

Not only size matters: achene morphology affects time of seedling emergence in three heterocarpic species of *Anacyclus* (Anthemideae, Asteraceae)

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Abstract

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The production of two or more distinct fruit types by an individual, i.e. heterocarpy, is considered as a mixed dispersal strategy in which a proportion of the offspring is able to colonize new sites, whilst others remain near the maternal location. Here, we aimed to explore the effects of achene morphology (winged vs. unwinged achenes) and achene size—measured here as achene mass—on post-dispersal life-history traits (probability and time of seedling emergence) in three heterocarpic *Anacyclus* species (Anthemideae, Asteraceae). Morphology, size and germination performance were studied in achenes from six populations of *Anacyclus clavatus* (Desf.) Pers., *A. homogamos* (Maire) Humphries, and *A. valentinus* L. Our results show that achene morphology and size were related to their position within the capitulum, such that outer, winged achenes were significantly heavier than the inner, unwinged ones. Additionally, winged achenes germinated faster than unwinged ones. This pattern may be related to the sequential achene time of release displayed by these species. Finally, our findings cast doubt on the role of wings as structures that favor dispersal by wind in these three species of *Anacyclus*.

Keywords: bet-hedging, Compositae, heterocarpy, mixed strategy, position effects, weeds, winged fruits.

INTRODUCTION

Seed dispersal is mainly determined by fruit characteristics, which usually vary continuously within an individual plant (Herrera, 2009). However, some plants produce two or more defined fruit types, a condition known as heterocarpy, in which distinct fruit morphs may show different behavior for dispersal, germination recruitment or seedling survival (Imbert, 2002). Heterocarpy is usually interpreted as a bet-hedging or mixed strategy in which different seed subsets of one individual may successfully germinate under different conditions in time and space. This offers the chance to colonize new sites, free from sibling competition or other local sources of stress, whereas the remainder of the offspring stays in the same habitat (Gadgil, 1971; Levin & al., 1984; Schoen & Lloyd, 1984; Venable & Brown, 1993; Imbert & Ronce, 2001). Various authors have proposed that a bet-hedging strategy is likely to be favored in temporally variable environments because it increases geometric fitness, even if indivi-

Resumen

Torices, R., Agudo, A. & Álvarez, I. 2013. No sólo importa el tamaño: la morfología del aquenio afecta al tiempo de emergencia de la plántula en tres especies heterocárpicas de *Anacyclus* (Anthemideae, Asteraceae). *Anales Jard. Bot. Madrid* 70(1): 48-55 (en inglés).

La producción de dos o más tipos de frutos diferentes por un mismo individuo, i.e. heterocarpi, es considerada como una estrategia mixta de dispersión en la que una parte de la descendencia es capaz de colonizar nuevos sitios, mientras que la otra permanece cerca de la planta madre. En este trabajo, nuestro objetivo fue explorar los efectos de la morfología del aquenio (aquenios alados vs. no alados) y de su tamaño—medido aquí como masa del aquenio—en la etapa del ciclo de vida siguiente a la dispersión (probabilidad de germinación y tiempo de emergencia de las plántulas) de tres especies heterocárpicas del género *Anacyclus* (Anthemideae, Asteraceae). Se estudió la morfología, el tamaño y la germinación en aquenios de seis poblaciones de *Anacyclus clavatus* (Desf.) Pers., *A. homogamos* (Maire) Humphries y *A. valentinus* L. Nuestros resultados indican que tanto la morfología del aquenio como su tamaño estaban relacionados con su posición en el capítulo, de manera que los aquenios más externos—alados—eran significativamente más pesados que los internos—sin alas—. Además, los aquenios alados germinaron más rápidamente que los no alados. Este patrón puede estar relacionado con la liberación secuencial de los aquenios que ocurre en estas especies. Por último, nuestros resultados ponen en duda la función de las alas como estructuras que favorecen la dispersión por viento de los aquenios en estas tres especies de *Anacyclus*.

Palabras clave: bet-hedging, Compositae, heterocarpi, estrategia mixta, efectos de posición, malas hierbas, frutos alados.

dual phenotypes may have a relatively lower mean fitness (Gillespie, 1977; Venable, 1985; Venable & al., 1987; Venable, 2007; Simons, 2011; Tielbörger & al., 2012).

