

THE INFLORESCENCES OF ASTERACEAE AS AN ADAPTATION TO UNPREDICTABLE CLIMATES

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Résumé

Les inflorescences monotèles des Asteraceae montrent des architectures variant entre la grappe composée définie (panicule) et la cyme. Dans un premier temps, il est montré que ces 2 extrêmes sont liés à des productions de capitules très différentes, plutôt simultanée dans le pôle panicule et étagée dans le temps pour le pôle cyme. Il en résulte que dans des conditions d'humidité prévisible, le système panicule devrait être favorisé, tandis que le système cyme le serait sous des climats imprévisibles. Des statistiques sur les proportions d'espèces du pôle cyme dans 21 localités du Maroc permettent de vérifier ces hypothèses.

Mots clés : *Asteraceae, inflorescence, cyme, anthèle, incertitude des précipitations, climat aride*

Summary

The monotelic inflorescences of Asteraceae show architectures varying between the definite grappe (panicule) and the cyme. It is first shown that these 2 extremes are related to very different production types of capitules, rather simultaneous in the panicule pole and staged in time for the cyme pole. It results that under conditions of foreseeable rainfalls, the panicule system should be favored, while the cyme system would be it under unforeseeable climates. Statistics on the proportions of species of the pole cyme in 21 localities of Morocco make it possible to generalize these assumptions.

Key words: *Asteraceae, inflorescence, cyme, anthele, rainfall uncertainty, arid climate.*

1. Introduction

Inflorescence designs the system of ramifications bearing the flowers (and not the vegetative buds): only the geometry of the various axes is concerned. One can extend this definition by replacing "flower" by "flower unit". Thus, the flower unit can be itself an inflorescence: ombelle, cyathe, capitules, etc... this is then a second order inflorescence. In the case of Asteraceae, inflorescence will be used in this extended sense. According to whether the inflorescence has or not a definite growth, two categories are distinguished. In a polvtelic inflo-

rescence, there is no flower (or another unit of flowering) at the top of the main axis. This axis thus remains indefinite after having developed a great number of lateral flowers. It is observed in the case of racemose system. In a monotelic inflorescence, a terminal flower (or any other unit of flowering) is located at the top of the main axis. The deep systematic unity of Asteraceae also results in the common monotelic type of their inflorescences.

The figure 1 presents the fundamental inflorescence architecture of herbaceous Asteraceae.

There is a terminal capitule (T) at the top of the main axis. The flowering order of the capitules terminating the successive secondary axes is indicated by thick arrows. The two arrows in contrary direction on the same portion of the main axis mean that, according to the species, the flowering order is ascending (acropetal) or going down (basipetal). Indeed, many examples illustrate decoupling between the order of flowering and the architecture of inflorescence [1]. One can clearly delimit two zones on the main axis: the higher one, or

enrichment zone, bears secondary axes equipped with capitules whatever (or almost) the conditions under which the plant grows. The number of capitules borne by these secondary axes increases from top to the base: 1 for the first, 2 for the second, 3 for the third and 5 for the fourth (fig. 1). The lower zone bears secondary axes equipped with capitules only when the conditions are favorable. In this case, these axes develop from top to the base. These axes do not generally bear as much capitules as the lower part of the enrichment zone. It is probable

that the higher zone exerts an inhibiting action on the development of the lower one (Sell, *in litteris*), and this one is also called inhibition zone. If the conditions are frankly drastic, it can even happen that the main axis corresponding to the lower zone is collapsed. According to Troll [2], [3] and Weberling [4], the increase in the number of flowerings units is mainly dependent on is the enrichment zone. The inhibition zone only rarely takes part in this increase.

Various categories of inflorescences are observed in Asteraceae (fig.2a-e). The example in fig.2a is a definite grape (panicle), b a corymb, c an anthele (term invented by Meyer [5] about *Juncus*), d is difficult to name and finally e is a dichasial cyme. Goebel [6] and Weberling [5] have pointed out the suspected physiological processes involved in the relative development of each bud compared to the others. If the most developed axillary buds are concentrated in the terminal part of the main axis, there is an acrotone development, leading to a sympodial system (d and especially e). If, on the other hand, the most developed secondary axes are the most distant from the top, the development is basitone (a). One can extend the logic of the system by adding the term of mesotony [7] when the most developed axes are located around the middle of the ramified part the main axis (b and c).

