny, M., Kaplan, J.O., 2013. The European Modern Pollen Database (EMPD) project. *Veg. Hist. Archaeobotany* 22, 521–530.
- Díaz Fernández, P.M., 1994. Relations between modern pollen rain and Mediterranean vegetation in Sierra Madrona (Spain). *Rev. Palaeobot. Palynol.* 82, 113–125.
- Djamali, M., Beaulieu, J.L., Shah-hosseini, M., Andrieu-Ponel, V., Ponel, P., Amini, A., Akhiani, H., Leroy, S.A.G., Stevens, L., Lahijani, H., Brewer, S., 2008. A late Pleistocene long pollen record from Lake Urmia, NW Iran. *Quat. Res.* 69, 413–420. <http://dx.doi.org/10.1016/j.yqres.2008.03.004>.
- Djamali, M., de Beaulieu, J.L., Campagne, P., Andrieu-Ponel, V., Ponel, P., Leroy, S.A.G., Akhiani, H., 2009. Modern pollen rain-vegetation relationships along a forest-steppe transect in the Golestan National Park, NE Iran. *Rev. Palaeobot. Palynol.* 153, 272–281.
- Djamali, M., Gambin, B., Marriner, N., Andrieu-Ponel, V., Gambin, T., Gandouin, E., Lanfranco, S., Médail, F., Pavon, D., Ponel, P., Morhange, C., 2013. Vegetation dynamics during the early to mid-Holocene transition in NW Malta, human impact versus climatic forcing. *Veg. Hist. Archaeobotany* 22, 367–380. <http://dx.doi.org/10.1007/s00334-012-0380-0>.
- El Euch, F., 1995. Le Sylvopastoralisme en Tunisie. Systèmes Sylvopastoraux. Pour un Environnement, une Agriculture et une Économie Durables. Cahiers Options Méditerranéennes No. 12 CIHEAM, Zaragoza, pp. 161–164.
- El Euch, F., 2000. Rôle de l'Acacia cyanophylla dans l'alimentation du cheptel en Tunisie. In: Sulas, L. (Ed.), *Legumes for Mediterranean Forage Crops, Pastures and Alternative Uses*. Cahiers Options Méditerranéennes No. 45. CIHEAM, Zaragoza, pp. 431–434.
- El-Moslimany, A.P., 1987. The late Pleistocene climates of the Lake Zeribar region (Kurdistan, western Iran) deduced from the ecology and pollen production of nonarboreal vegetation. *Vegetatio* 72, 131–139.
- El-Moslimany, A.P., 1990. Ecological significance of common nonarboreal pollen: examples from drylands of the Middle East. *Rev. Palaeobot. Palynol.* 64, 343–350.
- Fall, P.L., 2012. Modern vegetation, pollen and climate relationships on the Mediterranean island of Cyprus. *Rev. Palaeobot. Palynol.* 185, 79–92.
- Fletcher, W., 2005. Holocene landscape history of southern Portugal. University of Cambridge (Doctoral dissertation, University of Cambridge).
- Gaillard, M.J., Birks, H.J.B., Emanuelsson, U., Karlsson, S., Lagerås, P., Olausson, D., 1994. Application of modern pollen/land-use relationships to the interpretation of pollen diagrams—reconstructions of land-use history in south Sweden, 3000–0 BP. *Rev. Palaeobot. Palynol.* 82, 47–73.
- Ghorbel, A., Ben Salem-Fnayou, A., Chatibi, A., Tway, M., 1998. Towards a comprehensive documentation and use of Pistacia genetic diversity in Central and West Asia, North Africa and Europe. In: Padulosi, S., Hadj-Hassan, A. (Eds.), *IPGRI Workshop*, pp. 62–71. Irbid, Jordan.