Among members of Asteraceae, the occurrence of heterocarpy is relatively high (Mandák, 1997; Imbert, 2002). Heterocarpic species in this family usually produce different achene morphs within the same capitulum (reviewed in Imbert, 2002), although exceptions in which achene variation occurs between aerial and subterranean capitula are known in *Gymnarrhena micrantha* (Koller & Roth, 1964) and *Catananche lutea* (Ruiz de Clavijo, 1995; Ruiz de Clavijo & Jiménez, 1998), and in *Centaurea melitensis* (Porrás & Muñoz, 2000) between cleistogamous and chasmogamous capitula. Apart from these exceptions, most of achene variation is found within capitula. Besides variation in morphology, achenes may also vary markedly in size (Venable & al., 1987; McGinley, 1989; Maxwell & al., 1994; Imbert & al., 1996; Van Mólken & al., 2005; Brändel, 2007). Both traits, achene size and morphology, usually covary, such that achenes without dispersal structures are usual-

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ly the heaviest ones, whereas those adapted for greater dispersal are generally lighter (McEvoy, 1984; Tanowitz & al., 1987; Venable & al., 1987; Imbert & al., 1996; Imbert & Ronce, 2001; Brändel, 2004, 2007; Bastida & Menéndez, 2004, Bastida & al., 2010; among others). With regard to germination performance, recent research suggests that variation in achene size may be the main driver of divergent behavior exhibited by seeds from different achene morphs (Van Mólken & al., 2005; Torices & Méndez, 2010). Achene size can also affect performance in post-dispersal life-history traits, particularly in competitive conditions (McEvoy, 1984; Andersson, 1996; Ruiz de Clavijo & Jiménez, 1998; Meyer & Carlson, 2001; Ruiz de Clavijo, 2005; Van Mólken & al., 2005; Benard & Toft, 2007). Alternatively, seeds might have different behaviors in germination that are linked to the achene morphology, regardless of size, and which might also affect later stages in plant development (Imbert, 2002). In order to distinguish which of these situations applies in any particular species, we need to determine whether the achene morphology within a capitulum has direct effects on post-dispersal life-history traits, or whether this effect is solely mediated by achene size.

In spite of the high incidence of heterocarpy in the Asteraceae and its known influence on dispersal ability and germination performance, the proximate causes of achene variation remain unknown. As part of an ongoing project focused on the reproductive biology and population genetics of the *Anacyclus clavatus*, *A. homogamos* and *A. valentinus* species complex, we studied achene size variation and seedling emergence in these three species. *Anacyclus* is a Mediterranean genus of mostly annual weedy herbs that show an extraordinary variation in flower, achene morphology and sexual expression within capitula and among species (Bello & al., 2013). Achenes in *Anacyclus* vary from winged dorsiventrally flattened achenes to unwinged, from the outer to inner positions of the capitulum. Similar winged achenes are found in other Asteraceae (Anderberg & al., 2007; Manchester & O'Leary, 2010), mostly in the tribes Calenduleae (*Garuleum*, *Norlindbia*, *Triptaris*, etc.) and Heliantheae (*Silphium*, *Verbesina*, *Wedelia*, etc.). As far as we are aware, no studies have been conducted on the role of wings in these achenes. Bastida & al. (2010) argued that the winged achenes in *Anacyclus radiatus* Loisel. may favor dispersion by wind. Bastida & Menéndez (2004) found that in *A. radiatus* weight differ-

ences between the central unwinged achenes and the peripheral winged ones were not significant and also both morphs had non-dormant seeds.

We aimed to explore the effects of achene morphology (presence vs. absence of wings in achenes) and achene size on two important post-dispersal life-history traits in three *Anacyclus* species: probability and time of seedling emergence. Finally, we discuss the implications that winged achenes may have on different dispersal mechanisms and germination performance with regard to bet-hedging strategies in *Anacyclus* life-history.

MATERIAL AND METHODS

Study species and plant material

Morphology, size and germination performance were studied in achenes from a total of 6 different natural populations in *Anacyclus clavatus*, *A. homogamos*, and *A. valentinus* (Table 1). A total of 9-10 mature capitula of several individuals in each site were collected and preserved in darkness at -4°C with silica gel until their use.