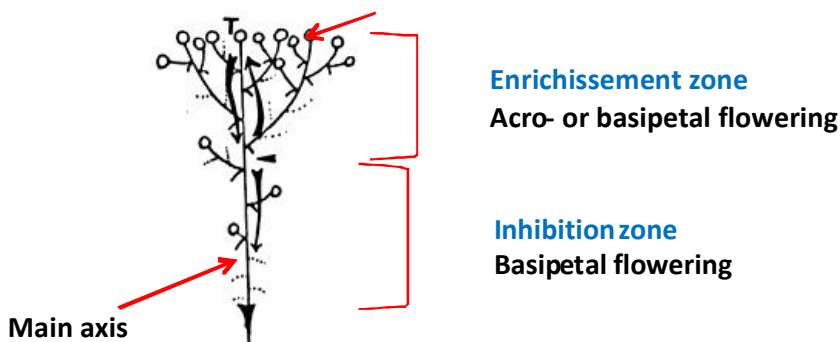


Figure 1. Organisation of inflorescence in Asteraceae

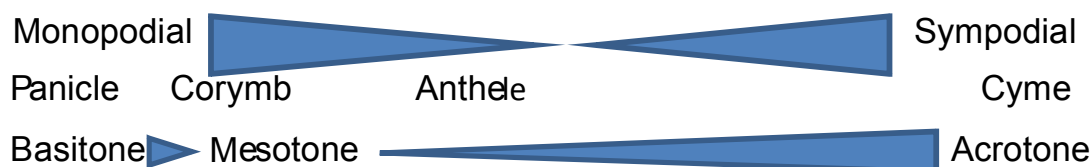
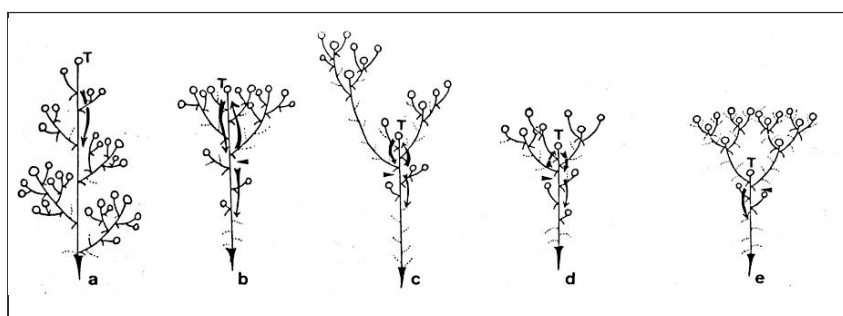


Figure 2. Monotelic inflorescences in Asteraceae

The works of Darwin on the flowers and inflorescences in especially in Orchidaceae tried to find traces of adaptation by natural selection process [8]. Indeed, the shape of the spur, or the position of the pollinies are related to entomophilous pollination (Bumblebee, Sphinx for example). These works played a pioneer part in the study of plant reproductive organs, and were followed by many authors who experimented some of his assumptions ([9, 10] for review). Nevertheless, the majority of works focused on the strategies of pollination.

The form of the inflorescences held more the attention of the morphologists than of the population biologists [4]. However, certain inflorescence architectures were tested as adaptive traits toward the constraints of environment. Plants in snowball, showing very condensed axes of flowers, covered with an important trichome, are commonly distributed in the Arctic zones and high mountains. These morphological features enabled the plant to store heat and thus to flower rather early in the season [11]. Theoretical work showed that the size of the inflorescences in self-incompatible plants depends on the availability of the resources, transport of the nutrients in the stem and the production of pollen and seeds per flower [12]. Nevertheless, the most significant work in term of strategy related to the polytelic inflorescences which are more frequent in the tropical zones, with regular rainfall, whereas the

monotelic ones dominate in temperate countries [13].

The goal of this work is to try to connect the morphology of inflorescences with various abiotic factors as climatic parameters. It is certain that the link is not direct since the production of the flowering units plays the role of intermediate variable. We first wish associating the various categories of inflorescence with the production rate of the flowering units. In a second time, it is necessary to establish a connection between inflorescences and climatic constraints. In order to get accurate result, we choose as model a group for which the systematic kinship is well-known, and showing a large panoply of inflorescences, which is verified in the case of Cardueae and Lactuceae of Morocco.

