Characteristics of the vegetation of tree stands on sacred sites in comparison to well-preserved forests in northwestern Morocco

Caractéristiques des peuplements forestiers des sites sacrés en comparaison des forêts bien préservées au nord-ouest du Maroc

Birgit FROSCH

University of Freiburg, Department of Geobotany,
Faculty of Biology, Schänzlestraße 1, D-79104 Freiburg, Germany
E-mail: birgit.frosch@biologie.uni-freiburg.de

Abstract

Muslim burial grounds and the surroundings of Saints' tombs (marabouts) in Morocco consist of spontaneous vegetation which is often protected from land use due to religious believes. Nevertheless many sacred sites are subjected to land-use practices like grazing or cutting of wood which alter the vegetation. In the present study, the vegetation of tree stands on 68 sacred sites (cemeteries and marabouts) in northwestern Morocco was analysed and compared to the vegetation of least disturbed stands of the corresponding forest communities. Those are thermomediterranean evergreen forest communities dominated by the tree species Quercus coccifera *L.,* Quercus suber *L. and* Olea europaea *L. The aim of the study was to determine the main factors affecting floristic differentiation of the sacred sites' stands and to assess their degree of 'naturalness'.*

The main gradient explaining floristic variance was associated with the proportion of annual species per plot and with the litter layer cover. Both were assumed to be proxies for the degree of land-use pressure, especially grazing. In heavily grazed tree stands, annual species replace woody and perennial plant species of the shrub and herbaceous layer ('therophytization'), while in little used, non-grazed forest stands annual species are rare or lack completely. Different stand structure types, like isolated trees, do not have a strong influence on the floristic composition. Quercus coccifera *stands from the examined sacred sites were mostly similar in their floristic composition to reference* Q. coccifera *stands, while* Olea europaea *stands showed no strong floristic similarity to reference stands.* Quercus suber *stands were partly similar, partly unsimilar to reference stands.*

Résumé

Dans les cimetières musulmans et dans les environs des tombes de Saints (marabouts) au Maroc existe une végétation spontanée que la croyance religieuse met souvent à l'abri de l'exploitation. Néanmoins la plupart des sites sacrés sont soumis à des exploitations comme le pâturage ou la coupe du bois, résultant en un changement de la végétation. Cette étude concerne l'analyse de la végétation des peuplements forestiers de 68 sites sacrés (cimetières et marabouts) du nord-ouest du Maroc et sa comparaison avec la végétation des peuplements les moins perturbés des groupements forestiers correspondants. Il s'agit des groupements forestiers thermo-méditerranéens sempervirents à Quercus coccifera *L.,* Quercus suber *L. et* Olea europaea *L. L'objectif de cette étude était de déterminer les facteurs principaux qui influencent la différenciation floristique des peuplements forestiers sur les sites sacrés et de déterminer leur degré de « naturalité ».*

Le principal gradient expliquant les différences floristiques était associé avec la proportion des espèces annuelles et l'importance de la litière.

Keywords: sacred grove, forest therophytization, grazing, Mediterranean evergreen forest, sclerophyllous species.

Mots clés : bois sacré, thérophytisation de la forêt, pâturage, forêt méditerranéenne sempervirente, espèces sclérophylles.

Les deux variables ont été considérées comme des proxies permettant d'évaluer le degré d'impact anthropique, particulièrement du pâturage. Dans les peuplements forestiers soumis au pâturage intensif, les espèces annuelles remplacent les espèces ligneuses et pluriannuelles de la strate arbustive et herbacée (« thérophytisation »), alors que dans les peuplements peu exploités, les espèces annuelles sont rares ou absentes. Les différents types structuraux, tels que les arbres isolés, n'ont pas d'influence forte sur la composition floristique. Pour Quercus coccifera*, les peuplements des sites sacrés étudiés ici sont assez proches des peuplements de référence en ce qui concerne la composition floristique. Les peuplements d'*Olea europaea*, au contraire, n'ont pas beaucoup d'affinités floristiques avec les peuplements de référence. Concernant les peuplements de* Quercus suber*, ils possèdent en partie une affinité floristique avec les peuplements de référence, mais s'en distinguent aussi profondément.*

Introduction

In recent years, international organisations have become increasingly interested in the cultural and biological heritage of sacred sites and in their potential for nature conservation (*e.g.* Dudley *et al.* 2006, Schaaf & Lee 2006). Sacred sites are natural elements like forests, single trees, caves, springs, lakes, mountains and/or embedded anthropogenic constructions like shrines or tombs. They are worshipped and protected by local communities for different religious, traditional or political reasons. This phenomenon is known from all continents (Bhagwat & Rutte 2006).

From North Africa to the Middle East, the existence of holy trees or 'sacred groves' (a term used for wooded sacred sites, but the usage is not consistent and the term is being used also for sacred sites in general) is in most cases linked to the worshipping of the tombs of Muslim Saints, although it is not always clear which existed first: the sacred vegetation or the tomb (Dafni 2006). In Morocco, sacred sites are a very common landscape feature. According to map analysis and ground checks the average density is 26 sacred sites/100 km^2 in the rural study area in northern Morocco investigated here (Deil *et al.* 2009). Usually the whole sacred site area is used as common burial ground, but sometimes sacred sites only consist of a building, the Saint's tomb in general. In the current study, the term 'sacred site' encompasses spatially extended sites with either a Saint's tomb or a common burial ground, or both. Preliminary results from 27 sacred sites in the study area suggest a small average size with considerable variation in size (85 m^2 to 5 ha with an average of 0.7 ha, Deil *et al.* 2009). Similar results were obtained in a survey conducted in southwestern Morocco (15 sacred sites between 360 m^2 and 6.9 ha, Petersen 2007).

During the last years, the investigation of sacred sites of Morocco and their vegetation gained momentum (Deil 2003; Deil *et al.* 2005, 2008, 2009; Taïqui *et al.* 2005, 2009; Demdam *et al.* 2008; Jäckle & Frosch 2008). First findings indicate that the floristic composition of the forested vegetation of northern Moroccan sacred sites reflects abiotic factors (Deil *et al.* 2009). However, due to human activities, the vegetation of sacred sites presents itself more often as a mosaic of different plant communities than as a dense impenetrable sclerophyllous forest (Deil *et al.* 2008). Only about 65% of the sacred sites consist in a little forest or tree stand larger than 500 m^2, while ca. 20% feature an isolated tree and are elsewhere covered by herbaceous and shrub species. Generally, sacred sites are not free from human influences. Human impact on sacred sites, leading to changes in vegetation and stand structure, is mentioned in all studies on sacred sites cited in this publication. Restrictions and rules associated with the religious status of sacred sites can be lifted or violated, which can ultimately result in sacred area loss (Byers *et al.* 2001, Campbell 2004).