These three species (Fig. 1) occur in Western Mediterranean and their distribution areas partially overlap. *Anacyclus clavatus* is present throughout the Mediterranean both in coastal and inland areas, while *A. homogamos* is mainly restricted to inland areas of Morocco and Algeria, and *A. valentinus* is found in coastal areas throughout the Western Mediterranean (Humphries, 1979; pers. obs.). In areas where these species coexist, morphological variation of flowers increases remarkably (e.g., the presence or absence of ray flowers within populations). In *A. homogamos* ray flowers are always lacking and all flowers are bisexual and tubular (i.e. hermaphroditic capitula), while *A. clavatus* and *A. valentinus* present female flowers in the periphery and hermaphroditic disc ones in the rest of the capitulum (i.e. gynomonocious capitula). Furthermore, while *A. clavatus* shows female ray flowers, in *A. valentinus* these are inconspicuously rayed to rayless and fewer in number.

Achene position and size

Each capitulum was manually opened up to separate the achenes, which were classified depending on their relative position within each capitulum in one of 5 categories (from the

Table 1. Sites and sampling for the three studied species of *Anacyclus*.

Species	Origin/Voucher	Sampling
<i>A. clavatus</i>	Spain: Granada, Carchuna (36°41'49"N; 3°27'33"W), 13 m, <i>Agudo 1</i>	one capitulum from each of 10 individuals (late summer 2011)
	Spain: Madrid, Miraflores de la Sierra (40°47'36.45"N; 3°43'46.97"W), 883 m, <i>Álvarez 2173</i>	one capitulum from each of 10 individuals (early autumn 2011)
<i>A. homogamos</i>	Morocco: Imouzzar (31°19'55"N; 7°24'32"W), 2224 m, <i>Gonzalo 1275</i>	10 capitula from an unknown number of individuals (summer 2009)
	Morocco: Asni (31°15'4"N; 7°58'40"W), 1160 m, <i>Álvarez 2115</i>	9 capitula from an unknown number of individuals (late spring 2010)
<i>A. valentinus</i>	Spain: Girona, Castelló d'Empuries (42°15'47.2"N; 3°7'45.5"E), 0 m, <i>Álvarez 2059</i>	10 capitula from 3 individuals (summer 2009)
	Spain: Málaga, Iznate (36°46'35"N; 4°10'45"W), 285 m, <i>Álvarez 2137</i>	one capitulum from each of 9 individuals (late summer 2011)

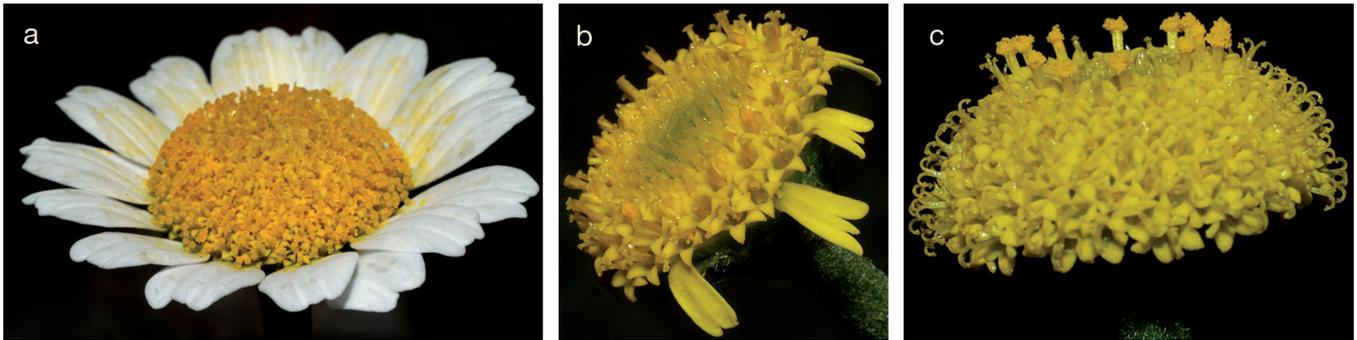


Fig. 1. Morphological variation among the capitula of the studied species of *Anacyclus*: **a**, *Anacyclus clavatus*; **b**, *A. valentinus*; **c**, *A. homogamos* (photograph: J. Fuertes).

outermost positions to the innermost): (1) winged, and produced by female peripheral flowers (only present in *A. valentinus* and *A. clavatus*), (2) outermost winged, (3) innermost winged, (4) outermost unwinged, and (5) innermost unwinged. Achene size was measured as achene mass. Since achenes were very light (< 0.1 mg), groups of ten were weighed for each category in all capitula using a Kern ABJ electronic precision balance (0.1 mg).