1. Material and methods

It is difficult to highlight tendencies of forms associated with a given environment, when the sampled species are heterogeneous by their taxonomy. To circumvent this difficulty, it is preferable to address groups of close species: the chances to discover new links are much greater by rigorous application of comparative biology method. The efforts were focused on the genera close to *Atractylis* because they were the subject of a revision in Morocco [14]. Measurements were taken on plants collected on the field and having finished their growth: from May for *Atractylis*, June for *Carlina* in the years 1984-1987.

For each station where it was possible, 7 individuals were studied, chosen among most vigorous and bearing the greatest number of capitules. Moreover, samples harboring less development strength were collected. Measurements were taken on plants having finished their growth. A given capitule is taken into account only when it contains achenes; those which are aborted or dry before the accomplishment of reproduction are indicated by a cross in the diagrams and are not taken into account in calculations. Many developmental stages were studied in addition to determine the flowering order of secondary and tertiary axes. In a low number of cases, the information concerning rare species was enriched using with measurements made on herbarium samples (RAB, MPU).

To modelling the number of capitules produced according to the strength of the plant and the duration of favorable conditions, a simple way consists in counting this number for each successive axis from the top the base, then to cumulate these numbers according to the rank of the secondary axis. Even if the order of flowering is not basipetal, this method makes it possible to homogenize counting. The result is that the transition between the enrichment zone and the inhibition zone is well highlighted because of the more or less abrupt reduction in the number of capitules.

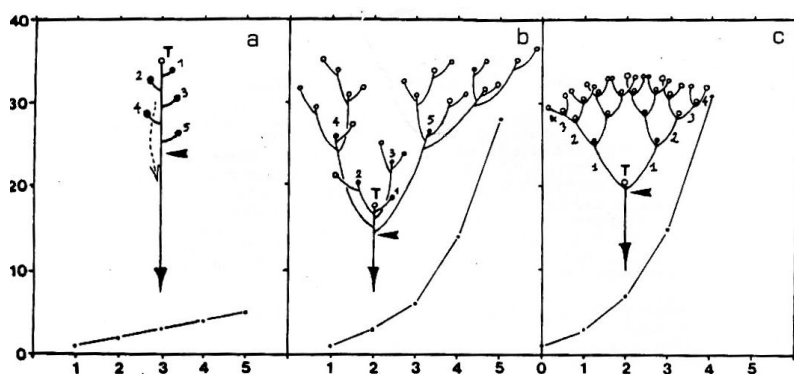


Figure 3. Enrichment curves of capitules in function of their position on the main axis

In abscissa, the ranks of secondary axes are given, and in ordinate, the cumulate numbers of corresponding capitules. a : panicle ; b : anthele ; c : dichasial cyme. In this last case, the rank is replaced by the order of secondary axes (see the text).

In the examples of figure 3, the cumulated numbers (y) increase in a variable way with the rank of the axes (x). In the panicle (fig. 3a), the increase follows a linear function, $y=ax + b$. In anthele (fig. 3b), the number of capitules increases according to a degree 2 polynomial function: $y=ax^2 + bx + c$. Lastly, for a dichasial cyme (figure 3c), counting must be made stage by stage, i.e. according to following: 1 (terminal capitule), 3 (the same one plus the 2 capitules terminating the primary ramifications), 7 (the same ones plus the capitules terminating the secondary ramifications), etc. The following of the cumulated numbers is according to: $y=1+2+2^2 + \dots$, i.e. $y=2^{x+1} - 1$ if the cyme is dichasial, but $y=1+3+3^2 + \dots$, i.e., $y=(3^{x+1} - 1)/2$ if the cyme is trichasial.

3. Results

3.1 Typology of inflorescences

Four architectural types can be defined in the genera *Atractylis* and *Carlina* (fig. 4).

- *Atractylis phaeolepis* type, characterized by an inflorescence of corymb-panicle type with mesotony or basitony, regular and non-null internodes. The curve of cumulated enrichment of capitules is close to a line: there is a weak difference between the enrichment and inhibition zones. In table 1, the adjustment was carried out with a polynomial model so as to facilitate the comparison with the other architectural types. It is clear that the coefficients of the second degree terms are lower those in the other cases. In this category, one finds *C. involucreta* and *C. hispanica*.

