

## COMPLEX DISPERSAL STRATEGY IN *PICRIS CUPULIGERA* (ASTERACEAE, LACTUCEAE)

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### Abstract

*Picriscupuligera* is an annual taxon of Lactuceae from North Africa living mainly in arid, semi-arid and sub-humid areas and with mild winters. We describe three kinds of dispersal: epizoochory of capitules linked to their peduncles, anemochory of free central achenes of capitules, and barochory of peripheral achenes stuck to receptacle and involucre bracts. The proportion of each kind depends on the habitat, as zoochory is more important in open than in woodl and habitat. Anemochory is the earliest mode of dispersal as it happens as soon as the involucre bracts are dried out. Barochory occurs more progressively and last peripheral achenes are released independently until January.

**Key words:** Zoochory, anemochory, barochory, bioclimatology, heterocarpy.

### INTRODUCTION

*Picriscupuligera* (Durieu) Walp. is an annual plant belonging to the tribe Lactuceae (Asteraceae) [1]. This species was first described from Algeria by Durieu de Maisonneuve in 1846 under the genus *Spitzelia* but was later included in *Picris* subgenus *Spitzelia* Schultz-Bip. in the flora of Algeria [2]. It was also recorded in Tunisia, Morocco and Spain [3]. *Picris* shares plumose pappus at the top of achenes with *Leontodon*, *Hypochaeris*, *Helminthotheca*, *Hedynois*, *Scorzoneroides*, and *Urospermum*. All these genera are classified within the Hypochaeridinae, a subtribe recently revisited by molecular phylogenetic approaches [4], [5].

According to these authors, *Hedynois* is now included in the genus *Leontodon* whereas the former subgenus *Oporinia* of *Leontodon* is separated from *Leontodon* s.s. and renamed as genus *Scorzoneroides*. Moreover, these authors extended the content of *Spitzelia* and they now include the perennial species *P. hispanica* and *P. scabra* in addition to

the annual species *P. cupuligera*, *P. coronopifolia*, *P. willkommii*, and *P. asplenioides*.

Heterocarpy is a feature consisting in the presence of two kinds of seeds on the same plant, allowing a diversification of dispersal modes. It can concern morphology (dimorphism) and/or physiology through differences in dormancy or germination [6], [7], [8]. Heterocarpy is an adaptation to unpredictable conditions which are often associated to arid and desert areas or disturbed habitats [9], [10]. It is assumed that each morph is advantageous for a special type of environmental conditions which vary as a function of years and habitats. Heterocarpy in *P. cupuligera* has long been recognized.

Indeed, in the Flora of Algeria [2], this species was included in the sub-genus *Spitzelia* which gathers annual taxa with dimorph achenes: peripheral ones without a beak surrounded by a scarious cupule and central ones with a long beak and a pappus of plumose hairs.

In a previous work related to Asteraceae [11], we showed that in Morocco, heterocarpy was more frequent in Lactuceae tribe than in Cardueae, and in annual and hemicryptophytic species than in perennial ones. In this paper, we describe an original case where heterocarpy is associated to another dispersal type, epizoochory, by means of the strong hairs born by outer bracts and by deciduous peduncles. The significance of this complex strategy is discussed in the light of bioclimatic constraints.

### Material and Methods

Individuals of *Picris cupuligera* were collected in two sites near Casablanca (Morocco) in June 1985 and May 1986. The first site is an ancient more or less abandoned cemetery (open habitat), where grows a degraded matorral with *Asparagus spp.*, *Chamaerops humilis*, *Asphodelus microcarpus* and *Urginea maritima* (altitude = 50 m, 33°34'42" N and 7°36'24" W). Herbaceous plants are dominant, including Poaceae, Brassicaceae and Asteraceae. The second one is a woodland with stands of *Eucalyptus spp.* in the area of Bouskoura, 10 km south of Casablanca (altitude = 138 m, 33°26'56" N and 7°38'55" W). The spontaneous vegetation is the same but less degraded with shrubs of *Pistacia lentiscus* and *Phyllirea*

*media*.

The collected specimens of *P. cupuligera* were dried and kept in herbarium sheets labeled with date and location and are now stored at the University of Limoges collection. The plant architecture was described according to [12]. The inflorescence is divided in two parts: the upper part (enrichment zone) with an increase in capitule number borne by successive axes and the lower part (inhibition zone) with a very low number of capitules. In order to quantify epizoochory among other types of dispersal, we used a device imitating the coat of a mammal. A small piece of wool was applied on each involucre so the strong hairs of outer bracts grip on it. The wool piece was hanged on a suspension spring that measured the strength necessary to detach the peduncles from the living plant. The length of the peduncle and the strength necessary to split it from the stem were recorded.