Achene morph and seed germination

Our aim was to study seed germination behavior in clearly distinct achene morphs: winged vs. unwinged achenes. Consequently, we selected only the outermost achenes which displayed the largest wings (excluding those achenes from female flowers) so as to have the same kind of achenes across all species, since *A. homogamos* does not have female flowers, and the innermost achenes, which never showed wings (Fig. 2). Five fertile achenes (i.e. achenes that were slightly swollen and hard, resistant to tweezers pressure) of each category in each capitulum were selected for study totaling 580 achenes. They were sowed on wet filter paper into Petri dishes and maintained under a 16h light, 8h dark regime and temperature ranging 10°-27°C in a glasshouse at the Real Jardín Botánico, CSIC. Filter papers were kept moist throughout

the study. The experiment was initiated on 20th January 2012 and seed germination was recorded daily until the experiment was terminated at 120 days.

Statistical analyses

We evaluated how position, which was completely correlated with achene morphology, influenced achene size, and afterwards, whether achene morphology and/or achene size affected seed germination traits. Firstly, to assess the effect of the achene position/morphology on achene size, we fitted Generalized Linear Mixed Models (GLMMs), via restricted maximum likelihood (Patterson & Thompson, 1971). GLMMs were employed because they provide a flexible way to model traits allowing the distinction between fixed and random factors in the model at the same time vs. a standard linear modeling. Satterthwaite's method was used to determine the approximate denominator degrees of freedom for these tests (Verbeke & Molenberghs, 1997). The explanatory variables included in the model were achene position, site and its interaction (achene position × site), whereas capitulum was included as a random factor. The response variable, achene size, was modeled using a gamma distribution with a log link function.

Secondly, we also evaluated the effects of achene morphology and achene size on the probability of seed germination and time of germination by fitting GLMMs. In these two cases the explanatory variables were achene size, achene morphology, site and its interaction (achene morphology × site). Again, the capitulum was the random factor. The probability of germination was modeled using a binomial distribution with a logit link function and time of germination was modeled using a Poisson distribution with a log link function. A different model for each species was fitted. All models were fitted using the GLIMMIX procedure of SAS (SAS Institute, Cary, NC) with the DIFF option in the LSMEANS statement.

RESULTS

Achene size variation

Achene size decreased from outermost/winged to innermost/unwinged positions in all three species at all studied sites (Table 2, Fig. 3). Furthermore, achene size also differed within two of the three species (Table 2). In *A. clavatus*, achenes

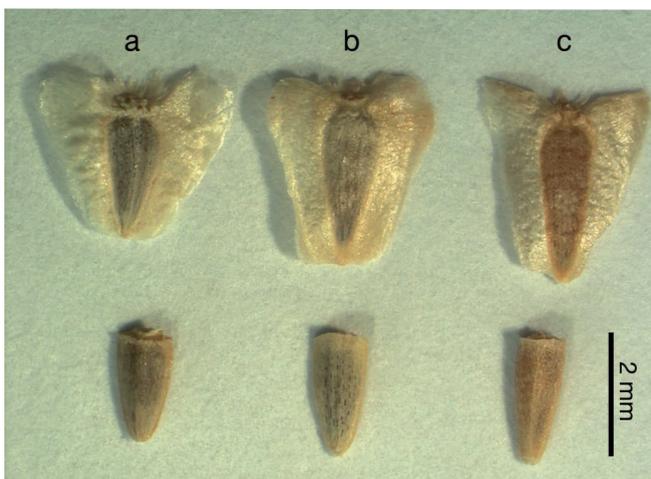


Fig. 2. Heterocarpy (winged vs. unwinged) in achenes of the studied species: **a**, *Anacyclus clavatus*; **b**, *A. valentinus*; **c**, *A. homogamos*.

Table 2. Effects of flower position and population on achene size of three *Anacyclus* species.

Fixed factors	<i>A. clavatus</i>		<i>A. valentinus</i>		<i>A. homogamos</i>	
	F	P	F	P	F	P
Position	70.15 _{4, 71}	< 0.0001	35.00 _{4, 62.04}	< 0.0001	20.37 _{3, 39}	< 0.0001
Site	4.07 _{1, 18.0}	0.0589	5.44 _{1, 16.92}	0.0322	0.88 _{1, 13}	0.365
Position × Site	1.26 _{4, 71}	0.2953	0.84 _{4, 62.04}	0.5034	1.38 _{3, 39}	0.2618
Random factor	Estimate	SE	Estimate	SE	Estimate	SE
Capitulum	0.047	0.017	0.050	0.019	0.035	0.015
Sample size	99		89		60	

Data represent the Wald-type F-statistic with the degrees of freedom as subindex for fixed factors (the sign indicating the direction of the effects), and the estimate for covariance parameter and its standard error for the random factor.

nes from Carchuna were significantly heavier than those from Miraflores de la Sierra, and likewise in *A. valentinus* those from Iznate were heavier than those from Castelló d'Empuries. Despite these differences, a general tendency for achene weight to decline towards inner positions was observed for each respective pair of sites (Fig. 3). In *A. homogamos* this tendency was less marked since only the innermost achenes were statistically different from the rest (Fig. 3).