- *Atractylis serratuloides* type, characterized by a plurichasial sympodic inflorescence, with acrotomy. The relative length of the secondary axes decreases gradually from the top to the base and the curve of the cumulated number of capitules follows an exponential to a degree 2 polynomial function. In this category, one finds *C. brachylepis*, *C. lanata* and *A.*

cancellata.

- *Carlina racemosa* type, characterized by an antheliform inflorescence: the relative length of the higher branches is lower than that of the middle branches. The accumulation curve of the capitules follows a degree 2 polynomial function.

- *Atractylis delicatula* type is derived from the *C. racemosa* type, in the sense that the first secondary ramifications start from the base of the main axis. This inflorescence is thus called flattened antheliform. Moreover, the internodes are null or almost in the enrichment zone. As a result, all the secondary axes belong to the enrichment zone. As previously, the curve of enrichment follows a degree 2 polynomial function. This model is illustrated by *A. prolifera*, *A. babelii*, *A. carduus* and even in certain situations, *A. cancellata*.

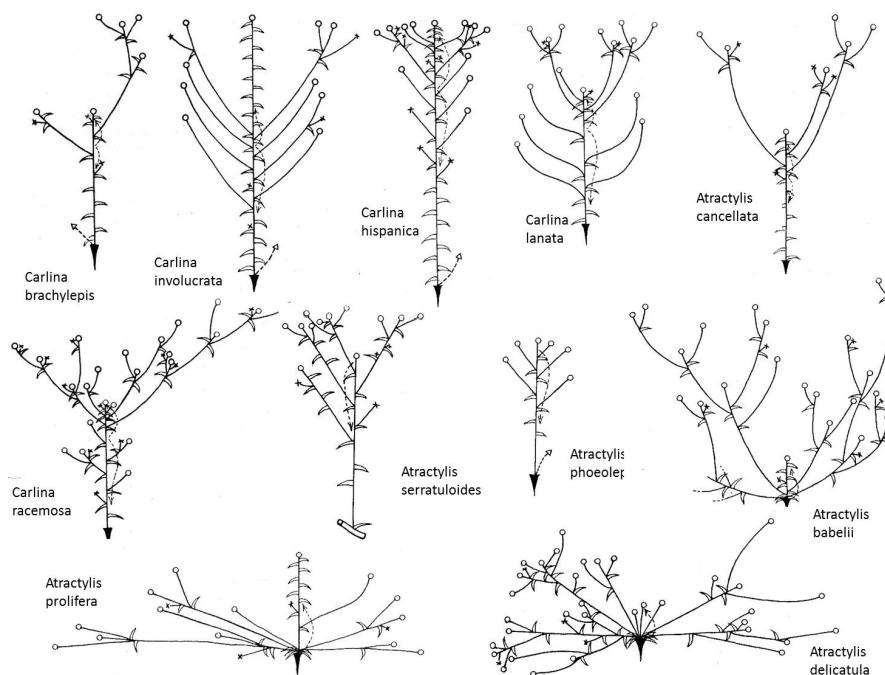


Figure 4. Architecture of inflorescences in the genera *Atractylis* and *Carlina*

Table 1. Characteristics of inflorescences in *Atractylis* and *Carlina*

Species	Inflorescence	Enrichment formula	Determination coefficient
<i>C. involucreta</i>	Corymb	$y = 0.0194x^2 + 1.0908x - 0.02$	$R^2 = 0.9949$
<i>C. hispanica</i>	Corymb	$y = 0.0816x^2 + 1.1959x - 0.1714$	$R^2 = 0.9987$
<i>A. phoelepis</i>	Corymb	$y = -0.055x^2 + 0.181x + 1.02$	$R^2 = 0.8301$
<i>C. brachylepis</i>	Sympodial	$y = 0.7667x^2 - 1.1667x + 3.6$	$R^2 = 1$
<i>A. serratuloides</i>	Sympodial	$y = 0.4667x^2 + 3.4x - 0.0667$	$R^2 = 1$
<i>C. lanata</i>	Sympodial	$y = (3^{n+1} - 1)/2$	
<i>A. cancellata</i>	Sympodial	$y = 2^{n+1} - 1$	
<i>A. cancellata</i>	Antheliform	$y = 1.025x^2 - 1.015x + 2.075$	$R^2 = 0.9984$
<i>C. racemosa</i>	Antheliform	$y = 0.7143x^2 + 0.0743x + 0.12$	$R^2 = 0.999$
<i>A. delicatula</i>	Flattened antheliform	$y = 0.2798x^2 + 0.9655x - 0.375$	$R^2 = 0.9882$
<i>A. babelii</i>	Flattened antheliform	$y = 3.5x^2 - 5.9x + 7$	$R^2 = 0.9901$
<i>A. prolifera</i>	Flattened antheliform	$y = 0.6667x^2 - 0.0667x + 0.5$	$R^2 = 0.9964$

3.2. Bioclimatology of species

The bioclimagrams of each species are presented in fig. 5.