- Gounot, M., Guillem, J.L., Schoenberger, A., 1965. Carte Phyto-Écologique de la Tunisie Septentrionale. Feuille 1. CNRS/CEPE et Gouvernement Tunisien, Secrétariat d'Etat au Plan et à l'Economie Nationale, Cap Bon – La Goulette – Sousse.
- Hadj Hamda, S., Ben Dhiab, A., Galan, C., Msalem, M., 2017. Pollen spectrum in Northern Tunisia. *Aerobiologia* 33, 243–251.
- Hansen, M.C., Stehman, S.V., Potapov, P.V., Loveland, T.R., Townshend, J.R.G., DeFries, R.S., Pittman, K.W., Arunarwati, B., Stolle, F., Steiner, M.K., Carroll, M., DiMiceli, C., 2008. Humid tropical forest clearing from 2000 to 2005 quantified by using multitemporal and multiresolution remotely sensed data. *Proc. Natl. Acad. Sci.* 105, 9439–9444.
- Havinga, A.J., 1984. A 20-year experimental investigation into the decay of pollen and spores in various soil types. *Pollen Spores* 26, 541–558.
- Hjelle, K.L., Mehl, I.K., Sugita, S., Andersen, G.L., 2015. From pollen percentage to vegetation cover: evaluation of the Landscape Reconstruction Algorithm in western Norway. *J. Quat. Sci.* 30, 312–324.
- INRE, 1976. Carte bioclimatique de la Tunisie selon la classification d'Emberger. Etages et Variantes (Scale: 1:1,000,000). Institut National de Recherches Forestières. République Tunisienne.
- Jaouadi, S., Lebreton, V., Mannai-Tayech, B., Lakhdar, R., Soussi, M., 2015. Apport de l'analyse pollinique des sédiments de la sebkha Boujmel (Sud-Est tunisien) à la reconstitution des paléopaysages et paléoclimats holocènes en milieu aride. *Méditerranée* 125, 39–49.
- Jaouani, A., 1976. La culture de l'amandier en Tunisie. CIHEAM – Options Méditerranéennes. vol. 32, pp. 67–71.
- Juggins, S., 2009. *Package 'rioja' – Analysis of Quaternary Science Data*. The Comprehensive R Archive Network.
- Kassab, A., 1981. L'agriculture tunisienne sur la voie de l'intensification. *Ann. Geogr.* 90, 55–86.
- Khrystal Engineering, 2003. Zone Sensible Littorale de Sidi Ali El Mekki. Rapport de Synthèse 50.
- Lebreton, V., Jaouadi, S., Mulazzani, S., Boujelben, A., Belhouchet, L., Gammar, A.M., Combourieu-Nebout, N., Saliège, J.F., Karray, M.R., Fouache, E., 2015. Early oleiculture or native wild Olea in eastern Maghreb: new pollen data from the sebkhalagoon Halk el Menjel (Hergla, Central Tunisia). *Environ. Archaeol.* 20, 265–273.
- Lisitsyna, O.V., Hicks, S., Huusko, A., 2012. Do moss samples, pollen traps and modern lake sediments all collect pollen in the same way? A comparison from the forest limit area of northernmost Europe. *Veg. Hist. Archaeobotany* 21, 187–199.
- Markgraf, V., 1980. Pollen dispersal in a mountain area. *Grana* 19, 127–146.
- McLauchlan, K.K., Elmore, A.J., Oswald, W.W., Sugita, S., 2007. Detecting open vegetation in a forested landscape: pollen and remote sensing data from New England, USA. *The Holocene* 17, 1233–1243.
- Moore, P.D., Webb, J.A., Collinson, M.E., 1991. *Pollen Analysis*. 2nd ed. Blackwell Scientific Publication, Oxford.
- Moussa, M., Baccar, L., Khemis, Ben, 2005. La lagune de Ghar El Melh: Diagnostic écologique et perspectives d'aménagement hydraulique. *Rev. Sci. Eau* 18, 1–248.
