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On the degree of adaptation of the moss flora and vegetation in gypsiferous zones of the south-east Iberian Peninsula

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INTRODUCTION

There are numerous papers on the physiological effects of high temperature and tolerance to desiccation in bryophytes (e.g. Mahmoud, 1965; Lee & Stewart, 1971; Krochko *et al.*, 1978; Bewley, 1979; Proctor, 1982) but fewer on their morphological adaptations to arid habitats (Vitt, 1981; Bell, 1982; Scott, 1982).

In this study we carried out an analysis of the occurrence of principal gametophytic adaptations, recognized as typical of xerophytic species, appearing in mosses in gypsiferous zones of south-east Spain (Fig. 1). By this means we obtained an objective view of the degree of adaptation to extreme dryness and high temperatures exhibited by the moss flora of this area where the dryness of the gypsiferous substrate (haplic gypsisols, petrogypsic gypsisols and lithic leptosols) (FAO-UNESCO, 1988) is exacerbated by the low rainfall (Fig. 2).

In the gypsiferous zones studied there is found the pioneering bryophytic community *Crossidium crassinerve–Tortula revolvens*, described by Ros & Guerra (1988) and which sometimes extends over a considerable area (up to 5–6 m^2), alternating with the lichen communities of gypsiferous crusts or rocks.

MATERIALS AND METHODS

We studied the seven largest gypsiferous outcrops in the south-east of the Iberian Peninsula (Fig. 1) and carried out 120 relevés from 9 to 100 dm^2, following Braun-Blanquet's (1951) method. This enabled us to recognize the moss flora and predominant bryophyte community. We then considered fifteen morphological adaptations to dryness and recorded their occurrence in the 67 moss taxa found in the area. From these data were obtained the results given below.

The nomenclature used is that of Corley *et al.* (1981), except for the genus *Didymodon* (section *Asteriscium*) where that of Guerra & Ros (1987) is followed.

Of all the relevés carried out on gypsiferous soils, the largest number belong to the *Crossidium crassinerve–Tortula revolvens* community, from which a table (available on request) has been constructed (Martínez-Sánchez, 1990), and where two principal groups of species have been distinguished (Table 1). Group 1 species (characteristic species) have high constancy class (cc) (e.g. *Crossidium crassinerve*), cover and gypsophilous tendency (e.g. *Aloina bifrons* and *Tortula revolvens*). Group 2 represents a group of numerous species with usually low constancy class and cover much lower than group 1. Species with a high ecological aptitude are

