Competition/colonization syndrome mediated by early germination in non-dispersing achenes in the heteromorphous species *Crepis sancta*

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INTRODUCTION

In ecology, the competition–colonization trade-off theory postulates to be a major factor shaping life-history traits and contributing to the maintenance of interspecific diversity in communities at the regional scale (Tilman, 1994; Kneitel and Chase, 2004). According to this trade-off, good competitors exhibiting low colonizing ability are favoured locally while good colonizers exhibiting poor competitive ability are favoured by recurrent colonization, overall favouring the maintenance of both types in the landscape. Although competition–colonization trade-offs have been considered in a variety of organisms, many of the empirical studies in plants have addressed this question by focusing on seed attributes. For instance, in wind-dispersed seeds, the trade-off can be captured by seed size, such that heavy seeds are good colonizers because of their substantial resources and small seeds are good colonizers because of their lightness (Salisbury, 1975; Fenner, 1985; Jakobsson and Eriksson, 2003). Interestingly, Smith and Fretwell (1974) demonstrated that this trade-off can emerge from resource partitioning when individuals have equivalent resources, such that an individual can produce either a few large seeds (competitive strategy) or many small seeds (dispersive strategy) (Geritz, 1995). The Smith and Fretwell (1974) model provides mechanistic support for competition–colonization trade-offs. While such theoretical models are appealing, empirical studies analysing such trade-offs in plants have reached conflicting conclusions (Jakobsson and Eriksson, 2003).

Although resource partitioning is at the heart of the competition–colonization syndrome, variation in seed size in plants encompasses a variety of seed traits that may modify individual fitness, which makes the problem more complex than a simple resource trade-off. As the first event in the plant life cycle, germination is likely to shape fitness components during the entire life cycle (Donohue et al., 2010). Harper (1977) proposed that plant success is determined very early in its development and is not only dependent on initial resources but also on the length of the growing period and interactions with competitive processes imposed by neighbouring plants. Empirical studies have shown that early germination provides a competitive advantage by increasing the growth period and also by limiting the impact of neighbouring plants, thus increasing individual fitness (Donohue et al., 2010). On the other hand, early germination may be costly in a seasonal environment because external conditions may not be favourable (e.g. frost, drought period) or simply because a longer life cycle increases the probability of exposure to stochastic disturbance (Donohue et al., 2010).

Seed attributes often vary continuously in plants at the individual level or at the population level; however, seed
heteromorphic plant species exhibit discrete variation in seed or fruit attributes and such heteromorphism has been shown to have evolved in many families and genera (Imbert, 2002). Seed heteromorphism is often associated with variation in dispersal ability and seed mass (Olivieri and Berger, 1984; Imbert, 2002). In particular, seed heteromorphism has evolved in many species of the Asteraceae family. For most Asteraceae species, the presence/absence of dispersal structures (pappus) is the most visible characteristic of seed heteromorphism (Imbert, 2002). In addition to morphology, dispersal attributes are sometimes associated with other traits such as dormancy, seedling emergence and seedling survival and growth (Olivieri and Berger, 1984; Venable, 1985; Imbert, 2002; El-Keblawy, 2003). Although these associations are often explained by differences in resource allocation among seed types, differences in physical seed structures may also be involved. For example, differences in the thickness and structure of the pericarp may vary among fruit or seed types, and play a major role in germination. As a result, water absorption by the embryo tissue and gas exchange may differ among fruit types and thus influence the variation in timing of germination of achenes (Imbert, 2002).

In this paper, we explore the possibility of a competition–colonization syndrome mediated by germination timing in *Crepis sancta*. In this species, achene dimorphism is strongly associated with dispersal ability (Imbert, 1999). Although both achene types are non-dormant (Imbert et al., 1996), Imbert et al. (1996) showed that the non-dispersing type tends to germinate earlier than dispersing achenes in Petri dishes. Using experimental conditions mimicking natural conditions, we test the possibility that the early germination of non-dispersing achenes may provide a competitive advantage over dispersing achenes, regardless of variation in resource allocation. More specifically, we address the following questions: (a) Do non-dispersing achenes germinate earlier than dispersing achenes in competitive stands? (b) Does early germination translate into fitness gains in both types of achene? (c) Do achene types differ in endosperm reserve?