While sacred sites in subtropical and tropical regions of the world are frequently described as sanctuaries for endemic or endangered plants or hotspots of floristic diversity (*e.g.* Jamir & Pandey 2003; Mgumia & Oba 2003; Ramanujam & Cyril 2003; Khumbongmayum *et al.* 2005; Sukumaran *et al.* 2008), the role of sacred sites for the study of climax-near forests or, more generally, rare and endangered vegetation types in otherwise altered landscapes is less often evaluated (*e.g.* Itow 1991; Tiwari *et al.* 1998; Byers *et al.* 2001; Aerts *et al.* 2006; Miehe *et al.* 2008).

References to the vegetation of sacred sites in Morocco are frequent in the literature and often emphasize that sacred sites shelter remnants or examples of natural forests (Emberger 1939; Sauvage 1961; Benabid 1984; Ajbilou *et al.* 2006). This stems from the fact that certain forest types are only described from sacred sites, because the surrounding landscape has been completely deforested due to land-use pressure (Emberger 1939; Benabid 1984). Additionally, striking differences in floristic composition and stand structure between non-sacred forests and well-preserved forest stands on sacred sites were reported (Sauvage 1961; Ajbilou *et al.* 2006; see also Hammi *et al.* 2007 for similar findings in community-preserved forests of Southern Morocco). However, no study has been carried out so far that investigated the 'naturalness' of the floristic composition of the sacred sites' tree stands in detail and only few studies have compared floristic data from sacred sites with reference data from non-sacred areas (Boraiah *et al.* 2003; Campbell 2004; Salick *et al.* 2007). In the current study, own data from randomly-stratified chosen sacred sites and reference floristic data have been analysed to fill this void. The term 'stand' is not used in the forestry sense (a group of trees of rather uniform age structure and species composition), but in a very broad sense to integrate all sorts of common tree-related structures found on sacred sites. The reference data was taken from a phytosociological work explicitly describing well-preserved stands of the respective forest types (Benabid 1984). Partly, the reference data was sampled on sacred sites due to the above mentioned fact that certain forest types only exist on sacred sites.

The objectives of this study were (1) to determine the main factors driving the floristic differentiation in northwestern Moroccan sacred sites' tree stands – are they abiotic factors or land use? – and (2) to assess the degree of floristic dissimilarity between sacred sites' stands and the least disturbed stands using reference data, and diagnose the causes of dissimilarity. Considering the detected differences in life form spectra and stand structure, two possible explanations for the dissimilarity between own and reference data were formulated and examined: a) dissimilarity is caused by different proportions of therophytes in own data and reference data, and b) dissimilarity is related to differing stand structure types.

Material and Methods

Study area

The study area is situated on the Tangier Peninsula in northwestern Morocco. It comprises a trapezoidal area of ca. 7300 km^2 delineated by the Atlantic coast north and south of the city of Larache and the Outer Ranges of the Rif Mountains (Prerif area). Within the study area, eight landscape sections of 36 km^2 each were investigated. The seasonal pattern of precipitation is characteristic of Mediterranean climate with a winter rainfall peak and a summer drought of several months. The eight landscape sections, where phytosociological fieldwork was carried out, are located in altitudes between 40 m a.s.l. near the Atlantic coast to about 900 m a.s.l. in the Prerif Mountains. This altitudinal gradient is associated with increasing precipitation. A mean annual precipitation of 600-1000 mm prevails, with only the highest peaks exceeding 1000 mm. All landscape sections and accordingly all sampled sacred sites are situated in the thermomediterranean belt (mean of the minimum temperature of the coldest month [m] > 3 ºC). Accordingly the bioclimate can be classified as subhumid to humid, applying the climate diagram for Morocco based on Emberger's pluviothermic quotient Q (in Sauvage 1963).

Bedrock along the western littoral parts of the study area is predominantly composed of Pliocene and Quaternary sands. On the ridges in the East, flyschs and Oligocene sandstones prevail, and the hilly area in between is dominated by marls. The potential natural vegetation is formed by forest, mainly composed of sclerophyllous Mediterranean oak species (*Quercus suber*, *Q. coccifera*, *Q. rotundifolia*) and wild olive, *Olea europaea* var. *sylvestris* (Emberger 1939; Benabid 1984). However, the actual vegetation is very different from the potential natural vegetation due to land-use pressure. In the lowlands, most of the forests have been cleared for agriculture. In mid altitudes, forests, predominantly with *Quercus suber*, are still quite common but submitted to pasturing and timber exploitation.

Sampling

The sampling on the sacred sites took place in a set of eight landscape sections of 36 km^2

each. All sacred sites in these landscape sections were investigated in the field. To obtain representative data for the different ecoregions from a small number of landscape sections, a pre-stratified random sampling procedure was applied. A landscape section is preset to have homogeneous geological and climatic conditions, and to contain at least five sacred sites. Landscape sections A1 and A2 are situated on littoral sands (subhumid climate), B1 and B2 on marls (subhumid climate), C1 and C2 on prerifian sandstone chains (humid climate). D1 and E are standalone landscape sections. Bedrock of landscape section D1 (humid climate) is the so-called "Beni Ider Flysch". Landscape section E (humid climate) was chosen as a particular example for a transition zone between sandstone and schist bedrock. To avoid spatial autocorrelation, a minimal distance of 20 km between the corresponding sections of a stratum was a further precondition.

On each sacred site, one to seven phytosociological plots were sampled applying the method of Braun-Blanquet (1964) including the original cover-abundance scale. According to stand structure type the plot area varied from 4 m^2 under isolated trees to 100 m^2 in larger stands. For the floristic assessment all plant species in the plot area were noted with their cover-abundance. A stratification of the vegetation was applied resulting in several different layers.

