

SIGNIFICANCE OF SPINES IN CARDUEAE (ASTERACEAE), BIOCLIMATIC STAGES, AND MAMMALIAN GRAZING

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Abstract

The significance of spines in Cardueae is tested through the analysis of their position in the different organs and their variations in different Moroccan stations. It appeared that the most constant presence of thorns is linked to capitule bracts. We also show that the spines are mostly developed in areas with arid stage and mild to hot winter, and areas with semi-arid to sub-humid stages with fresh winter. The climatic conditions prevailing in these areas allow a moderate biomass productivity. It is hypothesized that the development of spines is an adaptation to prevent damages to mammal grazing, and especially to protect capitules, where inulin reserves accumulate in the receptacle.

Key words

Cardueae, spines, mammal grazing, bioclimate, inulin reserves.

1- Introduction

The species of Asteraceae family show different strategies to prevent, or at least to limit damages caused by mammal grazing. We can broadly distinguish two possible answers of plants, not mutually exclusive: (i) chemical defenses involving a wide variety of molecules such as bitterness of sesquiterpenes lactones [1], or hepatotoxicity of pyrrolizidine alkaloids [2], and (ii) mechanical defenses as thorns on leaves, stems or reproductive organs (numerous Cardueae genera), glochidiate hairs with two hooks at the tips on the leaves which damage the tongue papillae (*Picris* and *Leontodon*). The plant can also reduce the damages of attacks by renewal shoots near the ground level. The Cardueae are a tribe of Asteraceae including around 2500

species and 83 genera [3], very diversified in the Mediterranean Basin and most species are thorny on leaves, stems or involucre. Several hypotheses can be held about the role of these spines: (i) adaptation to drought by reduction of transpiration surface, (ii) adaptation against grazing, and (iii) adaptation to enhance condensation of air humidity. The role of the spiny apparatus of Cardueae can be assessed by studying their distribution on the various parts of the plant [4], [5]. It appears that the spines can be restricted to the involucre bracts or be present on both involucre bracts and leaves. I recorded only few cases where the leaves are thorny but not the bracts: *Notobasis syriaca*, *Picnomonacarna*. However, in these species, the capitule is surrounded with very prickly upper leaves (figure 1).

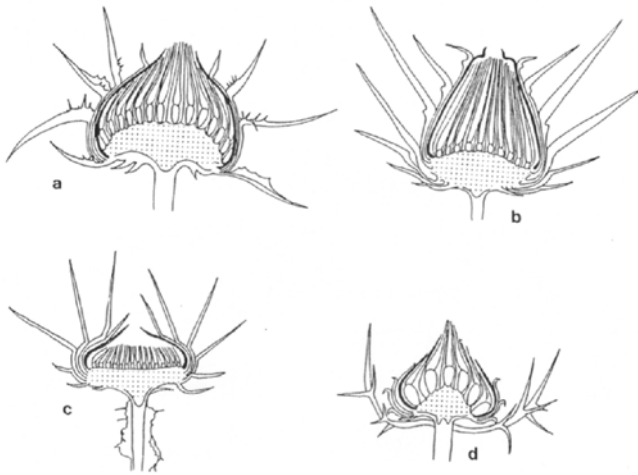


Figure 1.
Thorny capitule in Cardueae.
A: *Silybum marianum*,
b: *Cynara humilis*,
c: *Onopordum dissectum*,
d: *Notobasisis yriaca*.

My working hypothesis is based on a relationship between mammal grazing and climate. When growth is conditioned by a short window of favorable conditions due to drought (water shortage in summer) and/or low temperature (high altitude areas), biomass production is low resulting in a dramatic impact of mammal grazing. In response to this biotic pressure, plant has to adapt by different ways, including the development of spines. Of course, the original fauna present before Man on Earth, has a negligible influence by comparison with the actual domesticated Equidae and Bovidae [6], [7]. We have no record on the presence of the different Cardueae species in the last 20 000 years in Morocco. However, we hypothesize that each present combination of climatic parameters took place somewhere in Morocco before the arrival of domesticated mammals. Therefore, the pressure of ancient fauna is somewhat comparable to the one of present domesticated fauna if we take into account the environment determined by climatic parameters. To test the adaptation of plants, several methods can be undertaken in order to prevent bias

due to sampling. The first one requires complete inventories of species in a great number of sampling sites, including spine position and biological type of each species, and climatic parameters of each sampled station. The second one consists in considering the distribution of homogenous taxa presenting variations in spine aspect, according to a wide range of climatic conditions. In this paper, I followed this last strategy, and after successive eliminations, my choice focused on two perennial species of *Echinops* and on *Onopordum dissectum* in Morocco.