The results show that early germination provides a strong competitive advantage and we discuss the potential for the joint evolution of germination phenology and dispersal ability under natural selection.

**MATERIALS AND METHODS**

**Model species**

*Crepis sancta* is a winter annual Mediterranean herb (Asteraceae) commonly found in early to middle successional stages in the south of France (e.g. vineyards, old abandoned fields and anthropogenic habitats such as urban environments). Compared with other annual species, seedlings of *C. sancta* are one of the first to emerge in early autumn with the onset of the Mediterranean rain season. Individuals overwinter as a rosette and reproduce in early spring (March). At flowering, plants develop up to 100 inflorescences. Each inflorescence (capitulum) is composed of hermaphroditic ligulate florets. As in most heterocarpic Asteraceae, the florets located at the periphery of the capitulum produce large light-coloured achenes with floral seed coat tissues (0.27 ± 0.02 mg) without a pappus whereas the central florets produce small brown-coloured achenes (0.10 ± 0.01 mg) with a pappus (Fig. 1) (Imbert, 1999). The falling velocity of the peripheral and central achenes is 1.21 ± 0.03 m s$^{-1}$ and 0.23 ± 0.01 m s$^{-1}$, respectively (Imbert, 1999). Imbert (1999) found no evidence of inter-annual dormancy in either type of achene, and the absence of a seed bank has also been documented in this species (Dornier et al., 2011). Furthermore, the proportion of non-dispersing achenes has been shown to have evolved rapidly as a consequence of urban fragmentation (Cheptou et al., 2008).

**Sampling**

In May 2010, capitula from 30 individuals per population were sampled from eight populations in the south of France following seed maturation. The eight populations (three rural populations and five urban populations) were selected on the basis of a previous study (Cheptou et al., 2008) in order to maximize the variability in dispersal strategies encountered in natural populations in the south of France. Rural populations were sampled from vineyards <30 km from Montpellier: Fabrègues (hereafter FA, South West) and Claret (hereafter CL, North), and from a wasteland (Pic St Loup, hereafter PSL, North). The urban populations were located in the centre of Montpellier. Two (VV and SA) were large populations and the other three (AI, JC, DE) were fragmented.
patchy populations located in small patches around trees (Cheptou et al., 2008; Dornier et al., 2011).

Experimental design and statistical analysis

From 4 to 12 families per population were used (48 families in total). For each family, six non-dispersing achenes and six dispersing achenes (see Fig. 1) were randomly sampled from the same capitulum, giving a total of 576 achenes. To mimic natural conditions, the seeds were randomly sown outdoors at the beginning of June in six trays (1.2 × 1.2 × 0.5 m) filled with sterilized soil at the CEFE-CNRS experimental station. The achenes were positioned according to a 10 × 10 matrix spaced 10 cm apart (except at the four tray corners in order to generate competitive interactions close to those generated by natural seedling density (Cheptou et al., 2001). The co-ordinates of the achenes were recorded individually using a template. The trays were covered with netting to prevent the potential immigration of achenes. A total of 576 achenes were distributed among the six trays and non-dispersing and dispersing achenes were completely balanced within trays. After the first natural autumnal rainfall (September), the soil trays were kept moist by regular watering to minimize stochastic effects due to erratic rain, ensuring sufficient germination. Following the emergence of the first seedling (10 September 2010), the trays were examined every 2 or 3 d to record individual germination times until the number of germinated seeds remained the same for six consecutive days (8 October 2010). We thereafter recorded individual survival and measured individual dry mass (to the nearest 10⁻² g) at the end of the flowering period, as an estimate of total fitness (Cheptou et al., 2000).