Fieldwork was conducted between end of March and middle of June in 2008 and 2009. 140 plots of 68 sacred sites were included in the present analysis. They fit the following applied definition of 'forest': a stand with $\geq$ 10% tree layer cover (woody plants > 2 m high), with at least one of the tree species *Quercus suber*, *Q. coccifera*, *Q. rotundifolia*, *Q. canariensis*, *Olea europaea* s.l. (var. *sylvestris* and var. *europaea*), *Phillyrea latifolia* and *Fraxinus angustifolia* in the tree layer.

The following parameters were recorded in each plot: altitude, aspect and slope, height of the highest tree, estimated total cover of tree layer (woody plants > 2 m high), shrub layer (woody plants $\leq$ 2 m high), herbaceous and epiphytic layer (all in %), surface of litter layer, bare soil and stones/surface outcrop of rock (all in %), and stand structure type. Stand structure types were defined as follows: isolated tree ("IT") for 1-2 trees surrounded by non-forested vegetation types, tree group ("TG") for stands of up to 5-6 trees, forest edge ("FE") for plots under cover of a larger stand, but with non-forested vegetation types to one side, opened stand ("OS") for larger stands, crowns of overstory trees often without contact, large gaps, and closed stand ("CS") for larger stands, crowns in contact or overlapping, tree layer cover not necessarily high, as lightness of crowns was taken into account. On most sacred sites a topsoil sample was taken, if permitted to us by local authorities, and pH (H_2O) and lime content were determined. Grazing intensity as the main land-use factor could not be directly evaluated, as any information about stock density and the amount of time the animals spend grazing on the sacred sites was not available.

Data analysis

In order to identify the patterns of floristic differentiation and the impact of independent variables on the floristic composition, the plots were subjected to indirect as well as direct gradient analysis. Floristic variance was first assessed using Detrended Correspondence Analysis (DCA). The length of DCA axis 1 was long (4.5 SD for own data, 5 SD for own and reference data), indicating that analyses based on a unimodal model were most suitable for describing the data (ter Braak & Šmilauer 2002). Accordingly the chosen methods were Correspondence Analysis (CA) and Canonical Correspondence Analysis (CCA). The vegetation layers were merged to one layer for the present statistical analyses. This was done to obtain comparability with the external reference data. Species dominance/abundance values were recoded from r (solitary, < 1% cover), + (few, < 1% cover), 1 (numerous, but < 5% cover), 2 (5-25% cover), 3 (25-50% cover), 4 (50-75% cover) and 5 (75-100% cover) to a 1-7 numerical scale for multivariate analysis. Plant species with a frequency of < 5 were excluded from analysis. CA and CCA were performed with the following presetting: Hill's scaling with focus on inter-sample distances, no transformation of species data, and downweighting of rare species. In the CCA, the statistical validity of the association between environmental variables and variance in floristic data was tested using a Monte Carlo permutation test (1000 unrestricted random permutations).

The own data of 140 plots were ordinated in unconstrained and constrained analysis (CA-1, CCA-1). In CCA-1 the influence of the main environmental variables on the floristic composition of the sacred sites' woody vegetation was analysed quantitatively. The floristic data were classified to rankless groups: *Quercus suber* stands ("QS" in the analysis), *Quercus coccifera* stands ("QC"), *Olea europaea* var. *sylvestris* stands ("OE"), and a small number of plots representing other stands, dominated by *Fraxinus angustifolia* or *Quercus canariensis* ("other" in the analysis). Altitude, cover of tree layer, shrub layer, herb layer, litter layer, bare soil (all in %) and pH of topsoil were included as field-measured variables in the statistical analyses. Missing pH data were replaced by the mean pH of all other sacred sites. Climatic parameters were derived from the Wordclim database (Hijmans *et al.* 2005) and tested for explanation of the floristic variance. Most parameters were highly correlated and were therefore excluded. Only mean annual precipitation and mean minimum temperature of the coldest month were used. Additionally a spatial nominal parameter representing the respective landscape section was included ("A1", "C1", "D1", etc.).

Furthermore, proportions of life forms based on Raunkiaer's system were calculated on species presence for each plot in own and reference data. Three main groups were defined: proportion of therophytes ("PTh") including annual and biennial species, proportion of perennials ("PP"), including hemicryptophytes and geophytes, and proportion of woody species ("PW") including phanerophytes, nanophanerophytes and chamaephytes.

In the ordination diagram of the CA, only environmental variables with a correlation of > 0.3 (weighted correlation) with at least one of the first two axes were projected. Several parameters were excluded from the CCA due to correlation with other parameters, high multicollinearity, detected by high variation inflation factors, or due to poor correlation with the first four CA axes. Parameters directly derived from vegetation data were not included in the CCA. The inflation factor of the included variables was always < 20 in the CA and < 3 in the CCA.

In a second Correspondence Analysis (CA-2) the floristic affinity of the sampled tree stands on sacred sites with reference plots of the least disturbed stands of the respective forest types was evaluated (140 own plots and 100 reference plots). The reference floristic data consists of forest plots from northwestern Morocco recorded by Benabid (1984; data taken from tables 2, 3, and 6 therein). The reference data are present in the form of phytosociological plots after the method of Braun-Blanquet with plot areas of either 100 or 200 m^2. Plots are not stratified into different layers. They include the 29 plots of the thermomediterranean *Quercus suber* forests, referred to as "QS-REF" in the analysis (published as Myrto communis-Quercetum suberis), the 40 plots of the *Quercus coccifera* forests (Rusco hypophylli-Quercetum cocciferae; "QC-REF"), and the 31 plots of the *Olea europaea* forests (Tamo communis-Oleetum sylvestris, "OE-REF"). The purpose of this work was to document the floristic composition of natural or near-natural forest communities. Therefore the reference plots are considered to represent examples for the least disturbed expression of the forest types found on sacred sites in the present study. Reference plots of two of the forest communities (QC-REF, OE-REF) were almost exclusively recorded on sacred sites.

In order to analyse the influence of annual species the joint floristic dataset of 240 plots was subjected to a CA (CA-3) after exclusion of all annual/biannual species. For CA-2 and CA-3 a Mantel test was performed with 1000 permutations in order to estimate the difference in the ordinations with and without annuals.

The influence of different plot area in own and reference data was tested by evaluating Spearman's rank correlation coefficient for plot area and species number. The correlation result indicates that plot area did not bias species numbers (Spearman's rho -0.08, $p >$ 0.05). Nevertheless, other possible effects on own and reference plant data associated *e.g.* with different seasonal time and climatic conditions of fieldwork can not be completely ruled out (see discussion).

