American Journal of Botany
Celebrating 100 years 1914–2014

American Journal of Botany 101(5): 892–898. 2014.

THE EFFECTS OF ACHENE TYPE AND GERMINATION TIME ON PLANT PERFORMANCE IN THE HETEROCARPIC *ANACYCLUS CLAVATUS* (ASTERACEAE)[1]

ANA AFONSO[2], SÍLVIA CASTRO, JOÃO LOUREIRO, LUCIE MOTA, JOSÉ CERCA DE OLIVEIRA, AND RUBÉN TORICES

Centre for Functional Ecology and Department of Life Sciences, Faculty of Science and Technology, University of Coimbra, Calçada Martim de Freitas, 3001-401 Coimbra, Portugal

- *Premise of the study:* In heterocarpy, fruits with different morphologies have been associated with alternative strategies of dispersal, germination, dormancy, and seedling competitive ability. In heterocarpic species, it is common to find fruits with competitive or dispersal syndromes. The competitive advantage of nondispersing fruits has been frequently attributed to their larger size, but recent studies have suggested that this could also be mediated by germination time. The main objective of our study was to investigate which factor, fruit type or germination time, most affects plant performance and, consequently, competitive ability, using the heterocarpic species *Anacyclus clavatus*.
- *Methods:* To explore the effects of achene type and germination time on plant performance, we followed an innovative experimental approach including two experiments: one allowing for differences in germination time, and the other evaluating the effect of achene type alone by synchronizing germination time.
- *Key results:* A significant effect of germination time on several postdispersal life-history traits was observed: Achenes that germinated earlier produced plants with higher biomass and reproductive effort. When germination time was controlled, no significant differences were observed in any of the traits.
- *Conclusions:* The competitive advantage of achenes with different morphologies was mainly mediated by germination time and not by differences in size or other intrinsic traits. The consequences of these results are discussed in light of the dispersal–competition trade-off. Our experimental approach (i.e., the synchronization of germination time) revealed the importance of manipulative experiments for testing the effects of germination time on plant survival and performance.

Key words: achene type; *Anacyclus clavatus*; biomass; competitive ability; dispersal ability; gynomonoecy; heterocarpy; reproductive effort; winged fruits.

Heterocarpy is a strategy in which the reproductive output of an individual is partitioned between two or more groups of morphologically and ecologically dissimilar fruits. The production of fruits with different morphologies is associated with alternative strategies of dispersal, germination, dormancy, and seedling competitive ability. Thus, heterocarpy is commonly considered a mixed strategy whereby some offspring stay close to the mother plant, where competition is likely high (i.e., fruits with a competitive syndrome), and other offspring are dispersed to colonize new sites that are free of sibling competition or other sources of stress (i.e., fruits with a dispersal syndrome; Venable and Brown, 1993; Imbert and Ronce, 2001). Heterocarpy has evolved independently in several plant families, including Brassicaceae, Chenopodiaceae, Poaceae, and others. It is particularly common in Asteraceae (Imbert, 2002), in which the fruits (hereafter "achenes") that belong to the competitive syndrome are commonly placed on the outermost positions of the capitulum, being heavier and deprived of dispersal structures, whereas dispersing achenes are usually found in the inner positions of the capitulum and are lighter in weight and have dispersal structures (e.g., Ellner and Shmida, 1984; Kigel, 1992; Ruiz de Clavijo, 2001; El-Keblawy, 2003; Brändel, 2007; Sun et al., 2009).

The competitive advantage of nondispersing achenes has frequently been attributed to their larger size in comparison with dispersing achenes. Larger achenes typically have a higher percentage of viability, survival, and growth and may give rise to plants with greater competitive ability and higher reproductive success (Rai and Tripathi, 1987; Banovetz and Scheiner, 1994; Imbert et al., 1997; Torices and Méndez, 2010). Furthermore, plants that originated from larger achenes have been described as more stress tolerant than plants that originated from smaller ones (Venable and Levin, 1985; Imbert, 2002). However, it has recently been suggested that the competitive difference in plant performance could be mediated by germination time instead of achene size (Dubois and Cheptou, 2012). Early germination can provide a competitive advantage in diverse competitive environments (Donohue et al., 2010; Mercer et al., 2011). Dubois and Cheptou (2012) set up a competitive environment in which dispersing and nondispersing achenes of the heterocarpic *Crepis sancta* were sown together; regardless of the variation in achene size, the achenes that germinated earlier resulted in

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[1] Manuscript received 24 January 2014; revision accepted 11 April 2014.