Post-dispersal life-history traits (germination probability, germination timing, survival after germination and final plant biomass) were analysed using a nested generalized linear mixed model (R software, package lme4) (Crawley, 2007). For each trait, we compared the complete model with a model lacking the factor tested. The complete model included four categorical factors: tray, seed type, population, and seed type × population interaction as fixed effects, and family nested in the population as the random effect. Germination timing was added as a covariable for plant survival and plant dry mass. The population and seed type factors, seed type × population interaction and germination timing covariable were removed from the complete model when they were not significant. To estimate the effect of seed type, independently from germination timing, on plant survival and plant dry mass, we tested the effect of seed type with and without including germination timing in the model. Germination probability and individual survival were analysed using a logit link function with a binomial error structure. A log link function with a Poisson error structure was used for biomass and germination timing. Significance of factors was tested with a chi-square test excepting the presence of overdispersion where a Fisher test was used.

Anatomy of endosperm in dispersing and non-dispersing achenes

To evaluate resource allocation in dispersing and non-dispersing achenes, we randomly sampled one seed of each seed type in the same capitulum from 30 individuals randomly sampled in all the populations. We performed cross-sections of seeds at the largest section of the embryo, i.e. the inferior half of the seed (see Figs 1 and 5), and photographed them under a binocular microscope (Leica MZ16) using a highly sensitive digital camera (Leica DFC280). Pictures were analysed with ImageJ software (Abramoff et al., 2004) and nutrient reserves were estimated by measuring surface section approximated as the surface of the largest ellipse contained inside the area delimited by the pericarp. Differences in surface section between seed types were tested with a paired t-test.

RESULTS

Germination phenology and consequences for fitness

The mean estimated germination probability was 0.49 ± 0.14, and was significantly higher for non-dispersing achenes (0.56 ± 0.11) than for dispersing achenes (0.41 ± 0.11; Table 1). Germination was homogeneous across the eight populations and no significant population × achen type interaction was detected (Table 1). The mean time to germination for all seeds was 13.8 ± 6.8 d after the first rainfall. On average, non-dispersing achenes germinated earlier (12.32 ± 2.93 d) than dispersing achenes (15.72 ± 3.07 d) and there was no significant effect of population factor on germination timing or a population × achen type interaction (Table 1 and Fig. 2). A total of 296 seeds germinated and 237 survived

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F = 10.87^{**} \quad F = 15.33^{***} \quad \chi^2 = 1.02 \quad \chi^2 = 2.596
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F = 0.582 \quad F = 1.581 \quad \chi^2 = 9.3119 \quad \chi^2 = 3.46 \quad \chi^2 = 173.5^{***} \quad \chi^2 = 173.5^{***}
\]

Table 1. Results of the linear models

| Explanatory variables and covariable | Numerator d.f. | Germination probability | Germination timing | Individual survival | Individual mass |
|-------------------------------------|----------------|------------------------|--------------------|--------------------|-----------------|
| Seed type                           | 1              | F = 10.87**            | F = 15.33***       | \( \chi^2 = 1.02 \) | \( \chi^2 = 2.596 \) |
| Population                          | 7              | F = 1.902              | F = 0.725          | \( \chi^2 = 9.3119 \) | \( \chi^2 = 3.46 \) |
| Interaction seed type / Population  | 7              | F = 0.582              | F = 1.581          | \( \chi^2 = 20.25^{***} \) | \( \chi^2 = 173.5^{***} \) |
| Germination timing                  | 1              |                        |                    | \( \chi^2 = 20.25^{***} \) | \( \chi^2 = 173.5^{***} \) |