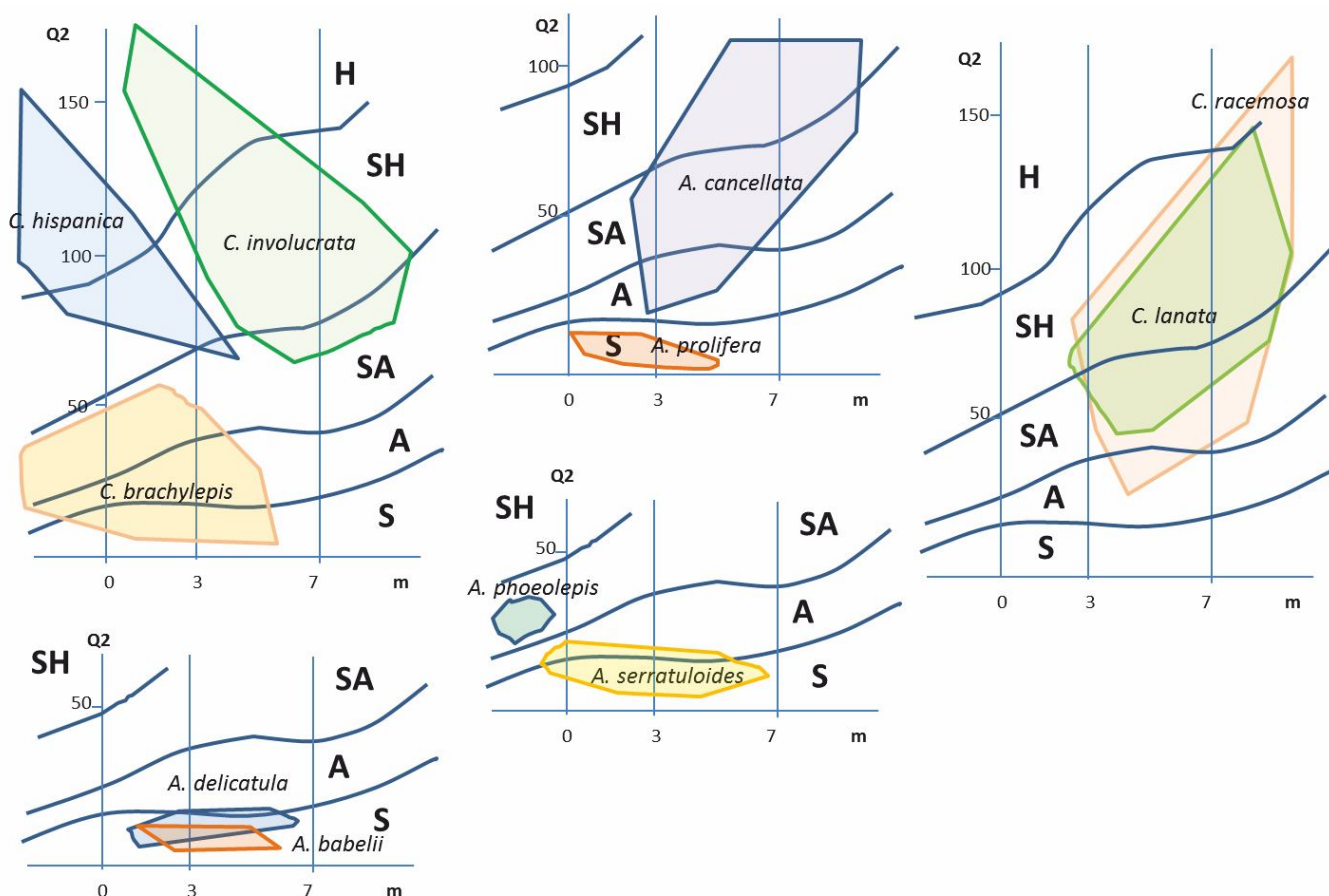


Figure 5. Climagrams of species.