The distribution of the species was deduced from our numerous field trips in Morocco during 1985 and 1986. A sample was collected in each locality where the species was present and further kept in herbarium. These data were used to assess the bioclimogram of the species which was drawn according to the method of [13] and [14]. Briefly, the Emberger-Sauvage pluviometric coefficient was

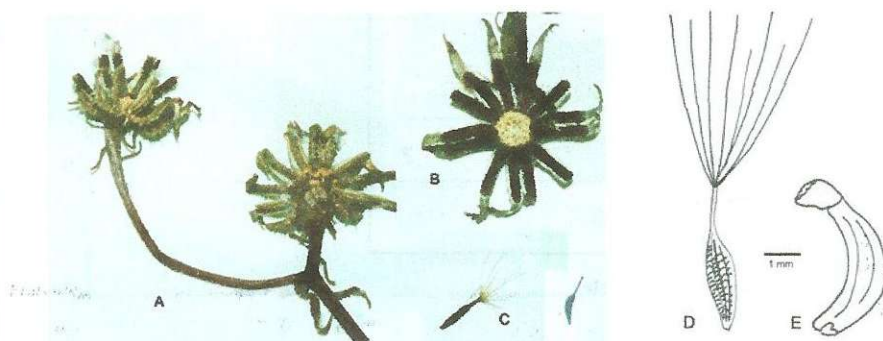
calculated using the formula:  $Q^2 = 3.43 P/(M-m)$ , with  $m$  = minima means of the coldest month (in °C),  $M$  = maxima means of the hottest month (in °C) and  $P$  = annual rainfall (in mm) [15]. The climogram was drawn using SYSTAT 12 [16].

The analyses of covariance (ANCOVAs) were used to compare the strength necessary for the breaking of peduncle between two stations, by considering their length as covariable. All the statistical analyses were performed using PAST 2.17 [17].

### Results

#### Description of achene heteromorphism

The body of central achenes is attenuate in a beak at the apex (about the third to the fourth of total length) and the wall bears longitudinal ribs with around 36 wrinkles. The pappus is composed of about 17 plumose bristles enlarged at the base and 17 thin ones. The body of peripheral achenes is slightly attenuate but never beaked, and is surrounded by a short scarious cupule (fig. 1). The central achenes are independently released as the involucre opens by desiccation, whereas the peripheral ones are clasped by the innermost involucre bracts.



**Figure 1.** Central and peripheral achenes of *Picris cupuligera*. Involucres open when they get dried (A) with outer achenes still attached to the receptacle and innermost bracts (B). Note the strong hairs on the outer bracts. The central achenes (C) have a deciduous pappus. D: central achene; E: peripheral achene.

The mean number of central achenes per capitule is  $34.63 \pm 4.98$  (standard deviation with  $N=16$  different plants). The number of peripheral achenes is more homogenous and we recorded a

mean number of  $12.75 \pm 0.45$  ( $N=13$ ). Their release occurs when the involucre bracts get broken several months later. For example in mid-January at the cemetery station, we considered the *P. cupuligera*

individuals still erect. In the two populations studied, the dispersal of more than 90% of peripheral achenes was already done and Chi2 test supported the homogeneity of results ( $p=0.28$ ).

**Table 1. Remaining peripheral achenes in mid-January at station 1.**

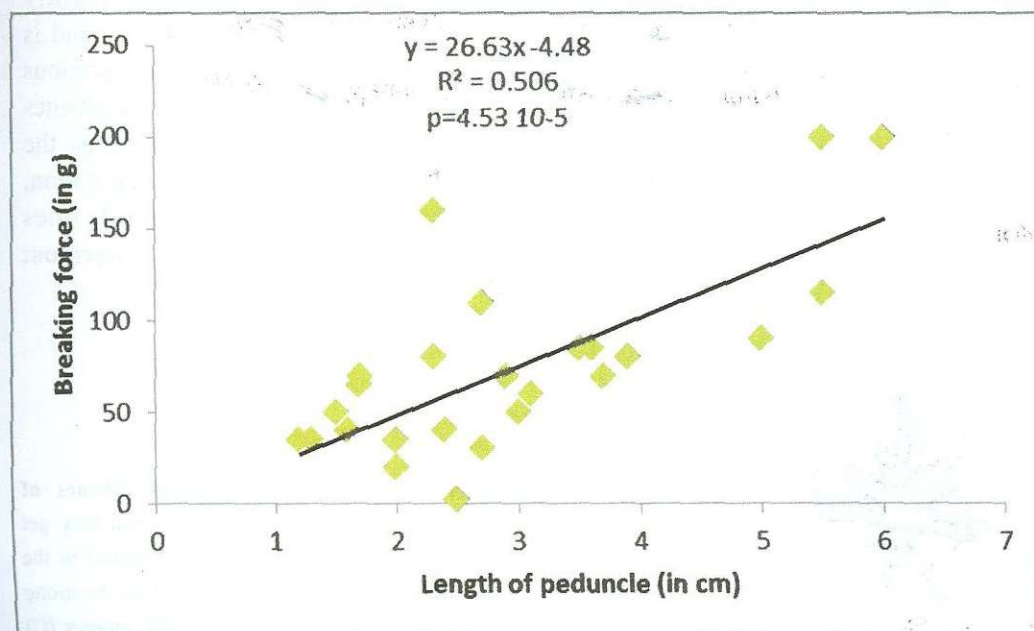
It is assumed that each receptacle retains a mean of 13 peripheral achenes.