Seed germination probability of winged vs. unwinged achenes

Mean percentage of total germination in all species analyzed was relatively high (74 %), while variation in observed germination within and among species was low. Seeds of winged vs. unwinged achenes did not show different germination probabilities for most of the sites (Table 3, Fig. 4a), with the exception of seeds of winged achenes from one site of *A. clavatus* (Miraflores) that germinated at a significantly lower percentage than unwinged ones, although seeds of winged achenes from this site germinated at the very high

rates found in the other two species (Fig. 4a). Achene size influenced positively the probability of seed germination in one species, *A. clavatus* (Table 3).

Additionally, our analyses indicated that the probability of germination was significantly different between sites within species (i.e.: 54 % in Carchuna vs. 91 % in Miraflores de la Sierra for *A. clavatus*; 66 % in Asni vs. 94 % in Imouzzar for *A. homogamos*; 56 % in Iznate vs. 85 % in Castelló d'Empuries for *A. valentinus*; Table 3).

Seedling emergence time of winged vs. unwinged achenes

Seeds showed an extraordinary variation in germination times, from one day after being sowed to more than 90 days. This variation was associated to achene morphology within each capitulum, so that in general, seeds of winged achenes germinated much faster than those of unwinged ones (Table 4, Fig. 4b). Only achenes of *A. clavatus* from Miraflores did not show this pattern (Fig. 4b). Time of seedling emergence varied significantly among sites in *A. clavatus* and *A. homo-*

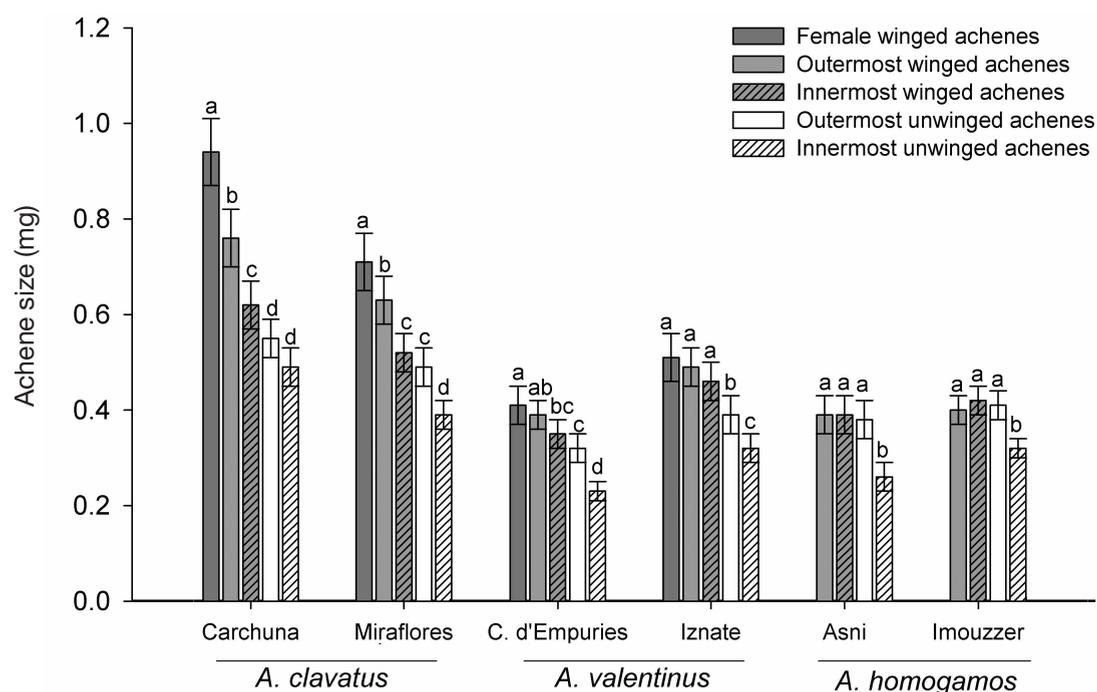


Fig. 3. Least-square means (\pm SE) of achene size of three species of *Anacyclus* from two sites each, and from different position within capitula. Means sharing a superscript were not significantly different at the $P < 0.05$ level.