Abbreviations. A: Saharan stage, A: arid stage; SA: semi-arid stage; SH: sub-humid stage; H: humid stage, m: minima means of the coldest months, in °C; Q2: Emberger-Sauvage [15] coefficient. $Q2 = Q2 = 3.43 P/M - m$, with M= maxima means of the hottest months, in °C, and P= annual rainfall, in mm.

The climagrams gather the species by sections of genera [16]. There is a good separation of the envelopes for *Carlina* of the *involucrata* group, and *Atractylis* of the *cancellata* and *serratuloides* groups. On the other hand, the bioclimatic areas of *Carlina* of the *lanata* group and *Atractylis* of the *delicatula* group are very overlapping.

4. Discussion

The fact that the same species (*A. cancellata*) can present a variable architectural model (sympodial, antheliform or flattened antheliform) according to the conditions is indicative of a kinship between architectures with depressed silhouette, i.e. with secondary axes more developed than the main axis. These 3 categories share an acrotone development and thus a certain similarity in the regulations of growth of the secondary axes. However, in the majority of cases, each species harbors a strict architectural type which makes it easily recognizable in the field. This feature argues that the architectural types are not the answer to climatic conditions but rather represent adaptations against the specific constraints of the various conditions of the environment.

In a preceding work, we showed that in Morocco, the absolute standard deviation of precipitations increases with precipitations, but that the relative standard deviation (or coefficient of variation) decreases with precipitations [17]. In other words, the so called « uncertainty of precipitations » in arid regions [18] means more exactly the « relative uncertainty of precipitations », increasing with aridity.

The inflorescences with convex to plane silhouette (defined

grapes, corymbs) would be favored in sub-humid and humid climates or semi-arid stage with cold winter. In the *A. phaeolepis* type, there is little differentiation between the axes borne by the enrichment and by the inhibition zones, which means that the increase in the cumulated number of capitules will be linear (according to the rank) if the conditions are favorable. The following assumption can be formulated: insofar as precipitations in these types of Mediterranean climates are less “uncertain” than in more arid climates [19, 20], natural selection will favor the architectural types able to produce a rather constant number of capitules according to the year, i.e. a better adjustment of their energy with the average conditions. The quantitative aspect of precipitations acts especially on the vigor of axes borne by the enrichment zone, the duration aspect on the number of axes borne by the inhibition zone with a downward flowering. In this case, these plants privilege the enrichment zone to take advantage of a favorable year, while exploiting the number of secondary axes likely to produce achenes. The increase in the number of capitules varies in a linear way with time, but with a relative simultaneity.

In the sympodial-antheliform type, the cumulated number of capitules increases in an exponential or degree 2 polynomial function according to the secondary axis rank on the enrichment zone, but linearly on the level of the inhibition zone. These plants are usually more frequent in arid or subhumid-humid climates with mild to warm winter, i.e. where there is a strong relative uncertainty of annual precipitations. It is rare that the studied species show a “perfect” example of sympode: generally, several capitules borne by

the secondary axes do not reach their maturity, mostly the upper ones in the species with ascending flowering. Moreover, in more than half of cases, *C. brachylepis* does bear only one secondary axis equipped with more than two capitules. This species, abundant in the arid and semi-arid regions, reaches its limit in Saharan area, *inter alia* because of its late flowering compared to *Atractylis* for example. It is probable that the water reserves in the ground are then insufficient to allow the complete development of a dichasial cyme. I only found 6 samples out of 60, and never in lower arid stage nor in Saharan stage.

As for *Carlina* of the *Mitina* section, *C. racemosa* usually produces more capitules (but smaller) than *C. lanata*. This result tallies well with the fact that this last species is never found in arid stage, contrary to *C. racemosa*. The flattened anthele *A. delicatula* type is frequently represented in Saharan stage. Indeed, in an environment where the pressure of pasture by the herbivores is strong, this architectural type is favored as it allows a renewal of the axes starting from buds at the base [21] and the release of achenes from capitules located close to the ground. It is speculated that in Saharan areas, the probability to be grazed is stronger than in the arid, semi-arid and humid areas. It is difficult to assess this issue by the only consideration of the distribution maps of Mammals in Morocco [22]. Indeed the local herbivorous Mammals (Oryx, Addax, Bubale, and Gazelle) do not seem to play an important role in this respect, their populations having undergone dramatic reductions under man hunting. Those which were introduced by man (Goat, Sheep, and Camels) have the strongest actual action on the vegetation.