	Plant numbers	Number of attached capitules	Theoretical number of peripheral achenes	Observed number of peripheral achenes	Percentages of remaining peripheral achenes
Population 1	18	159	2067	149	7.21
Population 2	12	192	2496	203	8.13

An original feature of *P. cupuligera* is that some capitules are attached to their peduncle and thus possibly dropped off as a whole. As a result, all the peripheral achenes are still linked to the head at the moment of dispersal. We investigated the

variability of attachment of peduncles to the stem. To measure the breaking strength, we took into account 28 measurements made on station 1 and 12 on station 2. Using this dataset, the strength necessary to split the peduncles from the stem

increases with the length of the peduncles ( $p=4.5 \cdot 10^{-5}$ ) (fig. 2). In other words, the shorter the peduncle, the higher the probability of breaking and transport by mammal coat.



**Figure 2. Breaking strength and length of peduncles**

We then compared the values recorded on the plants collected in cemetery and woodland sites. Given the strength-length relationship, we performed an ANCOVA with the same data. We checked the homogeneity of slopes between the two groups ( $F=1.917$ ,

$p=0.175$ ) as it is required for ANCOVAs, and no difference was recorded ( $F_{1,35}=0.004$ ,  $p=0.95$ ). We can conclude that the plants from both sites do not differ by intrinsic constitution of stems or peduncles. Both kinds of plants share the same strength-length of peduncle

relationships. It is interesting to note that the deciduous peduncles are mostly oriented toward the outside of the whole plant (fig. 3). These peduncles are characterized by a thickening at the base of the head.

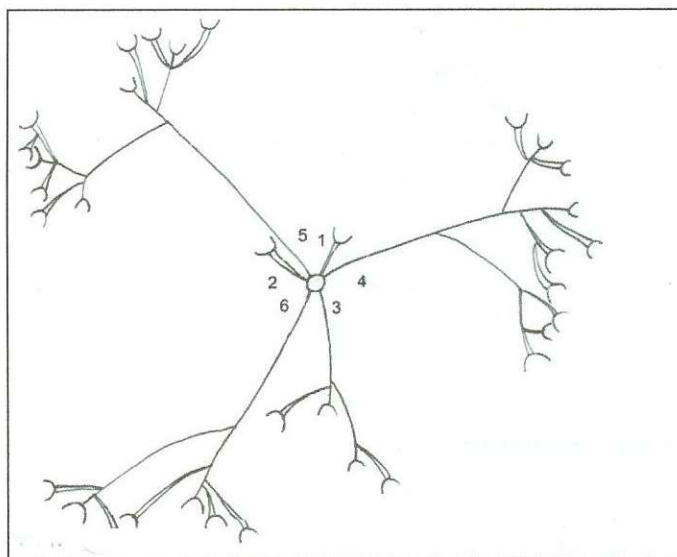


Figure 3. Deciduous peduncles (thickened at the top) and persistent peduncles (others).

The plant is seen from the top. The principal axis corresponds to the wide circle and the order of successive secondary axes are represented by numbers

We then counted the numbers of deciduous peduncles from 10 plants in both stations (fig. 4).