- Novikoff, G., 1965. Contribution à l'étude des relations entre le sol et la végétation halophile de Tunisie. Relations entre la végétation, l'érosion hydrique et la conservation du sol. Faculté des Sciences de Montpellier, Montpellier, p. 339.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szöcs, E., Wagner, H., 2016. *vegan: Community Ecology Package*. R Package Version 2.4-0. <https://CRAN.R-project.org/package=vegan>.
- Ouakad, M., 2007. Genèse et évolution des milieux laguno-lacustres du Nord-Est de la Tunisie (Garaet el Ichkeul, Lagunes de Bizerte et Ghar el Mehl). Thèse d'état es Sciences Géologiques. Faculté des Sciences de Tunis (461 pp.).
- Oueslati, A., 2004. Littoral et aménagement en Tunisie: des enseignements de l'expérience du vingtième siècle et de l'approche géoarchéologique à l'enquête prospective. Publications de la Faculté des Sciences Humaines et Sociales, Tunis.
- Parsons, R.W., Prentice, I.C., 1981. Statistical approaches to R-values and the pollen-vegetation relationship. *Rev. Palaeobot. Palynol.* 32, 127–152.
- Paskoff, R., Troussset, P., 1992. L'ancienne baie d'Utique: du témoignage des textes à celui des images satellitaires. *Mappemonde* 1, 30–34.
- Petanidou, T., Vokou, D., 1990. Pollination and pollen energetics in Mediterranean ecosystems. *Am. J. Bot.* 77, 986–992.
- Posner, S.D., 1988. *Biological Diversity and Tropical Forests in Tunisia*. Agency for International Development, p. 206.
- Prentice, I.C., 1985. Pollen representation, source area, and basin size: toward a unified theory of pollen analysis. *Qual. Res. Rev.* 23, 76–86.
- R Core Team, 2016. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. URL Vienna, Austria <https://www.R-project.org/>.
- Reille, M., 1992a. New pollen-analytical researches in Corsica: the problem of *Quercus ilex* L. and *Erica arborea* L., the origin of *Pinus halepensis* Miller forests. *New Phytol.* 122, 359–378.

- Reille, M., 1992b. Pollen et spores d'Europe et d'Afrique du Nord. Laboratoire de Botanique Historique et Palynologie, Marseille.
- Samaali, H., 2011. Etude de l'évolution de l'occupation et de l'utilisation du sol dans le delta de Mejerda par teledetection et systemes d'informations geographiques, Faculté des Sciences Humaines et Sociales de Tunis. Université de Tunis, Tunis, p. 375.
- Stuijts, I.-L., 1991. Kinderoffers in de Tophet (Carthago); houtskoolonderzoek. *Paleo-aktueel* 2, 58–61.
- Sugita, S., 1994. Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. *J. Ecol.* 82, 881–897.
- Sugita, S., Gaillard, M.-J., Broström, A., 1999. Landscape openness and pollen records: a simulation approach. *The Holocene* 9, 409–421.
- Traverse, A., 2007. *Paleopalynology*. second ed. Springer, Netherlands.
- Vuorela, I., 1973. Relative pollen rain around cultivated fields. *Acta Bot. Fenn.* 102, 1–27.
- Warnes, G.R., Bolker, B., Bonebakker, L., Gentleman, R., Liaw, W.H.A., Lumley, T., Maechler, M., Magnusson, A., Moeller, S., Schwartz, M., Venables, B., 2016. *gplots: Various R Programming Tools for Plotting Data*. R Package Version 3.0.1. <https://CRAN.R-project.org/package=gplots>.
- Williams, J.W., Jackson, S.T., 2003. Palynological and AVHRR observations of modern vegetational gradients in eastern North America. *The Holocene* 13, 485–497.
- Woodbridge, J., Fyfe, R.M., Roberts, N., 2014. A comparison of remotely sensed and pollen-based approaches to mapping Europe's land cover. *J. Biogeogr.* 41, 2080–2092.