The authors thank I. Álvarez for discussions and valuable comments on the manuscript; M. Castro, D. Tavares, A. Martins, L. DeSoto, A. Jorge, B. Moreira, and Y. García for technical assistance; and S. Perkins and J. Perkins for English review and editing. The research was partly supported by the project "Evolution in *Anacyclus* L. (Anthemideae, Compositae): Analysis of the *A. clavatus* (Desf.) Pers. and *A. valentinus* L. contact zone," funded by the Ministry of Science and Innovation, Spain (Plan Nacional de I+D+I, CGL2010-18039). S.C. and R.T. were supported by the Portuguese Foundation for Science and Technology (FCT/BPD/41200/2007) and the Spanish Ministry of Education (BVA 2010-0375), respectively.

[2] Author for correspondence (e-mail: ana.s.s.afonso@gmail.com)

doi:10.3732/ajb.1400030

plants with higher survival and performance than those that germinated later. Thus, rapid germination could be an advantage in favorable environments, despite the fact that it may also increase the risk of seedling mortality in unfavorable conditions (Mandák and Pyšek, 1999; Donohue et al., 2010; Dubois and Cheptou, 2012). In this scenario, germination phenology could be the main mechanism mediating the competition–colonization trade-off between the two types of achenes.

However, not only size and dispersal structures vary between achene types. For instance, nitrogen and calcium concentration in embryos of *Helianthus annuus* decreased exponentially from outer to inner achenes (Steer et al., 1988). Thus, other unmeasured characteristics of achenes may also affect postdispersal behavior, confounding the effects of germination time on plant competitive ability. In *Galinsoga parviflora*, the competitive ability of nondispersing achenes, which also germinate earlier than dispersing ones, was mainly attributed to a higher concentration of carbohydrates and proteins that lead to better growth of the seedlings (Rai and Tripathi, 1982, 1987). Therefore, other intrinsic traits (besides germination time) that are usually associated with each achene type might also influence their postdispersal behavior and their competitive ability.

We followed an innovative approach to control the effects of germination time by synchronizing germination, using as a study system *Anacyclus clavatus* (Desf.) Pers. (Asteraceae), a heterocarpic species in which achene types germinate at different times (Torices et al., 2013). In our experiment, the different achene types (dispersing and nondispersing) were manipulated to germinate at the same time, and these results were compared with an experiment in which achenes were sown simultaneously, allowing for differences in the time of germination. In this way, we could disentangle the effects of germination time from those related to achene type, including morphology, size, or other unmeasured physiological traits such as nutrient allocation. *Anacyclus clavatus* is an annual species whose achenes present two different morphologies: outer and heavier winged achenes, and small inner achenes that lack dispersal structures (Fig. 1A–C). Winged and unwinged achenes differ in germination time, with the winged achenes germinating earlier than the unwinged ones (Torices et al., 2013; Fig. 1D). In comparison with what has been described for Asteraceae (see above), this species could represent an exception to the common pattern because the smallest achenes are those that lack dispersal structures and germinate later, whereas the largest achenes that germinate earlier have a wing that could allow them to achieve greater dispersal distances. Considering all this, the main objective of the present study was to investigate which factor mainly affects the plant performance and competitive ability of *A. clavatus* plants—the achene type (winged dispersing vs. unwinged nondispersing) or the time of germination. We addressed the following specific questions: (1) Are there differences in survival rates and/or plant performance between dispersing and nondispersing achenes? (2) Are there differences in survival rates and/or plant performance between achenes with different germination times? And (3) if so, are those differences mediated by achene type or by germination time?

MATERIALS AND METHODS

Study system—*Anacyclus clavatus* (Desf.) Pers. (Asteraceae) is an annual self-incompatible herb (I. Álvarez, unpublished data) distributed throughout the Mediterranean basin, in which achene morphology and size vary within their capitula. Two types of achenes can be clearly observed in this species: winged and unwinged (Fig. 1A–C). Unwinged achenes always occupy the innermost positions within capitula and weigh less (Torices et al., 2013). The presence of a wing is hypothesized to be associated with higher dispersal ability in comparison with unwinged achenes (Bastida et al., 2010), but this has not yet been experimentally tested. A previous study has shown that winged achenes germinate faster than unwinged ones, possibly because of the sequential release time of each type of achenes produced by this species (Torices et al., 2013; Fig. 1D). In addition, sexual expression also varies within the capitulum: In this species, the capitulum presents one row of female rayed flowers at the outermost positions, and bisexual tubular flowers at the inner positions (gynomonoecy; Bello et al., 2013).