Table 3. Effects of achene morphology, achene size, and population on germination probability of three *Anacyclus* species.

Fixed factors	<i>A. clavatus</i>		<i>A. valentinus</i>		<i>A. homogamos</i>	
	F	P	F	P	F	P
Morphology	0.73 _{1, 45.8}	0.3983	0.23 _{1, 68.6}	0.6361	2.54 _{1, 149}	0.1131
Site	13.29 _{1, 18.5}	0.0018	4.71 _{1, 15.6}	0.0458	11.88 _{1, 11.9}	0.0653
Morphology × Site	7.91 _{1, 190}	0.0054	1.47 _{1, 188}	0.2267	0.64 _{1, 149}	0.4239
Achene size	+ 6.27 _{1, 24.1}	0.0194	0.25 _{1, 23.51}	0.6240	0.00 _{1, 26.3}	0.9840
Random factor	Estimate	SE	Estimate	SE	Estimate	SE
Capitulum	1.725	1.086	1.279	0.793	1.140	1.048
Sample size	195		193		154	

Data represent the Wald-type F-statistic with the degrees of freedom as subindex for fixed factors (the sign indicating the direction of the effects), and the estimate for covariance parameter and its standard error for the random factor.

gamos, but not in *A. valentinus* (Fig. 4b; Table 4). Thus, those sites having the fastest germinating seeds (Miraflores and Imouzzar) also showed smaller differences in germination time between seeds of winged vs. unwinged achenes (Fig. 4).

Achene morphology influenced the time of seedling emergence. However, whilst achene size had no significant effect in *A. homogamos*, in *A. valentinus* and *A. clavatus*, both achene size and morphology significantly influenced seedling emergence times, although in *A. clavatus* the effect of achene

morphology also depended on the site (Table 4). Beyond the significant effect of achene size on emergence time in these two species, achene morphology, with the exception of *A. clavatus* at the Miraflores site, also affected seedling emergence times, indicating that achene morphology could have a direct effect on the timing of germination independent to that of achene size in these three species (Table 4).

DISCUSSION

Achene size and morphology: their implications in dispersal

Our results show that in these three species of *Anacyclus*, achene size is related to position on the capitulum, so that outer achenes are significantly heavier than inner ones, as commonly occurs in other heterocarpic Asteraceae (McEvoy, 1984; Venable & al., 1987; McGinley, 1989; Maxwell & al., 1994; Imbert & al., 1996; Imbert, 2002; Brändel, 2007; Sun & al., 2009; Filho & Takaki, 2011; but see Rocha, 1996). Usually, in such heterocarpic species, variation in achene size and position is also correlated to the presence or absence of dispersal structures within the same capitulum. In *Anacyclus clavatus*, *A. homogamos* and *A. valentinus*, winged achenes were heavier than unwinged ones. This situation seems contrary to that found in most heterocarpic species in which achenes presenting structures to favor dispersion by wind (e.g. pappus) are the lightest. Therefore, the role of achene wings in *Anacyclus* dispersal is unclear. Although in *A. radiatus* achene size does not vary within a capitulum, Bastida & al. (2010) suggest that winged achenes in this species might be secondarily dispersed by wind.

Winged fruits and/or seeds are considered to be wind dispersed because wings reduce the descent rate of diaspores (Harper, 1977; Van der Pijl, 1982; Cousens & al., 2008). Although morphology may help to understand how diaspores disperse, the conventional assignment of a plant species to a particular mode of dispersal based only on the morphology of its diaspores could result in misleading conclusions (Tackenberg & al., 2003). Several lines of evidence indicate that wind may be only one of several possible vectors of dispersal of *Anacyclus* achenes. Firstly, the very low height of *Anacyclus* species (almost always below 1 m) limits the effective dispersal by wind, since wind dispersal is strongly correlated with plant height (Thomson & al., 2011). Secondly, in *Anacyclus*, achenes are protected by the persistent involucre bracts such