The ordinations were performed using CANOCO 4.5 (ter Braak & Šmilauer 2002). Further statistical analysis was performed using the R software package (version 2.10, R Development Core Team 2009) and additional package vegan (version 1.15-4, Oksanen *et al.* 2009).

Results

The floristic variation in the sacred sites' woody vegetation is high with total inertia of 4.98 in CA-1. The first and second ordination axes explain 10.4% and 7.2% of the floristic variation, while the third and fourth axes each explain 4%. A diagram of the first two axes with sample scores and selected environmental variables is presented in Figure 1. The three main forest types are clearly separated in the ordination plot, but the general distribution of the samples suggests a continuous variation of species composition in the data set. PTh is strongly positively correlated with Axis 1, while cover of litter layer (CovL) is strongly negatively correlated with Axis 1. Sample scores of *Quercus coccifera* (QC) stands are projected on the negative side of Axis 1, while those of *Olea europaea* (OE) stands are projected on its positive side. QC stands are poor in annual species and have a higher cover of litter layer in comparison to OE stands (in QC stands: mean PTh = 23.3%, mean cover of litter layer = 65.8%; in OE stands: mean PTh = 52.9%, mean cover of litter layer = 19.8%, see Table 1). Samples of QS stands are distributed along the length of Axis 1, indicating a considerable variability in floristic composition and life form spectra, from therophyte-poor to therophyte-rich stands. The projected arrow of PW is opposed to that of PTh. PW is highest in QC stands (Table 1) and negatively correlated with cover of herbaceous layer, whereas PTh is positively correlated with this layer (correlations given in Table 2). The second ordination axis of CA-1 is negatively correlated with pH. Correspondingly, samples of stands with *Quercus suber,* a tree species restricted to acidic soils, are distributed along the positive part of Axis 2. A gradient representing altitude and altitude-related climatic variables is detectable between QS stands positioned along the negative values of Axis 1, and OE stands. OE stands are mostly restricted to the lowlands

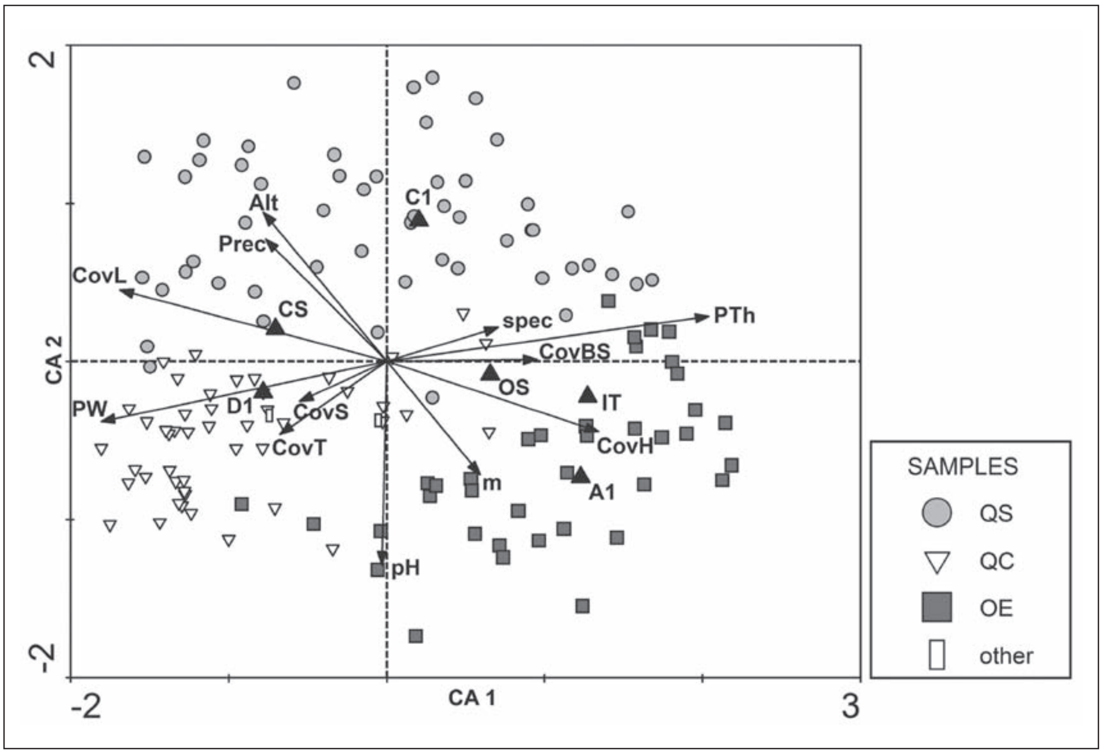

Figure 1 – Plot of a CA (CA-1) of 140 forest and tree stand vegetation plots from 68 sacred sites (Axes 1 and 2) with an overlay of explanatory variables. Number of included species 149 (species with < 5 occurrences excluded). Eigenvalues of Axis 1: 0.52, Axis 2: 0.36, total inertia: 4.98. Only variables with a correlation of > 0.3 (weighted correlation) with at least one of the first two axes are displayed.
Alt – altitude, CovBS – cover bare soil, CovH – cover herbaceous layer, CovL – cover litter layer, CovS – cover shrub layer, CovT – cover tree layer, CS – closed stand, IT – isolated tree, m – mean minimum temperature of coldest month, OS – open stand, pH – pH value, spec – number of species, Prec – mean annual precipitation, PTh – percentage proportion of annual species, PW – percentage proportion of woody species, A1, C1, D1 – landscape sections, QS –* Quercus suber *stands, QC –* Quercus coccifera *stands, OE –* Olea europaea *stands, other – other stands.

Table 1 – Arithmetic mean (± SD) and range of different proportions of life forms and cover of litter layer in the forest and tree stand plots of own and reference data (Benabid 1984) and of the total number of plots in own and reference data. CovL – cover of litter layer, n.d. – no data available, PW – proportion of woody species, PP – proportion of perennial species, PTh – proportion of therophytes, QS –* Quercus suber *stands, QC –* Quercus coccifera *stands, OE –* Olea europaea *stands, QS-REF, QC-REF, OE-REF – respective reference stands, own total – total number of plots in own data, ref total – total number of plots in reference data.