2. Material and Methods

2.1. Sampling sites

Many stations in Morocco were sampled in several seasons between 1984 and 1988. For each station, climatic parameters were obtained from [8] and [9]. In case of lack of data, these parameters were interpolated from the ones recorded in closest stations, taking into account exposition and altitude. As a result, the rule of decreasing 0.6 degrees for every 100 m was not systematically used. The Emberger-Sauvage pluviometric coefficient was calculated using the formula:

$$Q^2 = 2000 P / (M - m)(M + m)$$

with m = minima means of the coldest month, in K; M = maxima means of the hottest month, in K; P = annual rainfall, in mm. The climagrams were drawn according to the method of [10] and [11].

The identification of species was conducted using [12], [13], and [14].

2.2. The thorny apparatus of *Echinops spinosissimus* Turra and *E. bovei* Boiss.

Echinops spinosissimus Turra and *E. bovei* Boiss. are perennial hemicryptophytes, frequent in North Africa. Both species has thorny leaves. They differ from each other by the stem indumentum, the cutting out of the leaves, the corolla color, the length of the brush of capitules, etc. Briefly, *E. spinosissimus* subsp. *spinosus* has a tomentose and nonglandulose stem, whereas *E. bovei* Boiss. has a glabrous or glandulose stem. Each head is composed of monoflowered capitules [15], among which several ones (cornigere capitules) can bear hardened and acute bracts, clearly exceeding the normal capitules (fig 2).



Figure 2.

Echinopsbovei Boiss. (Tizi-n-Test). The arrow indicates cornigere capitules.

To characterize each station, I counted the number of cornigere capitules per head (capitules of second order) topping the main axis, on 35 individuals. The numbers obtained were distributed in 7 classes from 0 to 35. The stations were taken along a transect from Settate (375 m) in the North, towards Tizi-n-Test (2100 m) in the South. I also made observations at Amerzgane, on the Southern side of Atlas, at Talsinnt in Saharian Atlas, and finally at Demnate.

2.3. The thorny apparatus of *Onopordum dissectum* Mürb.

Onopordum dissectum Mürb. is a winter annual, developing a rosette in autumn, then a stem in spring, and blooms in early June [16]. In addition to the leaves and the wings of the stems (the leaves are decurrent), the thorny apparatus consists in involucral bracts ended in an acute appendix (fig. 3A for distribution map and 3B for bioclimogram).

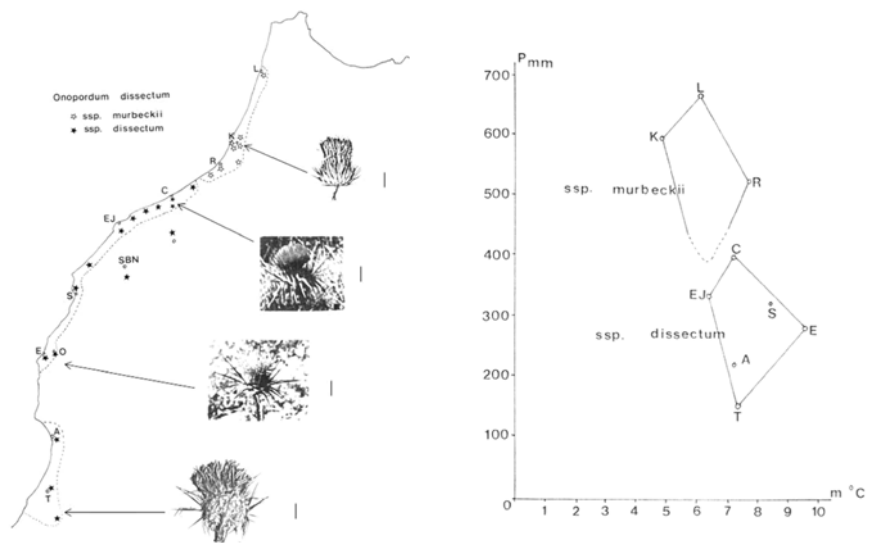


Figure 3. *Onopordum dissectum* in Morocco. 3A: Distribution; 3B: Bioclimogram.