Factor tested (in row) for the different fitness components (in column). The significances of the F-test or \( \chi^2 \) test are noted (*\( P < 0.05 \); **\( P < 0.01 \); ***\( P < 0.001 \)) and the residual degrees of freedom (d.f.) are given for each test. Column 2 lists the degrees of freedom used by explanatory variables that is the numerator degrees of freedom in the F-ratio.
until flowering. Germination timing had a highly significant effect on survival and dry mass (Table 1 and Figs 3 and 4). Seedlings that germinated early had a higher survival probability and a higher dry mass at the end of the life cycle. Importantly, seed type had a highly significant effect on dry mass ($\chi^2 = 23.812, P < 0.001$) and a marginally significant effect on survival ($\chi^2 = 2.9594, P = 0.085$) when germination timing was not included in the model, whereas it had no significant effect when germination timing was included (Table 1 and Figs 3 and 4). This emphasizes that germination timing captures a large part of the variance between seed types for plant survival and plant dry mass. Population had a significant effect on dry mass (Table 1), with populations FA, VV, SA, AI and JC producing larger individuals on average than populations DE, PSL and CL (approx. 1–2 g difference, on average, between populations). Only DE produced significantly smaller individuals relative to the other populations (Table 1).

Anatomy of endosperm in dispersing and non-dispersing achenes

Thirty achenes of each type were examined. Figure 5 shows a cross-section through the centre of the two achene types. In the case of the non-dispersing achene, the white part of the seed coat (epicarp) was removed to facilitate observation. The endosperm (i.e. seed nutrient reserves, labelled ‘e’ in Fig. 5) is clearly distinguishable in the central area, and is delimited by the internal part of the pericarp (‘p’ in Fig. 5). The paired $t$-test shows no significant differences between seed type (mean and standard error of the difference: $0.00507 \pm 0.00881$ mm$^2$, $t = 0.57$, d.f. = 29, $P = 0.5698$). We thus conclude that, in spite of the high morphological differences (seed weight, seed coat), there is no evidence of nutrient reserve differences between achenes.

DISCUSSION

In this study, we showed that non-dispersing achenes germinate about 4 d earlier than dispersing achenes in the heterocarpic weed Crepis sancta. This pattern was found to be significant and consistent over the eight populations sampled from both fragmented and non-fragmented habitats. We also
showed that early germination provided a fitness advantage in our experiment in which individuals were grown in a competitive environment. Interestingly, we showed that fitness for both achene types was nearly equivalent when controlling for germination timing, which shows that, among achenes, fitness variation was captured for a large part by the among-seed type difference in germination timing. This suggests a link between competitiveness and dispersal ability mediated by germination timing. The absence of significant difference in endosperm size among achene types supports the idea that resource variation is not responsible for the competitive advantage of non-dispersing achenes, as classically envisioned. Interestingly, these studies suggested a link between fitness advantage due to increased productivity (i.e. competitive ability) and early germination within the growing season (Venable et al., 1995; Fumanal et al., 2007), a trait that is known to be determinant in the competitive ability of plants either at the intraspecific or interspecific level (Harper, 1977; Donohue et al., 2010). In heterocarpic species, variability in the structure, shape and composition of achenes is likely to be involved in various traits other than those linked with dispersal. For instance, Imbert (1999) showed that dispersing and non-dispersing achenes of *Crepis sancta* differ not only in dispersal structure (presence or absence of a pappus) but also in the structure of the pericarp, which is not involved in dispersal ability per se. This illustrates the fact that heterocarpy encompasses a syndrome of traits that is not solely linked with

**Fig. 4.** Estimated individual dry mass as a function of germination timing and achene type. (non-dispersing and dispersing seeds, as indicated in the key). The continuous line and the dashed line represent the exponential relationship between germination timing and estimated mass for non-dispersing and dispersing seeds, respectively.

**Fig. 5.** Photograph of cross-sections in the medium position under binocular magnification of the two achene types sampled randomly in the same capitulum (small achene on the left and large on the right). The section zone surface of the pericarp (p) and the endosperm (e) (i.e. seed nutrient reserves) are identified. On the non-dispersing achene, the white part of the seed coat (epicarp) was removed to facilitate observation.
dispersal. In line with this, variation in pericarp structure (i.e. pericarp thickness) is likely to be involved in germination phenology (Imbert, 2002). Importantly, because the average ripening time difference between the two achene types is about 1 d (centripetal development of the capitula, see Cheptou et al., 2001), the ripening time alone cannot account for the average 4 d difference in germination timing. This suggests that germination timing results, at least in part, from adaptive processes.