		PW [%]			**PP [%]**			**PTh [%]**			**CovL [%]**		
Type	**n**	**mean**	**min**	**max**	**mean**	**min**	**max**	**mean**	**min**	**max**	**mean**	**min**	**max**
QS	53	32.1 ± 20.5	3.7	81.3	29.7 ± 13.4	0.0	57.7	38.1 ± 24.1	0.0	88.9	60.7 ± 30.9	1.0	98.0
QC	52	46.1 ± 22.6	8.0	100.0	30.2 ± 16.9	0.0	63.0	23.3 ± 23.2	0.0	80.0	65.8 ± 27.7	0.0	100.0
OE	33	23.3 ± 14.5	3.6	60.0	23.2 ± 13.2	0.0	50.0	52.9 ± 24.9	0.0	91.7	19.8 ± 20.0	0.0	60.0
QS-REF	29	72.0 ± 10.6	50.0	95.0	19.8 ± 10.4	4.4	40.9	8.2 ± 6.1	0.0	25.0	n.d.	n.d.	n.d.
QC-REF	40	69.8 ± 11.3	50.0	100.0	25.6 ± 10.8	0.0	50.0	4.6 ± 4.7	0.0	18.8	n.d.	n.d.	n.d.
OE-REF	31	53.0 ± 8.7	33.3	71.4	36.5 ± 8.0	13.3	52.9	10.5 ± 7.4	0.0	29.4	n.d.	n.d.	n.d.
Own total	138*	35.3 ± 21.9	3.6	100.0	28.4 ± 15.0	0.0	63.0	36.1 ± 26.4	0.0	91.7	52.9 ± 35.2	0.0	100.0
Ref total	100	65.2 ± 13.2	33.3	100.0	27.3 ± 11.9	0.0	52.9	7.5 ± 6.5	0.0	29.4	n.d.	n.d.	n.d.

* The two plots of forest type "other stand" are not included.

Table 2 – Spearman's rho rank correlations for variables directly related to vegetation. Numbers highlighted in grey for correlations ≥ 0.5. Bold numbers: correlation not significant (*p*-value > 0.05). Abbreviations given in Figure 1.

	CovT	**CovS**	**CovH**	**CovL**	**CovBS**	**spec**	**PW**	**PTh**
Cover of tree layer (CovT)	1.00							
Cover of shrub layer (CovS)	**– 0.13**	1.00						
Cover of herb layer (CovH)	– 0.31	– 0.34	1.00					
Cover of litter layer (CovL)	0.33	0.24	– 0.74	1.00				
Cover of bare soil (CovBS)	– 0.20	– 0.17	0.33	– 0.58	1.00			
Number of species (spec)	– 0.31	**– 0.03**	0.38	– 0.27	**– 0.01**	1.00		
Proportion of woody species (PW)	0.31	0.49	– 0.58	0.54	– 0.34	– 0.50	1.00	
Proportion of therophytes (PTh)	– 0.37	– 0.35	0.56	– 0.58	0.38	0.47	– 0.87	1.00

and are therefore linked to higher m (mean minimum temperature of coldest month) values and lower precipitation, while a part of the QS stands is associated with higher altitude and higher precipitation. Three landscape sections (A1, C1 and D1) correlate more than 0.3 with the first two CA axes. Sacred sites in D1 (predominant bedrock: flysch) are dominated by QC stands. Sacred sites in A1 (littoral sands) are associated with OE stands, while at sacred sites in landscape section C1 (sandstone) QS stands prevail.

Results of CCA-1 are presented in Table 3. The sum of all unconstrained eigenvalues is 4.98 comparable to CA-1; the sum of constrained eigenvalues of the nine chosen variables is 1.38 (28% of total variance explained). All canonical axes were significant according to the Monte Carlo test (F-ratio = 3.183, p-value < 0.001). The CCA identified cover of litter layer as the most important variable with 23.9% of constrained variance explained (0.33 of 1.38). Second most important environmental variable is pH. Climatic altitude-related parameters represented by mean annual precipitation as well as spatial effects represented by landscape sections A1, C1 and D1 also play an important role, while stand structure type (OS, IT, TG, FE) is less influential. Topographic factors like aspect or slope show no significant influence. The distribution of samples and environmental variables along the first two axes of the CCA ordination plot strongly resembled the one of CA-1 (Figure 1) and is therefore not displayed.

The first and second axis of CA-2 explains 10% and 7.4%, respectively, of the total inertia of 4.88. An identical dominant gradient as in CA-1 is revealed in CA-2. Again, Axis 1 is highly positively correlated with PTh (Figure 2). Samples of own plots (QS, QC, OE, other) are broadly scattered along Axis 1, similar to the ordination diagram of CA-1. Scores of the reference stands (QS-REF, QC-REF, OE-REF) are concentrated on the negative end of Axis 1. In the plane of Axis 1 and Axis 2 the distances between most samples of

Table 3 – Summary of a CCA (CCA-1) of 140 forest and tree stand vegetation plots from 68 sacred sites with selected environmental variables. Correlations between environmental variables and CCA Axis 1 and 2 are given. Lambda A is a measure of the additional variability explained by inclusion of each variable during forward selection. Statistical significance of Lambda A *was tested using Monte Carlo Permutation tests with 1000 unrestricted permutations.*

Variable		**Interset correlation with**				
		Axis 1	**Axis 2**	**Lambda *A***	***P***	***F***
Cover litter layer		– 0.790	0.082	0.33	< 0.001	9.90
pH		0.014	-0.601	0.17	< 0.001	5.13
Mean precipitation		– 0.417	0.319	0.12	< 0.001	4.03
Cover shrub layer		– 0.197	– 0.161	0.11	< 0.001	3.47
Cover tree layer		– 0.276	– 0.266	0.06	< 0.001	2.09
Landscape section	landscape section D1	– 0.504	– 0.270	0.14	< 0.001	4.22
	landscape section C1	0.042	0.563	0.09	< 0.001	3.14
	landscape section A1	0.501	– 0.298	0.07	< 0.001	2.14
Stand structure type	opened stand (OS)	0.324	– 0.001	0.05	< 0.001	1.72
	forest edge (FE)	0.099	– 0.151	0.05	< 0.001	1.83
	isolated tree (IT)	0.414	– 0.017	0.05	0.011	1.51
	tree group (TG)	0.165	– 0.037	0.04	0.008	1.50
Aspect	northness	– 0.151	0.007	0.04	0.013	1.43
	eastness	– 0.127	0.081	0.04	n.s.	1.09
Inclination		– 0.224	0.056	0.02	n.s.	1.02
Total variance explained (sum of constrained eigenvalues)				**1.38**		

n.s. = not significant (*p*-value > 0.05).

own QC stands and QC-REF stands are short, indicating high floristic affinity. The same can be observed for QS-REF stands and a part of own QS stands, while the other part of QS stands and QS-REF stands are clearly separated from each other on Axis 1. Also, all samples of OE stands and OE-REF stands are separated on Axis 1.