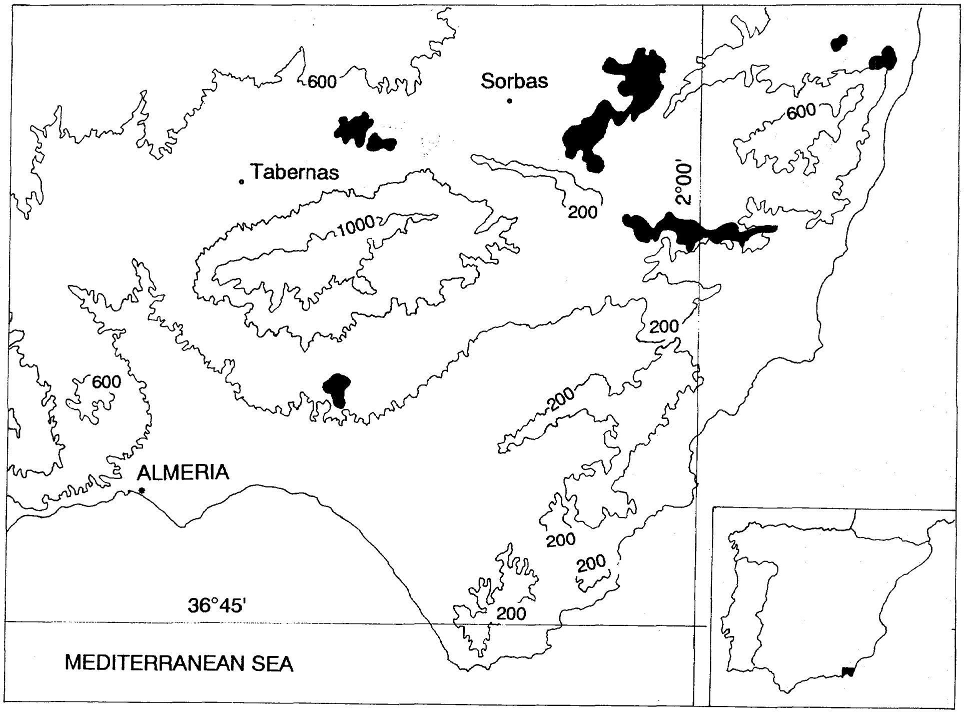

Fig. 1. Geographic situation. The shaded areas correspond to the gypsiferous outcrops studied.

aptitude are included in this group (e.g. *Bryum bicolor* and *Pseudocrosidium hornschuchianum*). A third group with cc = I is also considered (Table 1).

The degree of adaptation of each group to the conditions of the community was evaluated by calculating the index ϕ (ϕ = Tension) proposed by Bouderesque (1971) and Clauzade & Roux (1975). This idea of "Tension" is very important since it allows us to specify whether the group of species studied is well adapted to the habitat ($\phi > 1$) or not ($\phi < 1$) (see Clauzade & Roux, 1975; Roux, 1978).

In general terms, the estimation of this index begins with the calculation of the mean cover (*MC*):

(*a*) for a species in a table of *N* relevés:

$$MC = \sum_{i=1}^{n} \frac{C}{N}$$

where *C* represents the mean cover of this species in a relevé, calculated as a function of its cover-abundance (Braun-Blanquet scale) in the following way (Bouderesque, 1971; Mueller-Dombois & Ellenberg, 1974):

Cover-abundance	+	1	2	3	4	5
C (%)	0.1	2.5	15.0	37.5	62.5	87.5

(*b*) for a group of *p* species in a table of relevés: *MC* is the sum of the mean cover of each species in this group.

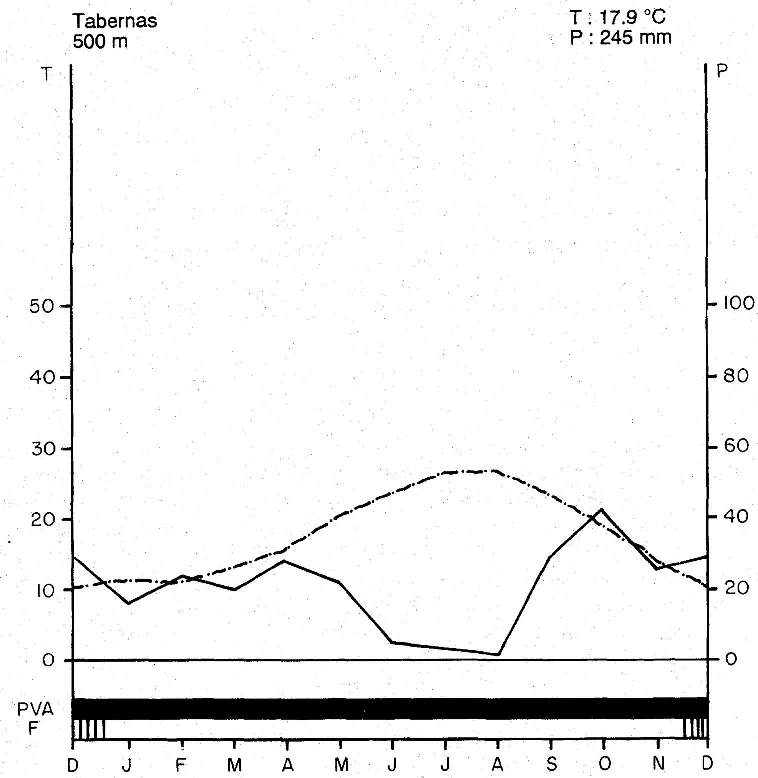

Fig. 2. Ombrothermic diagram of the area studied (weather station: Tabernas). PVA = period of vegetal activity, F = period of probable frosts.