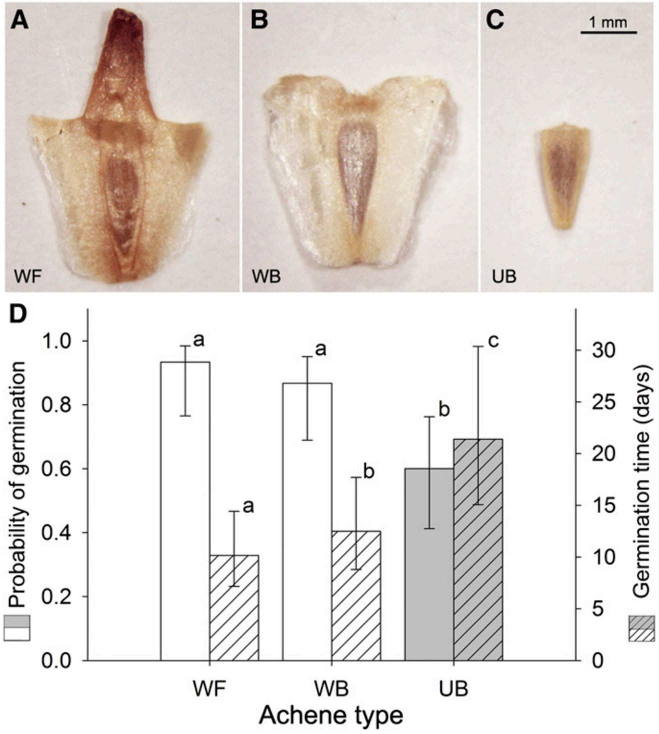

Fig. 1. Morphology and germination traits of the three types of achenes: (A) winged achenes from female flowers (WF); (B) winged achenes from bisexual flowers (WB); (C) unwinged achenes from bisexual flowers (UB); and (D) least squares means (± 95% confidence interval) of probability of germination (open columns) and germination time (hatched columns). White columns represent winged achenes, and gray columns represent unwinged achenes. The scale bar applies for all achene figures.

Achene material—In the summer of 2011, fruiting capitula were sampled from 37 different mother plants in a population from southern Spain (Carchuna, Spain, 36°41′49″N, 3°27′33″W, 13 m a.s.l.). All infrutescences were collected after complete seed maturation when the whole plant was dry.

In the laboratory, the achenes of each capitulum were manually separated into two categories: winged achenes (located at the outermost positions) and unwinged achenes (in the innermost positions). Furthermore, because this species presents two flower types at the outermost positions (i.e., female and bisexual), we included two categories of winged achenes: those from female flowers (hereafter "WF"; Fig. 1A) and those from bisexual flowers (hereafter "WB"; Fig. 1B), the latter located immediately after the row of female flowers. Because WF may reallocate resources saved in pollen production, the categorization of winged achenes is important for a more accurate comparison between winged and unwinged achenes of bisexual flowers. Unwinged achenes are produced by bisexual flowers located at the innermost positions only (hereafter "UB"; Fig. 1C).

Before sowing, all achenes were weighed to the nearest 0.1 mg. Because of their reduced weight, WF were weighed in groups of 2; WB and UB were weighed in groups of 10. Winged achenes were significantly heavier than unwinged ones at $P < 0.05$ (means ± SD: WF, 0.9 ± 0.2 mg; WB, 0.8 ± 0.2 mg; UB, 0.5 ± 0.2 mg; Kruskal-Wallis test: $H = 54.28$, $P < 0.001$).

***Experimental design*—**To explore the effect of achene type and germination time on plant performance, two experiments were performed: one allowing for differences in germination time between winged and unwinged achenes (experiment 1); and the other evaluating the effect of achene type alone, by synchronizing germination time and thus removing its effect from the experiment (experiment 2).

Experiment 1: Effect of achene type on plant performance, allowing for differences in germination time—In the first experiment, achenes were sown simultaneously in pots, to determine the effect of germination time in postdispersal plant traits. The three types of achenes (WF, WB, and UB) were obtained from 30 distinct capitula (representing 30 different maternal families), subsequently sown in 8.0 × 8.0 × 9.5 cm pots filled with a 1:2 mixture of gardening substrate and sand, and kept in a greenhouse. Two achenes from each category were sown per pot to ensure that at least one of the achenes germinated. Later, in cases where both seeds germinated, one of the seedlings was removed to ensure that each pot contained only one seedling.