The ordination along Axis 1 of CA-2 reflects the consistently low PTh in reference data (mean = 7.5%, range = 0-29%) in comparison to own data (mean = 36%, range = 0-92%; Table 1). A preliminary analysis revealed that PTh explained 4.8% of the floristic variance (result of a CCA of the 240 plots without annual species; p-value < 0.05), which was about half of the variance explained by the first species axis (10%). The hypothesis that the observed strong floristic differentiation between reference data and own data was based on considerably different PTh could be, however, only partially confirmed. A Mantel test on the distance matrices (Euclidian distance) of the CA of all plots of own and reference data with (CA-2) and without (CA-3) annual species nevertheless revealed a high correlation on the first four CA axes (Mantel statistic r: 0.897, $p < 0.001$).

PW and PTh were significantly different in a Mann-Whitney U-test ($p < 0.001$) between own and reference plots, and between the respective forest types of own and reference plots (*e.g.* QS *versus* QS-REF). Only PP was not significantly different ($p > 0.05$) in all plots of own and reference data as well as in QC stands of own and reference data. The differing life form spectra in own and reference data are illustrated in Figure 3. In reference data lower PW is mostly associated with higher PP, while annuals (PTh) play only a marginal role. In own plots decreasing PW is linked to decreasing PP and increasing PTh.

CCA-1 demonstrated that the influence of certain stand structure types (OS, IT, FE, TG) on the floristic composition of tree stands on sacred sites was marginal (Table 2). A more direct impression of the association of stand structure type with floristic composition was obtained by projecting the according stand structure types on the sample scores of the ordination plot of CA-2 (Figure 4). All samples of the reference data were presumed to belong to stand structure type closed stand (CS). Scores of the CS type are agglomerated on the negative side of Axis 1, where reference data and a part of the own data stands are plotted (see Figure 2). A number of *Quercus suber* stands located on the positive side of Axis 1 also belong to the CS stand structure type. Some stands of own data, which are plotted close to reference data scores on the negative side of Axis 1, belong to the tree group (TG) and forest edge (FE) type. Stands which are distributed along the positive val-

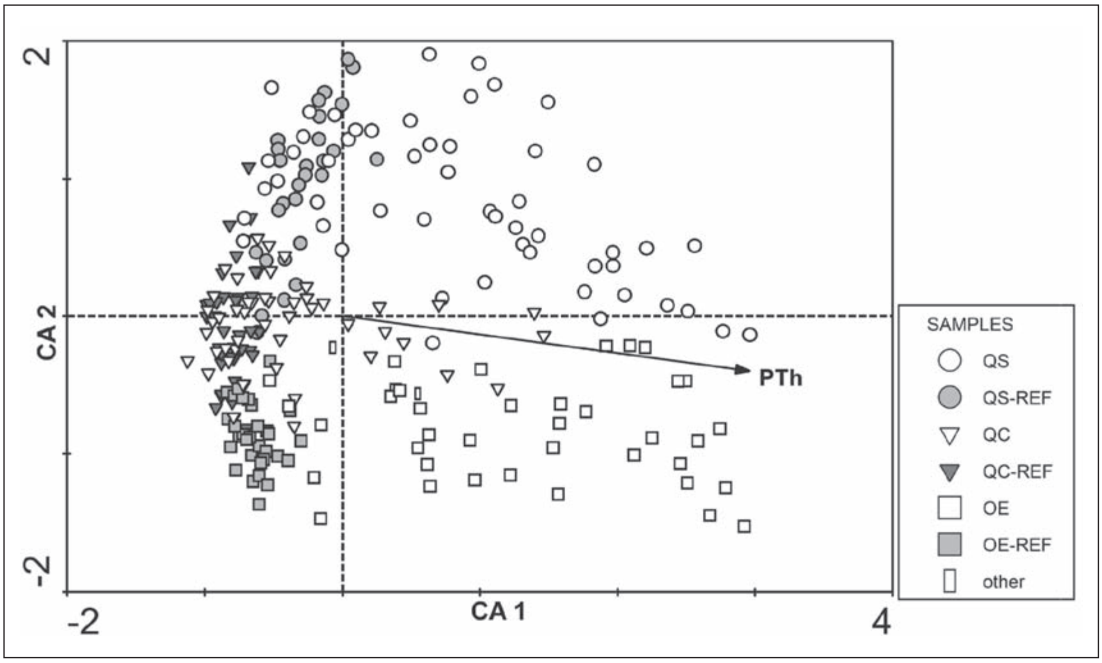

Figure 2 – Plot of a CA (CA-2) of 240 forest and tree stand vegetation plots (Axis 1 and 2) with one overlayed explanatory variable (PTh – proportion of therophytes); 140 plots from own data from sacred sites and 100 from reference literature partly from sacred sites (Benabid 1984, tables 2, 3, 6 therein). Number of included species 189 (species with < 5 occurrences excluded). Eigenvalues of Axis 1: 0.49, Axis 2: 0.36, total inertia: 4.88. Displayed are forest types: ***QS*** **–** Quercus suber ***stands, QC*** **–** Quercus coccifera ***stands, OE*** **–** Olea europaea ***stands, other – other stands, QS-REF, QC-REF, OE-REF – stands from reference literature.***