Actual mean ($\bar{Q}$) of a group of species in a table of relevés is simply the mean number of species of this group in the different relevés. If $S_1, S_2, S_3 \ldots S_n$ represent the number of species of the group under consideration in each one of the N relevés, then:

$$\bar{Q} = \sum_{i=1}^{n} \frac{S}{N}$$

Quantitative dominance (QD) is the dominance as a function of cover:

(a) the QD of a species (QD_i) in a table of relevés with n species is the relation of its MC (mean cover) with the total of the MC of the n species, multiplied by 100:

$$QD = \frac{MC}{\sum_{i=1}^{n} MC} \times 100$$

(b) the QD of a group of p species in a table of relevés is the sum of the QD of each species in this group:

$$\sum_{i=1}^{p} QD$$

Qualitative dominance (CD) of a group of species in a table of relevés comes from the expression:

$$CD = \frac{\bar{Q}}{M} \times 100$$

where M is the mean number of species per relevé in the table. This index represents the mean contribution in species of this group to the mean of the collection of relevés as a whole.

Tension (ϕ) of a group of species in a table of relevés is given by the expression:

Table 1. *Values of the parameters needed to obtain the degree of adaptation (Φ) of the groups of species in the* Crossidium crassinerve–Tortula revolvens *community. cc = constancy class, na = mean number of adaptations of each group of species. For abbreviations see text*

	cc	na	MC_i(%)	MC (%)	$\bar{Q}$	QD_i	QD	CD	Φ
Group 1 (characteristic species)		7.33		12.06	2.16		47.1	19.51	2.41
Crossidium crassinerve	V		5.07			19.80			
Tortula revolvens	VI		6.08			23.75			
Aloina bifrons	III		0.91			3.55			
Group 2 (other species, cc > I)		4.76		11.44	5.90		44.61	53.29	0.83
Pseudocrossidium hornschuchianum	V		1.29			5.03			
Bryum bicolor	IV		4.93			19.25			
Aloina aloides	IV		1.02			3.98			
Didymodon luridus	III		0.36			1.40			
Pottia starckeana	III		0.50			1.95			
Didymodon rigidulus	III		0.66			2.57			
Didymodon vinealis	II		0.34			1.32			
Didymodon acutus	II		0.79			3.08			
Phascum curvicolle	II		0.30			1.17			
Gymnostomum luisieri	II		0.56			2.18			
Crossidium squamiferum	II		0.20			0.78			
Bryum radiculosum	II		0.33			1.28			
Didymodon aaronis	II		0.16			0.62			
Others species (cc = I)		3.20		2.10	3.01		8.29	27.20	0.30

Adaptations Considered

The number preceding each adaptation is the reference number given in Table 2.

1. *Formation of cushions*. By means of this adaptation, exposure of the foliar surfaces to wind and sun is reduced. The space between stems and leaves is considerably reduced, preventing air turbulence which would cause rapid water loss (see Proctor, 1984). Several experiments have been carried out to demonstrate this

phenomenon (see Gimingham & Smith, 1971; Nobuhara, 1979). This adaptation is not very common in the species of the area, the clearest cases being *Grimmia crinita*, *G. orbicularis* and *G. trichophylla* among the saxicolous species, and *Bryum bicolor* and *Tortula revolvens* among the terricolous.

2. *Leaves with hyaline hair-points.* Hair-points are involved in the capture of water when the leaves are contracted and curved during periods of drought (see Bell, 1982). They are especially effective as captors of dew and are frequent in some cushion-forming species such as *Grimmia* spp. and some terricolous species of extremely dry soils such as *Aloina bifrons*, *Crossidium crassinerve*, *C. aberrans* and *Pottia lanceolata*. Water retention by these piliferous formations by means of surface tension must be considered very important. It is generally accepted that these structures also serve as a protection against desiccation and mechanical damage by sunlight (Scott, 1982).