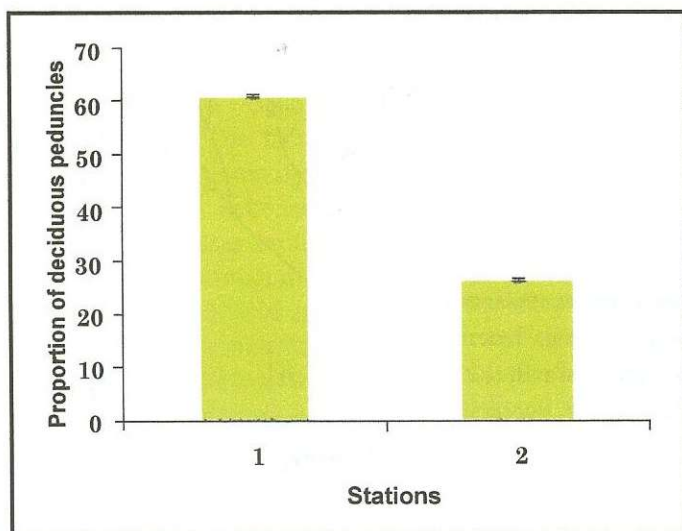


Fig. 4. Proportions of deciduous peduncles in plants of both stations (N=10)

There is a significant greater proportion of deciduous capitules in the station 1 than in station 2 (ANCOVA:  $F=11.45$ ,  $P=0.011$ ).

We then tested whether the lengths of peduncles differed between both stations. Indeed, there is a marginally significant difference (Kruskal-Wallis,  $p=0.063$ ). The

lengths observed in Bouskoura station are longer than in cemetery station. Moreover, there is a significant difference in the proportion of principal axis

corresponding to the inhibition zone (ANOVA:  $N=17$ ,  $F=12.85$  and  $p = 0.002$ , fig. 5).

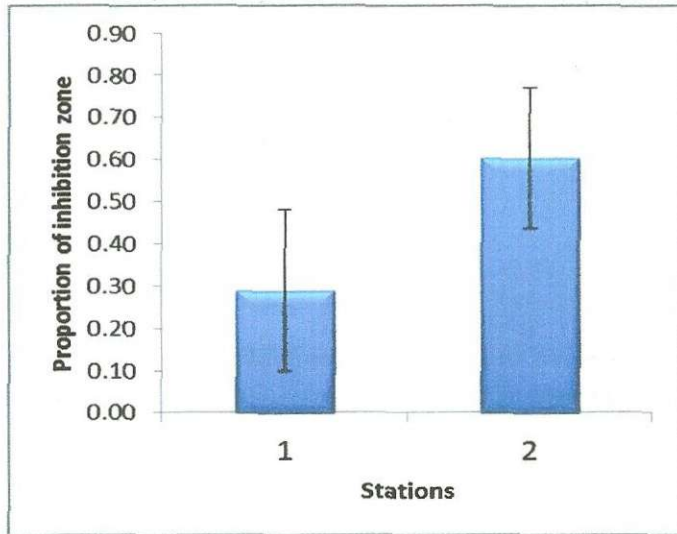


Figure 5. Proportion of inhibition zone in the plants of both stations ( $N=17$ )

We also tested whether there was a significant difference in the divergence angle of the successive ramifications from top to bottom between the plants of both stations. The means calculated with 5 plants from each site are given in table 2. They show that the angle, rather open in the first top ramifications, gets more and more acute downward. However, the angles recorded in station 2 are regularly more acute in station 2 than in station 1 (Wilcoxon,  $p=0.043$ ).

Table 2. Means of divergence angles in the successive ramifications of the principal axis

Order of ramifications	Station 1		Station 2	
	Angle mean	Standarddev	Angle mean	Standard dev
1	66.4	4.98	57	12.55
2	58	9.08	38.6	2.19
3	44	4.18	35.6	3.78
4	56.75	9.43	37.5	3.54
5	56.75	15.67	32	9.90

Wilcoxon  $p = 0.043$

In conclusion, the architectures of the plants from both stations are clearly different, and summarized in fig. 6. The deciduous peduncles are located lower above the ground and more distantly from the principal axis in the case of plants growing in open habitat (station 1) than those of woodland habitat (station 2).