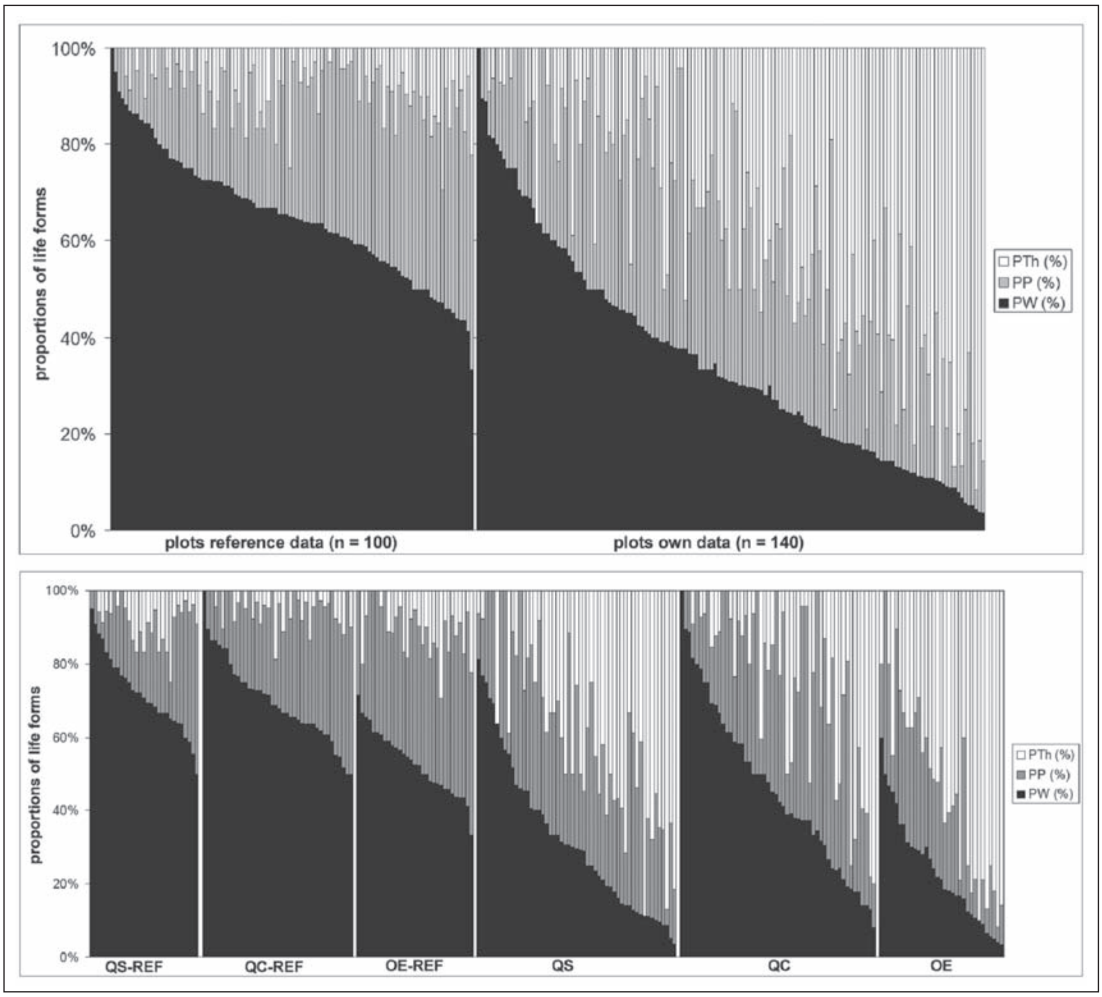

Figure 3 – Proportions of species of different life forms in reference and own vegetation plots. Above: in all plots, below: in all plots distinguished after forest types: PW – proportion of woody species, PP – proportion of perennials, PTh – proportion of therophytes, QS – **Quercus suber** ***stands, QC –*** **Quercus coccifera** ***stands, OE –*** **Olea europaea** ***stands, QS-REF, QC-REF, OE-REF – respective reference stands.***

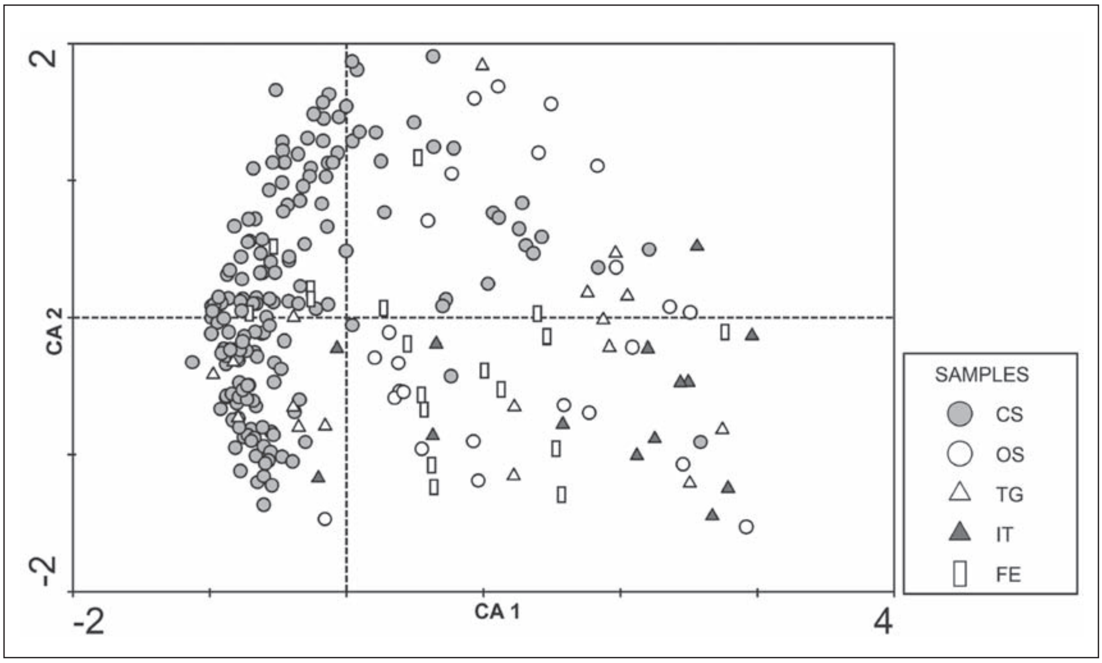

Figure 4 – Plot of a CA (CA-2) of 240 forest and tree stand vegetation plots (see Figure 2). Displayed are stand structure types: CS – closed stand, OS – opened stand, TG – tree group, IT – isolated tree, FE – forest edge.

ues on Axis 1 can belong to any of the defined stand structure types. TG, IT, FE or OS do not show a clearly agglomerated pattern as CS. FE is predominantly found in the central part of the ordination plot in OE stands (negative values on Axis 2), while IT is loosely linked to samples scores of OE stands more to the right side of the plot (most positive values on Axis 1, negative values on Axis 2).