3. *Leaves bordered with special cells.* These cells are usually of a different size, shape etc, from those of the rest of the leaf and are the first to dry, thus forming a protective barrier for the rest of the foliar cells, retarding their desiccation (Watson, 1914).

4. *Involuted leaf margins.* Numerous xerophytic moss species have an involuted margin in the upper part of the leaf, forming a sacciform structure which protects the adaxial face of the leaf and reduces evaporation.

5. *Revolute leaf margins.* An equally widely distributed adaptation among xerophytic mosses (e.g. *Pseudocrossidium hornschuchianum*, *P. revolutum*, *Crossidium aberrans*). As with the previous adaptation it seems to favour the flow of water from the apex to base (Bell, 1982). Unfortunately there are no experimental data on this particular phenomenon.

6. *Cucullate leaves.* The apex of leaves boat-shaped and forming a cavity in which water is retained longer than in the rest of the leaf (e.g. *Phascum cuynetii*).

7. *Concave leaves.* Numerous species from dry habitats have concave leaves which act as efficient water retainers (Proctor, 1984). This retention is particularly favoured when the leaves are appressed to each other forming bud-like shoots.

8. *Papillose or mamillose leaves.* This is one of the most common and important adaptative characteristics among xerophytic mosses. The papillose leaf surfaces speed up the transport of water, acting as a capillary system without interrupting gaseous exchange (Rundel & Lange, 1980). Although it is unwise to generalize as regards the function of any type of structure, the above seems to be widely confirmed (see Vitt, 1981; Bell, 1982; Proctor, 1984).

9. *Incrassate cells.* The thick walls of some leaf cells undoubtedly offer resistance to desiccation and are found in many species (e.g. *Aloina aloides*, *Didymodon fallax*).

10. *Bistratose leaf cells.* A frequent adaptation in xerophytic species or those with a tendency to occur in arid habitats. Bistratose cells are frequently found in the upper part of the leaves (e.g. *Tortula caninervis* subsp. *spuria*, *Dicranella howei*, *Didymodon australasiae*).

11. *Nerve enlargement.* This produces a marked stiffening of the leaf and gives mechanical support during desiccation. It might also be interpreted as a mechanism to retain water (Bell, 1982).

12. *Leaves spirally twisted when dry.* Regardless of the posture of leaves when moist, they frequently become spirally twisted when dry. By this means the leaves

Table 2. *List of species and the adaptations they present. Numbers 1–15 correspond to the reference numbers in the text*