Experiment 2: Effect of achene type alone on plant performance—In the second experiment, the germination time was manipulated to evaluate the effect of achene type per se. Previous studies have shown that outermost achenes (WF and WB) germinate within 1–2 d after watering, whereas the innermost achenes (UB) germinate ~10 d later (Torices et al., 2013). Thus, achenes from the inner positions (UB achenes) belonging to 29 different capitula (representing 29 different maternal families) were first placed in plastic Petri dishes filled with sand, and achene germination was monitored daily. When the first UB achenes of a given capitulum germinated (achenes were considered to have germinated after radicle emergence), the WF and WB achenes of that capitulum (same maternal family) were immediately planted to germinate in the same conditions. With this approach, the obtained seedlings resulted from germination within the same day or in the day after, removing the effect of germinating time from the experiment. One seedling from each type of achene was transplanted to pots from the Petri dishes at the same time, as described above.

Experimental conditions and variables measured—Both experiments began in October 2012, when all the pots were transferred into the greenhouse, and were grown until June 2013, when all the plants completed their life cycle. During this period, pots were watered 3 d wk^{-1} with a defined volume of water (50 mL) and were monitored weekly to record plant survival and flowering duration (i.e., the number of days that each plant was flowering). For experiment 1, germination rates were also monitored weekly until January and monthly until June. After senescence, plants were harvested, and flowering heads, stems and leaves (aboveground biomass), and roots (belowground biomass) were separated into paper bags, dried at 68°C for 48 h and weighed in an analytical scale to the nearest 0.1 mg. Plant performance was measured as total biomass, including total and percentage biomass of vegetative and reproductive structures, and belowground biomass (calculated in relation to the total biomass), which allowed us to evaluate the proportion of resources allocated by the different types of achenes. Reproductive effort of each plant was estimated as the biomass allocated to reproductive structures (i.e., the production of capitula) and as flowering duration.

***Statistical analyses*—**The two experiments were analyzed with generalized linear mixed models (GLMMs; Bolker et al., 2009), allowing the distinction of random and fixed factors.

Experiment 1: Effect of achene type on plant performance, allowing for differences in germination time—Two statistical approaches were followed to evaluate the effects of achene type and germination time on plant performance. First, the effect of achene type (the explanatory variable) was analyzed using maternal family as a random factor and probability of germination, germination time (number of days that have passed since achenes were sown), total biomass, aboveground and belowground biomass, reproductive biomass, biomass proportions, and flowering duration as response variables. The probabilities of germination and survival were modeled with a binary distribution, while germination time and flowering duration were adjusted to a Poisson distribution, and total, aboveground, belowground, and reproductive biomass were fitted to a Gaussian distribution. The biomass proportions were fitted to a gamma distribution. Differences between achenes types were analyzed using least squares means (LSmeans; i.e., the group means after having controlled for the covariates).

Second, the effect of achene type on plant performance was analyzed using germination time as a covariate, employing a GLMM approach similar to that described above. For this model, achene type and germination time were the explanatory variables and maternal family was the random factor. Plant performance was evaluated using the same traits as in the first mode, excluding probability of germination and germination time. Error distributions and link functions were set as above. Statistical differences between the different achene types were also analyzed using LSmeans. In both models, we used Satterthwaite's method to determine the approximate denominator degrees of freedom for these tests as suggested for unbalanced designs and small sample sizes (Verbeke and Molenberghs, 1997).

Experiment 2: Effect of achene type alone on plant performance—The effect of achene type on plant performance was analyzed using the first GLMM used in experiment 1 (i.e., achene type as the explanatory variable and maternal family included as a random factor). Plant performance was evaluated using the same traits as above, except for the probability of germination and germination time. Error distributions and link functions were set as above. Statistical differences between the different achene positions were analyzed using LSmeans.

All models were fitted using the GLIMMIX procedure for SAS, with LSMEANS option (SAS Institute, Cary, North Carolina, USA).

RESULTS

***Effect of achene type on plant performance allowing for differences in germination time (experiment 1)*—**Achene type significantly affected all the analyzed postdispersal life-history traits, except survival rates (Table 1 and Fig. 2A–D). The WF and WB achenes presented a statistically significant higher probability of germination than the UB achenes (Table 1 and Fig. 1D). As previously described for the study species, winged achenes also germinated significantly earlier than unwinged ones (Table 1 and Fig. 1D; Torices et al., 2013). Winged achenes also presented the highest values of total, aboveground, and belowground biomass (Table 1 and Fig. 2B; see Supplemental Data with the online version of this article: Appendix S1, panels A and B). The proportion of biomass allocated to aboveground and belowground growth was also significantly affected by achene type. The WF achenes produced plants that allocated proportionally higher biomass to belowground organs and less to aboveground organs, whereas WB and UB achenes showed the opposite pattern of resource allocation (Appendix S1, panels C and D).