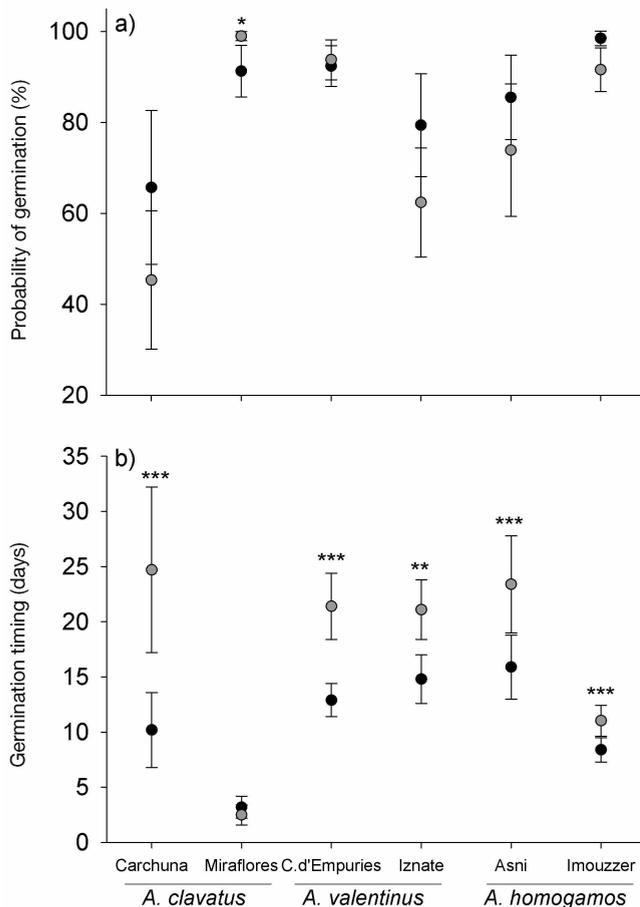


Fig. 4. Least-square means (\pm SE) of a) probability of germination, and b) germination timing of winged (black) and unwinged (grey) achenes of three species of *Anacyclus* from two sites each. Significant differences among winged and unwinged achenes are shown above each site (* < 0.05, ** < 0.01, *** < 0.001).

Table 4. Effects of achene morphology, achene size, and population on time of seedling emergence of three *Anacyclus* species.

Fixed factors	<i>A. clavatus</i>		<i>A. valentinus</i>		<i>A. homogamos</i>	
	F	P	F	P	F	P
Morphology	2.03 _{1, 147}	0.1563	19.47 _{1, 151}	< 0.0001	22.06 _{1, 133}	< 0.0001
Site	15.92 _{1, 17.4}	0.0009	0.12 _{1, 18.9}	0.7299	10.06 _{1, 13.2}	0.0072
Morphology × Site	47.79 _{1, 147}	< 0.0001	3.30 _{1, 151}	0.0714	1.20 _{1, 133}	0.2750
Achene size	-42.30 _{1, 147}	< 0.0001	-17.21 _{1, 151}	< 0.0001	1.64 _{1, 133}	0.2022
Random factor	Estimate	SE	Estimate	SE	Estimate	SE
Capitulum	0.799	0.304	1.226	0.047	0.150	0.062
Sample size	152		156		138	

Data represent the Wald-type F-statistic with the degrees of freedom as subindex for fixed factors (the sign indicating the direction of the effects), and the estimate for covariance parameter and its standard error for the random factor.

that dry capitula become resistant structures that may remain on dead plant for long periods of time, resulting in an aerial seed bank (Bastida & al., 2010; pers. obs.). This type of capitulum is present in other Asteraceae that grow in arid and semi-arid environments (Zohary, 1950), in which moisture seems the main factor for achene release (i.e., ombrohydrochory). Achenes are retained in the capitula until the rainy season, and are then sequentially released during different periods of rain (Gutterman & Ginott, 1994, in *Asteriscus pygmaeus* (DC.) Coss. & Durieu; and Aguado & al., 2012, in *Anthemis chrysantha* Gay). This mechanism may be advantageous in fluctuating environments such as Mediterranean Climate zones because it increases the probability of establishment during different pulses of precipitation when the likelihood of establishment success is maximal (Gutterman, 1994; Peters & al., 2009). A similar mechanism was described in *A. radiatus* (Bastida & al., 2010), and observed in other *Anacyclus* species, in which achenes dampened by rain are released centripetally, so that unwinged inner achenes may be liberated several months after the outermost. Consequently, it is expected that heavy rains rather than winds may be the main dispersal vector in all such ombrohydrochorous species. Furthermore, small diaspores, such as *Anacyclus* achenes, usually show a high capacity to float which may allow secondary dispersal by temporary watercourses (e.g. Telenius & Torstensson, 1989; Redbo-Torstensson & Telenius, 1995; Fumanal & al., 2007; Cousen & al., 2008; Lu & al., 2010). Finally, capitula with some achenes persisting (the aerial seed bank) can be observed after the rainy season when conspecific individuals are in flower. These capitula also might act as dispersal units attached to animals (goats, sheep, etc.) or by human activity (transport by roads and/or railroad). In this way, various agents may contribute to achene dispersal apart from winds, and the effective dispersal of each achene morph will depend on which dispersal agent(s) is predominant.