Scale bar: 1 cm. A: Agadir, E: Essaouira, EJ: El-Jadida, L: Larache, K: Kenitra, O: Ounagha, S: Safi, SBN: Sidi Bennour, R: Rabat, T: Tiznit.

This species is composed of two subspecies recognizable by the length of the florets, stamens and achenes: (i) *O. dissectum* subsp. *dissectum*: short florets, stamens and achenes, and (ii) *O. dissectum* subsp. *murbeckii*: long florets, stamens and achenes. Both subspecies presents variations in the length of the thorny bract appendices according to the populations. To characterize each station, I measured the length of the bract appendices in a medium position on the terminal capitules of 10 individuals.

In addition to the prospected localities, I considered herbarium material available in RAB (Institut Scientifique Chérifien de Rabat) and P (Museum National

d'Histoire Naturelle de Paris). In these cases, only one individual was taken into account. Insofar as the collectors were not especially interested in the length of bract appendices, I hypothesize that they collected an average individual and thus introduced few bias sampling. It would be highly desirable to multiply the sampling sites so as to better determine the amplitude of the variations.

3. Results

3.1. Cornigere capitules of *E. spinosissimus*

The number of cornigere capitules regularly increases from north to south and from the plain towards the Atlas summits (fig. 4).

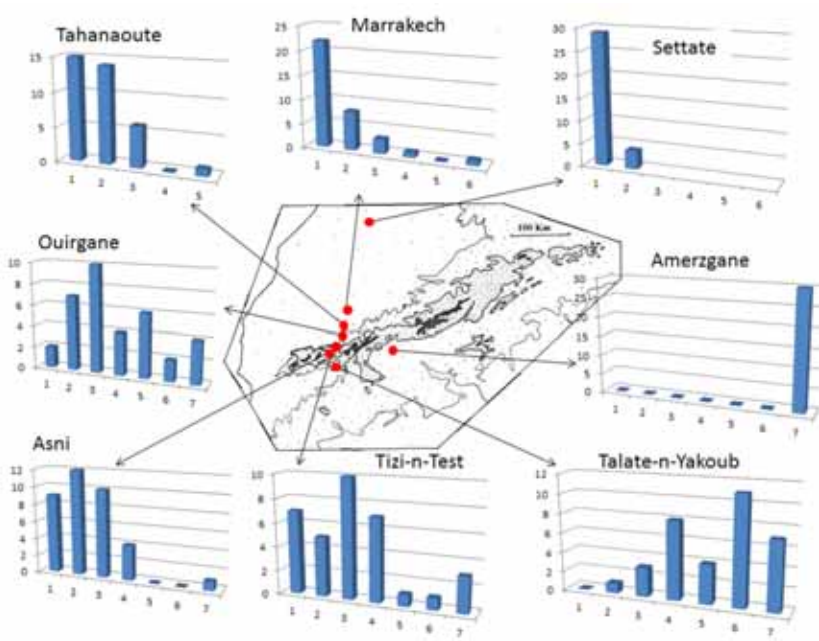


Figure 4. Variations in the number of cornigere capitules of *Echinopsin* different Moroccan localities. The histogram classes are from 0 to 5, 5 to 9, etc. Altitudes: light dots (0 to 1000 m), medium dots (1000 to 2000 m), dense dots (2000 to 3000 m), and black background (>3000 m).

These data, transformed into averages, can be plotted onto the pluviothermicdiagram (fig. 5) of Emberger--Sauvage[9]. It appears that the abundance of the cornigerecapitules is linked to the Saharan stage on the one hand and to dry mountains with arid to semi-arid climate on the other.

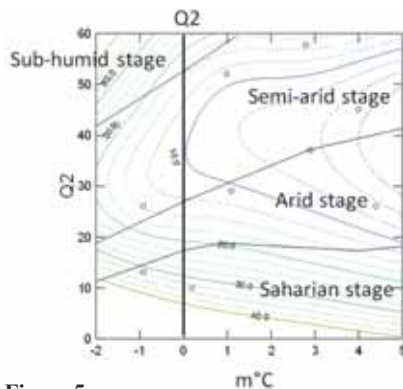


Figure 5. Climatic distribution of the different abundances of cornigere capitules. A circle between the 30 and 40 isohyets corresponds to a locality where a mean number of 30 to 40 cornigere capitules per head was observed. The abscissa indicates the minima mean of the coldest month, in °C, and the ordinate the Q2 Emberger-Sauvage coefficient (see text).