Species	Adaptations															Number of adaptations
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Acaulon dertosense							X	X	X			X			X	5
Acaulon triquetrum							X		X						X	3
Aloina aloides				X		X			X		X			X	X	6
Aloina bifrons		X		X		X			X		X			X	X	7
Barbula unguiculata					X			X				X			X	4
Bryum argenteum	X	X										X				3
Bryum bicolor	X				X		X					X				3
Bryum caespiticium	X	X	X		X							X				5
Bryum dunense	X	X			X							X				4
Bryum gemmilucens	X				X							X				3
Bryum radiculosum	X				X							X				3
Bryum ruderale	X				X							X				3
Bryum torquescens	X	X	X		X							X				5
Ceratodon conicus	X								X			X				3
Crossidium aberrans		X			X		X	X			X	X		X	X	8
Crossidium crassinerve		X			X		X	X			X	X		X	X	8
Crossidium squamiferum	X				X		X				X	X		X	X	7
Dicranella howei					X					X						2
Didymodon aaronis					X	X	X	X		X			X		X	7
Didymodon acutus	X				X		X		X			X				5
Didymodon australasiae					X		X			X			X		X	5
Didymodon fallax	X				X			X	X			X				5
Didymodon insulanus					X			X				X				3
Didymodon luridus					X		X		X			X				4
Didymodon rigidulus	X				X			X	X		X		X			6
Didymodon trivialis					X		X	X		X		X			X	6
Didymodon vinealis	X				X			X				X				4
Encalypta vulgaris								X				X			X	3
Ephemerum recurvifolium											X				X	2
Fissidens incurvus			X													1
Fissidens viridulus			X						X							2
Funaria pulchella							X					X				2
Grimmia crinita	X	X					X		X	X		X			X	7
Grimmia orbicularis	X	X			X				X	X		X			X	7
Grimmia pitardii					X				X				X		X	4
Grimmia trichophylla	X	X			X				X			X			X	6
Gymnostomum luisieri	X							X				X				3
Gymnostomum mosis								X		X		X				3
Homalothecium aureum												X			X	2
Hypnum cupressiforme					X		X								X	3
Leptobarbula berica								X	X						X	3
Phascum cuynetii					X	X	X	X	X		X		X		X	8
Phascum curvicolle					X		X	X							X	4
Phascum longipes					X		X	X				X	X		X	6
Pleurochaete squarrosa	X		X					X							X	4
Pottia caespitosa				X			X	X	X			X	X		X	7
Pottia commutata					X			X							X	3
Pottia lanceolata		X			X			X				X		X	X	6
Pottia minutula					X			X				X			X	4

Table 2. *Continued*

Species	Adaptations															Number of adaptations
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Pottia mutica					X	X					X				X	4
Pottia starckeana					X			X				X			X	4
Pseudocrossidium horschuchianum					X		X	X				X				4
Pseudocrossidium revolutum					X		X	X				X				4
Pterygoneurum ovatum		X					X		X			X	X	X		6
Pterygoneurum sampaianum		X					X		X			X	X	X		6
Pterygoneurum subsessile		X				X	X					X		X	X	6
Rhynchostegium megapolitanum															X	1
Tortella humilis	X						X	X				X	X		X	6
Tortula atrovirens					X	X	X	X			X	X	X		X	8
Tortula brevissima		X			X		X	X			X	X		X	X	8
Tortula muralis var. *obcordata*		X			X			X				X			X	5
Tortula revolvens var. *obtusata*	X				X		X	X			X	X			X	7
Tortula caninervis subsp. *spuria* var. *spuria*	X	X			X			X		X	X	X	X		X	9
Trichostomum brachydontium	X							X				X	X		X	5
Trichostomum crispulum	X					X		X				X	X		X	6
Weissia controversa	X			X			X	X				X	X		X	7
Weissia triumphans	X			X		X	X	X				X	X		X	8

expose, almost exclusively, the upper parts only where there are such adaptations as hyaline hairs, curved margins, bistratosity or greater density of papillae, which reduce desiccation and sunlight damage.

13. *Leaves curving when dry.* In numerous xerophytic species the upper leaves curve towards the stem, resulting in a smaller degree of leaf exposure (e.g. *Grimmia pitardii*, *Phascum cuynetii*, *Pterygoneurum sampaianum*).

14. *Leaves with lamellae or filaments on the adaxial side of the nerve.* Some species of arid biotopes have filaments or lamellae on the adaxial face of the leaves. These structures can be interpreted as increasing the photosynthetic surface, allowing rapid growth of the gametophyte and development of the sporophyte during the short periods of moisture (e.g. *Crossidium* spp., *Pterygoneurum* spp., *Aloina* spp.).

15. *Hyaline basal cells.* Numerous species of dry habitats have special large hyaline cells that retain water (e.g. *Tortella* spp., *Pleurochaete squarrosa*, *Weissia* spp.).