The effects of achene morphology on seedling emergence

Achene morphology and size influenced different stages of the post-dispersal life-history traits in these *Anacyclus* species, supporting previous findings on direct and indirect effects. The probability of seed germination was mainly related to achene size rather than achene morphology in *A. clavatus*. Within an individual, seeds of larger achenes usually showed a higher probability of germination than those of smaller ones

(Rai & Tripathi, 1982; Pandey & Dubey, 1988), regardless of the achene dispersal ability (McEvoy, 1984). Such differences in germination have been mainly attributed to seed size rather than to differences in achene morphology (Van Mólken & al., 2005).

In contrast, timing of seedling emergence in all the studied species was directly influenced by morphology. Thus, independently of achene size, seeds of winged achenes germinated faster than those from unwinged ones. This pattern may have resulted from a coupling of seedling emergence to the sequential mechanism of capitulum opening and achene release displayed by these species. Consequently, we would expect a divergent selection on seedling emergence times of outer winged achenes vs. inner unwinged ones, leading to a mixed strategy in germination. However, since morphology and position within capitula are fully coupled, we cannot disentangle at present whether the observed effects should be solely attributed to achene morphology or to its position within a capitulum. To answer this question, manipulative experiments on wing size would be needed to assess the potential effects of winged morphology, achene position and achene size on emergence times in this genus.

The differences in the timing of seedling emergence of winged vs. unwinged achenes may also influence the potential dispersal distance of each achene morph. If the main dispersal agent is a passive one such as water and/or wind, then, the time of exposure to dispersal vectors might influence the final ability of achieving longer distances, such that unwinged achenes have more time to be secondarily dispersed once they have been released from capitula. By contrast, seed of winged achenes germinate quickly, sometimes within 24 h, thus reducing the probability of being secondarily long-dispersed. This reduction in the probability of secondary dispersal occurs in other species with diaspores released by rains in harsh environments (Parolin, 2006). Thus, contrary to expectation, the heavier winged achenes might achieve shorter, or at least similar distances to the unwinged and lighter ones. Whether achene release and achene variation in emergence times are adaptive strategies developed through selection to cope with unpredictable rains and disturbed habitats, we would expect that both traits (1) vary along a gradient of unpredictability in rains, and (2) were heritable in some way.

An alternative explanation for the rapid germination of winged achenes might be an adaptive response triggered by competence with neighbors. It is expected that accelerated

germination is selected when competition in the neighborhood is likely to be high (Orrock & Christopher, 2010). In another Asteraceae, *Crepis sancta*, early emergence of heavier achenes provides a competitive advantage that might have been selected to cope with sibling competition (Dubois & Cheptou, 2012). Thus, winged achenes may be adapted to compete with siblings rather than to be long dispersed since they are able to germinate rapidly. But then, does having wings have any adaptive significance beyond dispersal? Wings might contribute to the ecophysiological mechanism by means of which the time of seedling emergence is controlled, because they are membranous expansions of the pericarp that increase the surface through which water and gas can enter into the embryo to initiate germination. It is known that the timing of germination can be influenced by the pericarp anatomy of achenes (Imbert, 2002). For instance, thick pericarps restrict gas exchange and water absorption by the embryo tissue (McEvoy, 1984; Tanowitz & al., 1987; Prinzie & Chmielewski, 1994).

Despite our lack of knowledge of the effective dispersal agent(s) for each achene morph type, several traits (i.e., high percentage of germination, non-dormancy, fast seed germination rate of the first subset of achenes released, lack of a seed soil bank, and differences in seedling emergence coupled with achene release) are consistent with a bet-hedging strategy that ensures progeny establishment in different optimal germination frames.

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