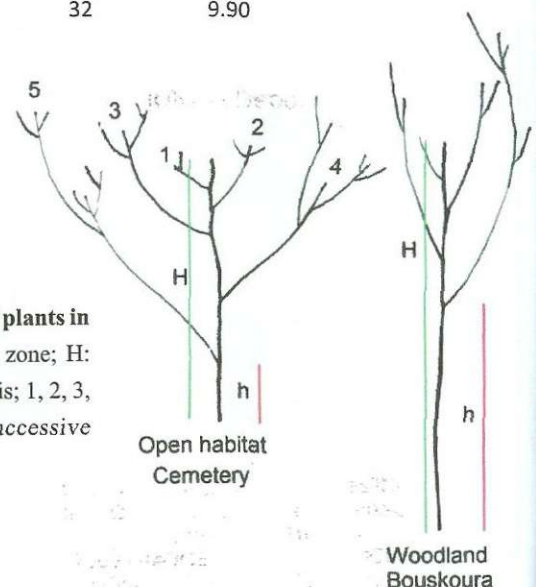
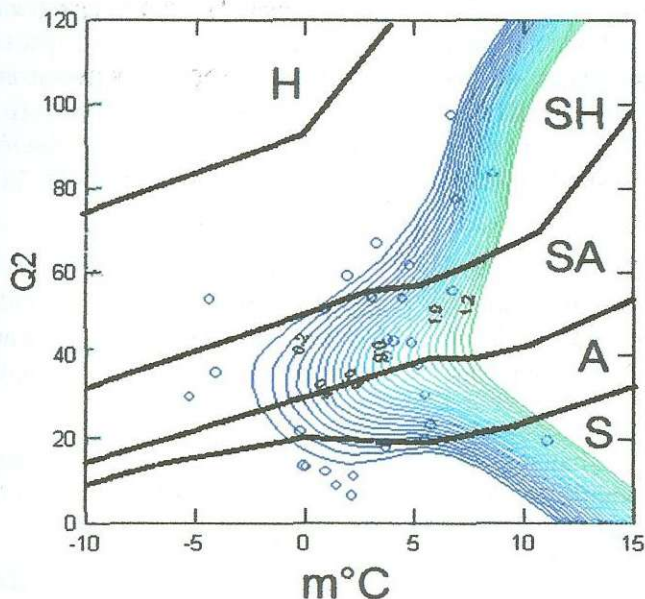


Figure 6. Architectures of plants in both stations. h: inhibition zone; H: total length of principal axis; 1, 2, 3, 4, 5: order of the successive ramifications.

## Bioclimatology

According to fig. 7, *Picriscupuligera* is mainly found in arid, semi-arid and sub-humid stages, with mild winters ( $m > 4^{\circ}\text{C}$ ).



**Figure 7.** Bioclimogram of *Picriscupuligera*. The lighter the blue lines, the higher the probability of presence of *P. cupuligera*. S: saharian stage, A: arid stage, SA: semi-arid stage, SH: sub-humid stage, and H: humid stage.

## Discussion

*Picriscupuligera* is an annual plant showing an original mode of dispersal. Indeed, the relatively common dimorphism of achenes, associated to anemo- and barochory, is enriched by the possibility of epizoochory. It is possible to quantify the theoretical proportion of types of dispersal in open habitats. During the first days after capitule desiccation, the central achenes are the first to be released and brought away by anemochory. They represent about the 75% of total seeds per capitule. The facultative epizoochory allows diversifying the fate of peripheral achenes. The proportion of capitules brought by the fur of mammal is random but the maximum is around 60% in open habitats. So the percentage of barochory is something between 10% (numerous mammals walking around the plant) to 25% (no mammal present).

We demonstrated that epizoochory depends on the plant architecture

since there are deciduous peduncles that are dropped as a whole, bearing all the peripheral achenes of a same capitule at the same time. We recognize here the synaptospermy described by Zohary [18] in the Near-East (several seeds stuck together). However, this feature is facultative and varies according to the habitat. The shade due to woodlands has an effect on the shape of the plants by comparison to individuals grown in sunny habitats: (i) the secondary axes are closer to the principal axis, (ii) the axes bearing the deciduous peduncles are more elevated above the ground, and (iii) the peduncles are generally longer. As a result, the deciduous peduncles are about twofold less frequent and less accessible to the fur of mammals than in open habitat. So the epizoochory is predicted to be as at least twofold more effective for dispersal in open than in woodland habitat, assuming an equal abundance of mammals in both environments.

Barochory should be the system of security as the mother plant found favorable conditions to develop and produce seeds. However this strategy is not appropriate in the case of arid environment. Indeed, the water supply is low from the end of spring (flowering time) until the first autumn rainfalls and it would lead to a strong competition between the seedlings. At this time, it is unlikely that the released achenes can germinate due to strong dormancy. As several Hypochaeridinae living in Mediterranean climates, we hypothesize that the germination occurs during early spring rainfalls [8], [19]. Of note, we showed that most peripheral achenes were already dropped off in mid-January. It means that their release is progressive, limiting the attraction of harvester ants such as *Messor sp.* in autumn [20]. The possibility to escape from competition is enhanced by epizoochory.

In conclusion, the climatic constraints prevailing in arid and semi-arid stages have favored the development of complex dispersal strategies. Epizoochory, an original feature of *Picriscupuligera*, contributes to limit the intraspecific competition and the predation by harvester ants which are very abundant in these areas.

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