The reproductive effort was also significantly affected by achene type (Table 1). The biomass allocated to reproductive structures decreased from the winged, larger achenes to the unwinged, smaller achenes, in accordance with the trend in plant size, as seen above (Fig. 2B) for the total biomass. However, when analyzing the biomass allocated to reproductive structures proportional to the total biomass, the opposite pattern was observed (i.e., the proportion of biomass allocated to reproduction was higher in unwinged achenes than in winged ones; Table 1 and Fig. 2C; Appendix S1, panel E). Finally, a significant effect of achene type in flowering duration was also observed, with plants from WB achenes presenting a significantly shorter flowering period than WF and UB (Table 1 and Fig. 2D).

When the time of germination was included in the models as a covariate, some of the significant effects of achene type disappeared, leaving germination time as the only significant factor (Table 1). The time of germination significantly affected all traits, except the proportional patterns of resource allocation. Achene type still significantly affected some traits, such as total

TABLE 1. Effects of achene type on postdispersal life-history traits (WF = winged achenes from female flowers, WB = winged achenes from bisexual flowers, and UB = unwinged achenes from bisexual flowers) as analyzed with a generalized linear mixed model for achenes that germinated simultaneously in pots, with achene type as the explanatory variable and maternal family as a random factor (experiment 1) or with achene type and germination time as explanatory variables and maternal family as a random factor (experiment 1 with germination time as covariate). *F*-statistic with degrees of freedom (df) is shown for the explanatory variables, with significant *P* values highlighted in bold. When the differences were statistically significant, a sign that indicates the direction of the germination-time effect was added. Variance estimation and SE are shown for the random factor, and sample sizes (*n*) are provided.

	Experiment 1					Experiment 1 with germination time as covariate									
	Achene type			Maternal family		Achene type			Germination time			Maternal family		
Variables	df	*F*	*P*	Variance	SE	df	*F*	*P*	df	*F*	*P*	Variance	SE	*n*
Germination traits														
Probability of germination	2, 87.0	4.98	**0.009**	0.2159	0.6690	—	—	—	—	—	—	—	—	—
Germination time	2, 69.0	56.56	**<0.0001**	0.7919	0.2166	—	—	—	—	—	—	—	—	—
Survival														
Probability of survival	2, 62.0	0.69	0.505	0.7840	0.7630	2, 61	0.29	0.752	1, 61	+4.49	**0.038**	0.6441	0.7667	65
Plant performance														
Total biomass	2, 24.7	4.91	**0.016**	0.0015	0.0014	2, 24.7	2.97	0.070	1, 24.6	−16.27	**0.001**	0.0004	0.0012	39
Aboveground biomass	2, 25.3	3.59	**0.042**	0.0010	0.0009	2, 26.2	2.00	0.155	1, 23.9	−14.93	**0.001**	0.0002	0.0008	39
Belowground biomass	2, 21.0	6.85	**0.005**	0.0001	0.0001	2, 20.4	5.05	**0.017**	1, 27.9	−12.85	**0.001**	0.0000	0.0000	39
Aboveground biomass (%)	2, 36.0	5.36	**0.009**	0.0000	0.0000	2, 26.4	4.48	**0.021**	1, 24.7	1.42	0.245	0.0003	0.0014	39
Belowground biomass (%)	2, 36.0	5.20	**0.010**	0.0000	0.0000	2, 28.9	4.30	**0.023**	1, 26.2	1.58	0.219	0.0034	0.0211	39
Reproductive traits														
Reproductive biomass	2, 23.6	3.19	0.059	0.0003	0.0002	2, 23.6	1.78	0.190	1, 27.2	−12.59	**0.001**	0.0001	0.0001	39
Reproductive biomass (%)	2, 23.7	2.80	0.081	0.0033	0.0117	2, 25.7	3.44	0.168	1, 25.6	1.91	0.075	0.0037	0.0096	39
Flowering duration	2, 36.0	6.31	**0.005**	0.2310	0.0833	2, 35.0	5.35	**0.009**	1, 35.0	−7.82	**0.008**	0.1991	0.0759	39

biomass (marginally significant), belowground biomass, proportional allocation to aboveground and belowground growth, and flowering duration (Table 1), producing patterns similar to those described above (Fig. 2E–H; Appendix S1, panels F–J). Germination time positively affected the probability of survival: Achenes that germinated earlier had a lower probability of survival than achenes that germinated later (Table 1 and Fig. 2E, I). By contrast, germination time negatively affected other plant performance traits, particularly total biomass, aboveground biomass, belowground biomass, reproductive biomass, and flowering duration (Table 1 and Fig. 2J–L). Overall, achenes that germinated earlier (i.e., WF and WB) had higher total, aboveground, and belowground biomass (Table 1 and Fig. 2F, J; Appendix S1, panels F and G) and showed a higher reproductive effort than achenes that germinated later (i.e., UB; Table 1 and Fig. 2H, L; Appendix S1, panel J).