In the light of the evolutionary theory of dispersal (Ronce, 2007), we propose an adaptive scenario linking germination timing and dispersal ability in Crepis sancta. The presence of empty patches caused by extinction in the landscape is known to favour dispersal, whereas various costs of dispersal (physiological costs, probability of dispersal into unsuitable habitats) select against dispersal. According to this scheme, non-dispersing achene have a high probability of suffering from high competitive pressure in local undisturbed populations, whereas dispersing achene are more likely to fall into empty disturbed patches where competition is low. As a consequence, we expect competitiveness to be favoured in the non-dispersing achene, which can be achieved by early germination. Because competition is lower in empty patches, we do not expect early germination to evolve in dispersing achene. Interestingly, selection gradients for early germination have been found to increase with density in experimental stands (Winn, 1988). The scenario described here is consistent with ruderal plants that colonize disturbed habitats and have rapid demographic growth. This is typically the scenario encountered in the species Crepis sancta in rural Mediterranean regions (Cheptou et al., 2000). The competitiveness of non-dispersing achenes may also be advantageous in the context of interspecific interactions (Imbert et al., 1997). Populations in advanced successional stages (crowded) will favour early germination while young successional stages will show lower selection for competitiveness. However, for this scenario to hold, early germination has to be costly so that it is disadvantageous for plants that are not subjected to competition to germinate early. For most plants, the timing of germination depends on the presence of a set of environmental conditions such as water, temperature and light that ensure suitable conditions for the development and growth of seedlings (Harper, 1977). Germinating early thus increases the risk of seedling mortality, particularly in a seasonal environment, and such a risk is expected to fluctuate from year to year. For instance, the winter annual Crepis sancta usually germinates with autumn rainfall. Seeds that germinate too early (i.e. in late summer) would have a low survival due to scarce and erratic rainfall. Early germination costs may also apply to plants germinating in spring when early germinating plants could be exposed to late frosts.

In line with this scenario, Venable et al. (1995) showed that in a Mexican population of Heterosperma pinnatum, earlier germination is favoured in non-hazardous germination conditions compared with hazardous germination conditions (such as semi-arid sites) where precipitation events are more scarce and unpredictable. This may be understood as a cost of competitiveness due to early germination. In contrast to our data on Crepis sancta, Venable et al. (1995) showed, in the heterocarpic species Heterosperma pinnatum, that dispersing central achenes on average germinate earlier than non-dispersing peripheral achenes, i.e. the opposite pattern to that observed in Crepis sancta. Unlike in the Mediterranean population of Crepis sancta, the low intensity of local competition and high variability of costs due to early germination in semi-arid habitats may explain the observed germination timing/dispersal association in Heterosperma pinnatum.

Conclusions

Overall, our results show that the competition–colonization syndrome is more complex than simple partitioning of resources among seed types. The link between germination timing and dispersal strategy has previously been studied mainly by focusing on inter-annual delayed germination dynamics (i.e. dormancy) (Venable and Lawlor, 1980; Olivieri and Berger, 1984; Venable and Brown, 1988; Olivieri, 2001; Imbert, 2002). However, the way in which evolutionary processes shape the joint evolution of dispersal and germination phenology within a season (without dormant seeds) has rarely been considered. Our study suggests that germination timing is important, even in species without dormancy. Since the impact of crowded conditions is central in the evolution of dispersal (Comins et al., 1980; Olivieri et al., 1995; Ronce et al., 2000; Parvinen et al., 2003), competitive ability mediated by phenology is likely to co-evolve with dispersal traits. Importantly, we have shown here that the classical competition–colonization trade-off can evolve without considering physiological constraints on resource allocation, thus shedding new light on an old question in ecology.

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