3.2 Bract appendage length in *O. dissectum*

There is a very significant correlation ($r = -0.79, p < 0.02$) between the length of bract appendages and the annual rainfall averages (fig. 6). The appendices recorded in subsp. *murbeckii* are shorter than in subsp. *dissectum*.

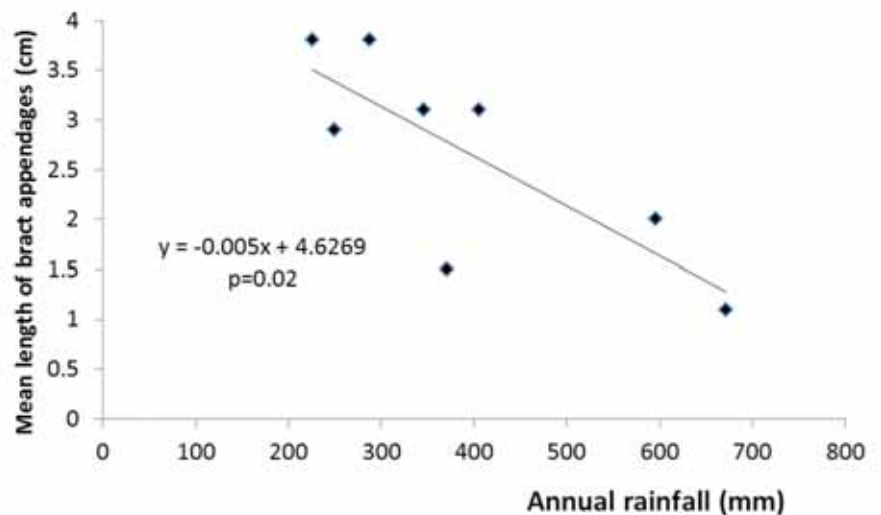


Figure 6. Correlation between annual rainfall and mean length of bract appendages of *Onopordumdissectum*.

3. Discussion

From the two studied species, it appears that the spines are mainly developed in arid and semi-arid stages with fresh winter. It corresponds to areas where biomass productivity is low, supporting our hypothesis of grazing impact in these bioclimatic conditions. The reserves contained in the receptacle of capitules are coveted by herbivorous mammals. When these reserves are abundant, as in the genera *Cynara*, *Onopordum*, and *Silybum*, the involucre is strongly thorny.

Most concerned species are winter annuals or perennial hemicryptophytes to geophytes, so it is interesting to understand the interest of capitule reserves, in connection to the life-cycle of species. Their life-cycle begins with a rosette of leaves in autumn, followed by the development of the stem in the next spring. According to the experiments conducted on different *Cynara cardunculus* varieties (globe artichoke, i.e. var. *scolymus*, wild and cultivated cardoon, i.e. var. *altilis*), Melilli and Raccuia [17] showed that inulin-type fructan reserves accumulated at a very high degree of polymerization (over 100) in the root to prevent drought stress in winter time and during the stalk and capitula formation. They also measured that inulin content was maximal before the beginning of flower formation, and then deeply decreased as a result of capitulum growth and grain ripening. As indicated by Daniel [6], this functioning is also observed in *Onopordum*, where inulin reserves are used for final development of the florets and achenes. According to this last author, the maximal content of inulin can be reached earlier, in

the beginning of the development of the florets, as in *Carduus nutans* or *Centaurea calcitrapa*. In summary, the translocation of inulin from underground organs to receptacle, for a further use in flower or achene development, allows a very fast development of the capitules of *Cardueae*. This feature is well adapted to Mediterranean climate, as rosette formation is linked to autumn rainfall, and development of stems and capitules to spring humidity. However, in Saharian stage, the life-cycle can be reduced: *Onopordum arenarium* (Desf.) Pomel is an annual species and not a winter annual.

Conclusion

Following other papers on *Asteraceae* adaptation to climate constraints [18], [19], this study shows that the spines of *Cardueae* seem to be mainly associated to the protection of capitule reserves located in the receptacle against mammal grazing. These inulin reserves are further used for the quick development of florets and achenes. The thorny protection gets more developed in areas where biomass productivity is low, as a result of arid conditions or semi-arid and sub-humid stage with fresh winter.

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