Effect of achene type alone on plant performance (experiment 2)—When the germination time was controlled and all achenes were manipulated to germinate at the same time, achene type had no effect in any postdispersal life-history trait (Table 2 and Fig. 2M–P; Appendix S1, panels K–O), which suggests that all the differences observed between different achenes detected in experiment 1 were mediated mainly by differences in germination timing.

DISCUSSION

Our results reveal a significant effect of germination time in several postdispersal life-history traits. Considering that germination time is directly linked with achene morphology, the type of achene also influences, indirectly, the postdispersal traits. In *A. clavatus*, the achenes that germinated earlier produced plants with higher biomass (total, aboveground, and belowground) and higher reproductive effort. These results are in accordance with the assumption that early emergence influences the fitness of the plant, producing plants with higher performance (Rai and Tripathi, 1987; Imbert et al., 1997; Imbert, 2002; Donohue et al., 2010; Mercer et al., 2011). Consequently, winged achenes produced larger plants with a higher investment in reproduction than unwinged ones. Still, it should be noted that these differences were not directly due to achene type, given that they disappeared when achenes were manipulated to germinate at the same time. Therefore, our results indicate that the competitive advantage of winged achenes compared with unwinged ones was mediated mainly by their ability to germinate earlier, and not by their greater size or other intrinsic traits.

Our results support those of previous studies in *C. sancta* that suggest that germination time may result from an adaptive process linked to the competitive ability in plants within Mediterranean ruderal regions that have fast population growth and are able to colonize disturbed habitats (Dubois and Cheptou, 2012). Imbert et al. (1997) also pointed out that germination appeared to be the main factor, surpassing the possible effect of achene type. Previous studies have suggested that the effect of germination time seems to be stronger in controlled conditions than in the field, because of the unlimited availability of nutrients and water resources (Verdú and Traveset, 2005). In the present study, although the experiment occurred in controlled conditions, the resources were very limited (both water and nutrients), and our plants reached smaller sizes than those