Discussion

Findings indicate that the vegetation of less disturbed stands on sacred sites dominated by *Quercus suber* is comparable to that of the best-conserved non-sacred *Quercus suber* forests in the region. They also indicate that at least in the study area lowland *Olea europaea* stands are mostly highly disturbed and floristically distinct from the best conserved stands on sacred sites with *Olea europaea*. *Quercus coccifera* stands on the contrary are for the most part well preserved and floristically near to reference data from other sacred sites. The relative proximity of the reference data sample scores in ordination space in comparison to the highly scattered ordination of own sample scores indicates a higher floristic affinity between reference stands than between own stands.

Indirect and direct ordination of own data illustrates that floristic composition is best explained along a gradient associated with the proportion of annual species (PTh) on the one hand and the proportion of the litter layer cover on the other hand. An increase of annual species and a decrease of perennial species is part of several global models of grazing effects on vegetation (Díaz *et al.* 2007) and a main characteristic of grazed Mediterranean grasslands (Fernández Alés *et al.* 1993). Analyses of the differences in life form spectra between grazed and un-grazed woodlands of Mediterranean Europe and of Mediterranean regions worldwide indicate similar patterns. In several studies significant differences in annual species proportion between grazed and un-grazed or abandoned woodlands were detected. In grazed woodlands the proportion of annuals was higher (Pettit *et al.* 1995; Debussche *et al.* 2001; Dimopoulos & Bergmeier 2004; Tárrega *et al.* 2009). Nonetheless in some systems no significant differences in annual species proportion between grazed and abandoned sites were detected (Peco *et al.* 2005). Continuous grazing or overgrazing can also lead to a decrease of annuals (Gauquelin *et al.* 1999). Considering own observations as well as the evidence from literature, a high PTh is estimated to be a useful indicator for high grazing intensity in the present study. PTh in turn is inversely correlated with the litter layer cover. A reduction of the litter layer due to grazing was observed in grazed forests in the Mediterranean (Gutman *et al.* 2000; Dimopoulos & Bergmeier 2004). The litter layer can be reduced to zero under heavy grazing by cattle (Gutman *et al.* 2000). Correspondingly, a high cover value of the litter layer is judged to act as an indicator for low grazing intensity in the present study.

In the examined tree stands of the present study, a reduction of the litter layer was highly correlated with an increasing proportion of annual species and with an increasing coverage of the herbaceous layer, but there was only a weak correlation with tree layer cover (Table 2). In other words, litter layer and perennial and woody species can be gradually replaced by annual species and bare soil under a more or less intact tree cover. This process is called 'forest therophytization', and is interpreted as a form of hyperdegradation due to heavy grazing in Mediterranean forests (Barbéro *et al.* 1990; Quézel & Médail 2003). Forest therophytization has to be regarded as a commonly occurring process in the investigated stands on sacred sites. Trees are protected from being felled, but the undergrowth is intensely used, mainly as forage. However, different proportions of annual species in own and reference data could not explain floristic differentiation on their own. This result could be interpreted in the context of forest therophytization. The shift in life form spectra towards annual species might be linked to a disappearance of characteristic woody and perennial species. However, a strictly linear connection should not be expected, because species number increases with increasing PTh (see Table 2). Forest therophytization was most common in *Olea europaea* stands, frequently appeared in *Quercus suber* stands, and was almost never encountered in *Quercus coccifera* stands.

Land use, above all grazing, thus constitutes the main factor explaining floristic variation in the tree stands of the examined sacred sites and between own and reference stands. This is supported by the result of the comparison between own data and reference data. The sample scores of the reference data set, considered as representing the stands least affected in their floristic composition by land use, are poor in annual species and therefore had the most negative values along CA Axis 1. However, it has to be kept in mind that the very strong differences in PTh between own and reference data could at least partly result from different seasonal sampling periods. Therophytes are known to exhibit high intra- and interannual fluctuations in cover and presence due to inter- and intra-annual variations in rainfall patterns in the Mediterranean region (Peco *et al.* 1998).

The second-most important gradient in the analysis was pH, a result confirmed by both indirect and direct ordination. This is not surprising considering that the occurrence of one of the forest types (*Quercus suber* stands) is restricted to lime-free bedrock and acidic soils (Sauvage 1961). Climatic and spatial factors are also important in explaining floristic variation, but they are less influential than land use and pH. Stand structure type is not among the most significant variables in explaining floristic variation, although distinct floristic differences of plots with closed stands (CS) to plots with more open or isolated stands of the other stand structure types (IT, OS, FE, TG) are detectable. However, neither IT, OS, FE or TG alone is associated with floristic patterns displayed in the CA diagram. On the contrary, the position of sample scores of the different stand structure types in ordination space indicates a considerable floristic affinity. This implies that *e.g.* the ground vegetation under an isolated tree could be similar to the ground vegetation under an opened stand of considerable size. Nevertheless, heavily grazed stands of the different forest types are still distinguishable from each other according to their floristic composition in the CA along Axis 2, which represents the pH gradient. In other words, even in heavily grazed *Quercus suber* and *Olea europaea* stands a 'characteristic' species composition is developed in the surveyed sacred sites, presumably due to the different acidity of the soil.

Although the presented results contribute to our knowledge about the vegetation of sacred sites in Morocco, some questions remain open. Undoubtedly the conservational value of sacred sites with *Quercus coccifera* as examples of near-natural forests is high (Benabid 1984; Deil *et al.* 2009). However, the more disturbed character of most of the *Olea europaea* stands and part of the *Quercus suber* stands does not imply a negative evaluation of their conservational value. In northern Morocco, forests with non-cultivated *Olea europaea* constitute a strongly endangered vegetation type mostly restricted to sacred sites, just like *Quercus coccifera* forests (Benabid 1984). Even small, grazed woodland patches on sacred sites can play an important role as species refuges and seed source for forest restoration in areas which have been completely deforested elsewhere (Aerts *et al.* 2006). They can provide important information about the former vegetation, and in deforested mountainous regions they also serve as indicators for the potential timberline (Miehe *et al.* 2008). Finally, even singular trees can shelter a rich fauna. The faunistic value of isolated trees (stand structure type IT) in the Mediterranean in general is estimated as being high (Grove & Rackham 2001).

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