In summary, our studies show that the species of the arid and specially Saharan areas share an inflorescence architecture which, by privileging the enrichment zone against the inhibition one, enables them to produce quickly a number of capitules as much larger than precipitations of a given year are higher. The strong pressure of grazing by the domestic mammals introduces a modification towards a basal ramification of the secondary axes. On the other hand, the species with inflorescences with plane to convex silhouette would be favored in wetter conditions. One can generalize these ideas by testing, in the total Cardueae and Lactuceae tribes in Morocco, the adaptive tendency of antheliform to sympodial inflorescences with respect to arid regions. In a preceding paper, it had been shown a positive correlation between the frequency F of the species presenting this type of inflorescence and the relative uncertainty of precipitations [17].

In this work, we can draw a synthetic climagram based on 21 Moroccan localities where the climatic parameters and the frequencies F (fig. 6) are recorded. It shows that the frequency F increases with aridity, especially with mild to warm winters.

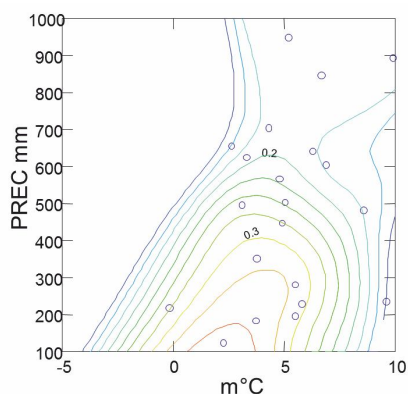


Figure 6. Antheliform and sympodial inflorescences frequency in the bioclimatic space.

Abbreviations. m = Minima means of the coldest months, in °C; Prec = annual rainfall, in mm. The warmer the color, the higher the frequency.

It appears that the tendency illustrated by the examples of *Carlina* and *Atractylis* is well supported by the analysis of the tribes of Lactuceae and Cardueae taken in their entirety. It can be predicted that other families also present adaptations to arid conditions by their inflorescence architecture. In Apiaceae, the *Eryngium* genus gives a good illustration of this tendency, although panicles or grapes are not represented. The most common species in the arid steppes and Saharan ermes (*E. ilicifolium*) has a sympodial inflorescence slightly different from the *A. serratuloides* type, as its main axis presents generally reduced internodes, as in the *A. delicatula* type.

In Zygophyllaceae, the herbaceous genera of Morocco and Sahara also deserve attention [18]. *Peganum harmala* (inflorescence with a rather plane silhouette) is widespread in arid and semi-arid regions limited to the Northern fringe of Sahara, but is absent from really desert conditions. The genera able to colonize the Saharan areas (*Tribulus*, *Setzenia*, *Zygophyllum* and *Fagonia*) present all sympodial inflorescences. However, it does not mean that all the Saharan herbaceous plants have modified their architecture: Resedaceae and Brassicaceae, families relatively well represented in this desert [18], have the same inflorescences as in Europe: racemes.

Apart from the areas subjected to Mediterranean climate, it could be tested if there exist environments where the disturbances are strong enough for replacing uncertainties of precipitations. In a preliminary approach, the examination of plant lists extracted from work of French phytosociologists [23] allowed to note associations where the frequency of antheliform-sympodial

inflorescences is high. It appears that the garden adventitious grasses developed on rich ground (Alliance of Polygono-Chenopodiopolyspermi) are interesting to consider. On the 6 quoted species, 4 present inflorescences with depressed silhouette: *Sonchus oleraceus* and *S. asper* represent the *C. racemosa* type, *Euphorbia helioscopia* (Euphorbiaceae) and *Geranium dissectum* (Geraniaceae) the *A. serratuloides* type. These associations share two characteristics with the Mediterranean arid regions: (i) open environment, and (ii) a strong disturbance, but here caused by the spade of the gardener.

One can hypothesize that, in certain cases at least during evolution of flowering plants, the appearance of anthele and sympodial inflorescences was favored under the constraint of the disturbance of the environment, as the relative uncertainty of precipitations, or the random impact of animals.

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