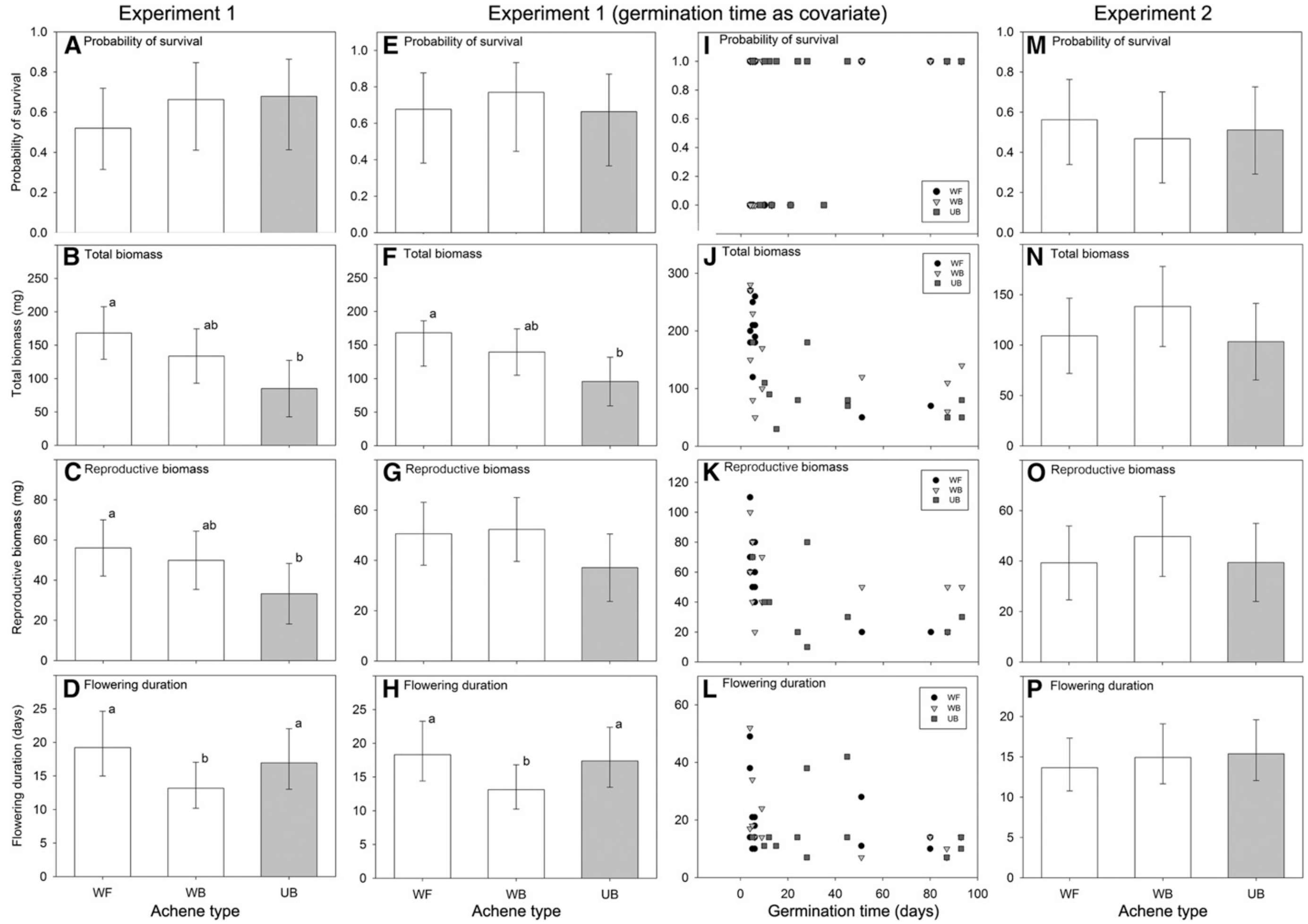

Fig. 2. Effects of achene type on postdispersal life-history traits. Experimental and statistical approaches are organized vertically as follows: (A–D) experiment 1, in which achenes germinated under different times; (E–H) experiment 1, using germination time as a covariate; (I–L) experiment 1, including the relationship between germination time and postdispersal life-history traits; and (M–P) experiment 2, in which achenes germinated at the same times. Least squares means (± 95% confidence interval) of postdispersal life-history traits analyzed across all the approaches are organized horizontally as follows: (A, E, I, M) probability of survival; (B, F, J, N) plant total biomass; (C, G, K, O) reproductive biomass; and (D, H, L, P) flowering duration. Achene types: WF = winged achenes from female flowers, WB = winged achenes from bisexual flowers, and UB = unwinged achenes from bisexual flowers. In panel I, probability of survival 1 is for seedlings that survived and 0 is for seedlings that did not survive. White columns represent winged achenes, and gray columns represent unwinged achenes. Means with the same superscript letter were not significantly different at $P < 0.05$ (see Tables 1 and 2).

from the same population in natural conditions (results not shown). Early germination has been shown to be advantageous in habitat patches with high plant density, allowing for plant growth before competition started (Orrock and Christopher, 2010). Also, several studies have shown that early germination leads to higher survival (Forsyth and Brown, 1982; Venable and Levin, 1985; Rai and Tripathi, 1987; Mercer et al., 2011). Still, in situations when competition is low, early germination is less likely to provide a benefit, and probably bears costs related to unpredictable environmental changes (Orrock and Christopher, 2010; Dubois and Cheptou, 2012). Under this scenario, it is expected that plants that germinated earlier can suffer a higher risk of seedling mortality (Dubois and Cheptou, 2012). Interestingly, when we let the achenes germinate freely, those achenes with delayed germination showed a higher survival probability than early-germinating ones (Table 1 and Fig. 2I). Therefore, early germination can be advantageous under a competitive environment but may increase the risk of mortality even for plants that are not subjected to competition. In our experiment, plants were grown individually in different pots and, hence, were free of neighborhood competition. Even without competition, achenes that germinated earlier showed significantly higher plant performance (growth and fecundity), which indicates that this effect might be higher under strong competition scenarios. Studies to address this issue are already being performed in our laboratory and will be important in shedding further light on the link between germination time and competition.