FREQUENCY OF ADAPTIVE STRUCTURES

The most commonly encountered adaptation in the species of the study zone was the presence of twisted or overlapping leaves (71% of the species). This is very marked, for example, in *Crossidium crassinerve*, *Pottia lanceolata* and *Pseudocrossidium hornschuchianum*. The next most common adaptations were hyaline basal cells (62.6%), revolute leaf margins (59.7%) and papillose leaf cells (55.2%). The most infrequent adaptations were leaves with modified marginal cells (7.4%) and involute leaves (7.45%) (Fig. 3).

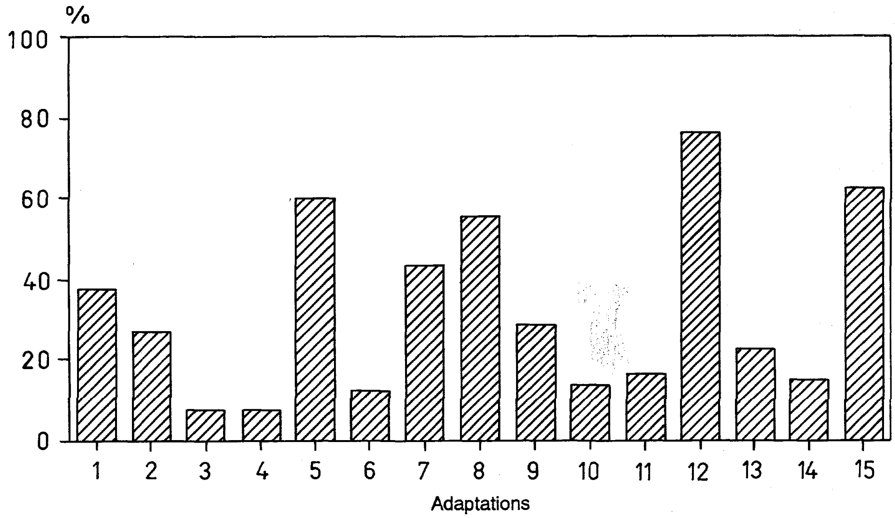

Fig. 3. Frequency of the adaptive structures. Numbers 1–15 correspond to the reference numbers of the text.

Degree of Adaptation of the Moss Flora

It is of interest to know the percentage of species and their different number of adaptive structures to evaluate the degree of adaptation of the moss flora. Table 3 shows the following as being noteworthy. It may be seen that 18.4% of the species show 6 adaptations characteristic of dry conditions; 40.7% present 5 to 7 adaptations, while 9 adaptations (the highest number) are shown by only 2.98% of the species. This last percentage also corresponds to species with one adaptation only. It is clear that the moss flora in the zone studied shows a high degree of adaptation to dryness.

Table 3. *Percentage of species with different number of adaptations*

Number of adaptations	1	2	3	4	5	6	7	8	9
Species (%)	2.98	7.48	17.91	20.89	11.94	18.41	10.44	8.95	2.98

Degree of Species Adaptation within the Community

The results obtained by calculating the indices explained in the methods section (Table 1) demonstrate that *Crossidium crassinerve*, *Tortula revolvens* and *Aloina bifrons* constitute a group of species which can be considered characteristic of moss vegetation of the gypsiferous soils of the south-east of the Iberian Peninsula and probably of the Mediterranean basin. In a recent work (Frey *et al.*, 1990) this community has been described in the Middle East and the same characteristic species proposed.

The degree of adaptation of this group ($\phi = 2.41$) is clearly higher than that of group 2 ($\phi = 0.83$) and this is in agreement with the notable difference in the mean number of adaptations presented by the groups (na = 7.33 and na = 4.76, respectively). In addition, as already indicated, these species are typical of gypsiferous soils and constitute the largest part of the bryophyte biomass.

Summary

The occurrence of fifteen xeromorphic adaptations in mosses of gypsiferous sites in south-east Spain, the most arid part of Europe, was analysed. The characteristic species of a gypsophilous moss community (*Crossidium crassinerve*, *Tortula revolvens* and *Aloina bifrons*) were evaluated in order to compare their degree of adaptation to the habitat with the degree of adaptation of other groups of species of this association.

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