Commonly, in other heterocarpic species without dormant seeds, the achenes with the competitive syndrome usually are larger, lack dispersal structures, and germinate faster compared with dispersing achenes (Imbert et al., 1996, 1997; Dubois and Cheptou, 2012). In our study system, as well as in other *Anacyclus* species (e.g., *A. radiatus*, *A. valentinus*, and *A. homogamos*), achene morphology does not follow this pattern (Bastida and Menéndez, 2004; Torices et al., 2013). The competitive achenes (i.e., those that are larger and germinate earlier) are the

TABLE 2. Effects of achene type on postdispersal life-history traits (WF = winged achenes from female flowers, WB = winged achenes from bisexual flowers, and UB = unwinged achenes from bisexual flowers) as analyzed with a generalized linear mixed model for achenes germinated at the same time (experiment 2), with achene type as the explanatory variable and maternal family as a random factor. *F*-statistic with degrees of freedom (df) is shown for the explanatory variable. Variance estimation and SE are shown for the random factor, and sample sizes (*n*) are provided.

	Achene type			Maternal family		
	df	*F*	*P*	Variance	SE	*n*
Survival						
Probability of survival	2, 79.0	0.21	0.814	1.4740	0.8946	82
Plant performance						
Total biomass	2, 19.9	1.94	0.169	0.0041	0.0018	41
Aboveground biomass	2, 20.4	1.78	0.195	0.0027	0.0012	41
Belowground biomass	2, 20.5	1.31	0.293	0.0001	0.0001	41
Aboveground biomass (%)	2, 29.8	1.47	0.246	0.0001	0.0008	41
Belowground biomass (%)	2, 29.2	1.55	0.230	0.0019	0.0171	41
Reproductive traits						
Reproductive biomass	2, 21.5	1.05	0.368	0.0005	0.0002	40
Reproductive biomass (%)	2, 27.2	0.00	0.999	0.0084	0.0070	40
Flowering duration	2, 37.0	0.65	0.526	0.1789	0.0667	40

ones provided with a broad wing, theoretically linked with increased dispersal ability (Bastida and Menéndez, 2004; Bastida et al., 2010). Therefore, this species could represent an exception to the competition–dispersal trade-off that hypothesizes that wings increase the dispersal probability and distance, enabling the winged achenes to escape from competition. However, the role of the wings as dispersal structures has been questioned on the basis of the plant's natural history. In particular, the protection of the achenes with persistent involucral bracts that retain the seeds until the rainy season and the sequential release during rainy periods, together with the fast germination after contacting with water (frequently within 24 h), reduces the potential of winged achenes for dispersal. Additionally, by germinating significantly later, unwinged achenes increase their likelihood of being dispersed farther by passive agents such as strong winds or temporary heavy rain (seeds have the ability to float). Furthermore, wings could be involved in other functions besides dispersal, such as water imbibition, by increasing the pericarp surface for water uptake (for further discussion, see Torices et al., 2013). To ascertain whether this species is an exception to this trade-off, future studies should evaluate the effective dispersal distance of both achene types and the functional role of the wings in *Anacyclus* achenes.

The pattern observed in *A. clavatus* could be an adaptive strategy to the high environmental unpredictability of the disturbed open habitats and roadside habitats where this species commonly occurs. In these environments, winged and larger achenes are the first to be released from the capitulum immediately after the first autumn rains; the higher probability of rapid germination will be an advantage when competing with siblings, with other individuals of the same species or even with different species. The unwinged achenes are released with subsequent rains through the winter and may constitute a reservoir to replace seedlings lost due to mortality events after winter or early spring disturbances (Bastida et al., 2010). Interestingly, all *Anacyclus* species with variation in germination timing (*A. radiatus*: Bastida and Menéndez, 2004; *A. clavatus*, *A. valentinus*, and *A. homogamos*: Torices et al., 2013) are winter annuals distributed in Mediterranean disturbed habitats. The only perennial species within the genus, *A. pyrethrum*, characteristic of subalpine meadows and rocky habitats of the Atlas Mountains (in Morocco and Algeria), has homomorphic achenes with very small wings (Humphries, 1979), which supports the hypothesis that the wings could be involved in facilitating germination more than dispersal. Future comparative studies are needed to test this hypothesis.

In conclusion, the results of the present study showed that, in *Anacyclus*, the phenology of achene germination was the main factor affecting postdispersal life-history traits related to competitive ability and reproductive success. Still, knowledge of the effective dispersal ability of different types of achenes (i.e., winged and unwinged) will be fundamental for better understanding the role of the dispersal–competition trade-off on the evolution of dispersal strategies such as the ones observed in this heterocarpic genus. Finally, our experimental approach (i.e., the synchronization of germination time, experimentally controlled for the first time in the present study) revealed the importance of manipulative experiments to clearly perceive the effects of germination time in plant survival and performance.

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