

Chapter III

Environmental study of reproductive and dispersal efforts of the common weed *Cirsium arvense* on a metapopulation level

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Abstract: We examined the effect of succession on *Cirsium arvense* reproductive and dispersal outputs. *Cirsium arvense* is a dioecious, insect pollinated clonal plant. Female and male plants were collected in three populations of early successional stage and in ten populations of late successional stage. Among others, succession caused a number of important phenotypic changes in *C. arvense* including a significant decrease in the number of flowering shoots per population (-48%; $P < 0.01$), the number of flower heads per shoot ($P < 0.01$ in females; not significant in males) and the number of flowers per flower head ($P < 0.1$ in females and not significant in males). However, there was no relationship between successional stage and average mass of an achene or germination rate ($F = 0.07$; $P = NS$ and $F = 0.14$ $P > 0.71$ respectively). Based on recent theoretical models about the reproductive effort in metapopulation context (Ronce and Olivieri, 1997; Ronce et al., 2000b), we suggest that the differences found may result from evolutionary changes in the genotypic composition of populations because of increasing intraspecific selection pressures when the habitat is maturing. This idea is supported by previous AFLP analysis of *C. arvense* populations (Solé, et al., 2004). However, we found no changes in the dispersal potential (pappus length) of *C. arvense* and we discuss the suitability of this trait for estimating the dispersal potential in this species.

Key words: Reproductive effort, dispersal capacity, succession, mixed reproductive system, *Cirsium arvense*, metapopulation.

Introduction

Succession, which corresponds to all biotic and abiotic changes associated with the development of a juvenile community into a mature one, is often studied in ecology and more recently in population biology (Quinn et al., 1972; Beasleigh and Yarranton, 1974; Escarré et al., 1985; Escarré and Thompson, 1991; Escarré et al., 1994; Welham and Setter, 1998; Ross and Quinn, 1977; Peroni, 1994; Piquot et al., 1998). During succession, populations encounter different selection pressures: from density-independent selection pressures following colonisation of a new habitat to density-dependent selection when the habitat reaches its carrying capacity. Therefore, succession can lead to temporal and spatial variability in the expression of some plants life history characters, especially reproduction and dispersal, which can evolve rapidly when affected by changes in the selection regime (Fisher, 1930; Reznick et al., 1990; Li and Margolies, 1994; Cody and Overton, 1996).

Most perennial plants have a mixed reproductive system with sexual reproduction through seeds and clonal reproduction through different modes of vegetative propagation. These plants are usually called clonal plants. Limited availability of resources or a limited capacity for resource uptake may generate, at every age in clonal plants a trade-off between different life history components, if these compete for the same resources (Stearns, 1992). Therefore, if reproductive effort represents the proportion of resources that an individual allocates at a specific age into reproduction compared with the proportion allocated into maintenance (survival) or growth (Williams, 1966), a trade-off is expected between reproductive effort and clonal reproduction (van Noordwijk and de Jong, 1986; Hautekeete et al., 2001; Stearns 1992). If selection pressures change through time during succession, then we can expect population age-specific patterns of reproductive effort and clonal reproduction in each successional stage (Ronce and Olivieri, 1997; Piquot et al., 1998).

Likewise, different selection pressures may act on dispersal rate over time (Quinn et al., 1972; Olivieri et al., 1983; Peroni, 1994; Welham and Setter, 1998). For many clonal plants, dispersal by vegetative means is limited and seed dispersal is the only way to colonize a new habitat. Thus, genotypes with a high dispersal and reproductive output will more likely occur in early successional habitats. In late successional habitats however, density dependant selection should favour genotypes with high competitive ability i.e. plants that allocate more resources into vegetative reproduction and survival. Density dependant selection may also act against seed dispersal because of the immediate cost in local competitiveness once the carrying

capacity is reached (Ronce et al., 2000a). However, the evolutionary relation between reproductive effort and dispersal is not trivial as demonstrated by recent theoretical models (Ronce et al., 2000b).

Studies looking at the evolution of these two traits in natural conditions are rare (Quinn et al., 1972). The aim of this study was to investigate reproductive and dispersal outputs in natural populations of the clonal dioecious plant *Cirsium arvense* in different successional states. We asked the following questions: 1) is there a relation between the reproductive output and succession? 2) is there a relation between dispersal and successional state? 3) do dispersal and reproduction coevolve?

In order to determine which possible factors might be responsible for changes in *C. arvense* reproductive effort and dispersal, we looked among others in the field at the plant height, sex ratio, fruit-set frequency distribution, seed weight and seed germination.

Materials and Methods

Plant biology

Canada thistle (*Cirsium arvense*, Asteraceae) is a major perennial weeds of Eurasia and Northern America. As most perennial plants, *C. arvense* has a mixed sexual-asexual reproduction system. Clonal reproduction occurs by means of very efficient lateral roots, which can spread up to 12m a year (Donald, 1994; Moore, 1975; Bostock and Benton, 1979) and lead to the production of large ramets (i.e. all aerial shoots coming from the clonal propagation of a single root). With regard to its flowering biology, *C. arvense* is often described as a subdioecious-dioecious species. Female plants are strictly female with only pistillate flowers (Moore, 1975). Males are morphologically hermaphrodites with vestigial ovaries, but functionally males. *C. arvense* is insect pollinated and produces a large number of plumed achenes with a long pappus easily dispersed by wind. New populations are mainly founded by achenes, as natural long distance dispersal of vegetative propagules is strongly limited or quasi-impossible (roots are deeply buried in the soil).

Early and late successional stages

Our study area is an experimental zone of 15 km² located in Southern Germany (11°50'E 49°35'N) that we regularly investigated over the last ten years (Eber and Brandl, 1994; Eber and Brandl, 1996; Eber and Brandl, 2003). It is a rural area composed of several types of habitats (meadows, agricultural fields, wastelands, old fallows, roadsides). In September 2000, we sampled three natural populations of *C. arvense* in early successional stage and 10 populations in late successional stage. For easiness, populations in early successional stage are called young populations whereas populations in late successional stages are called old populations. Young populations represent the first step after population establishment (i.e. colonisation phase). To locate young populations, we prospected and recorded *C. arvense* stands that had never been observed in previous studies. Young populations of *C. arvense* typically occurred on bare patches in disturbed grazing area, or in disturbed areas recently ploughed or mowed. Within these habitats, the vegetation cover was below 75 %. The plant communities were exclusively composed of herbaceous species in which *C. arvense* was the dominant species.

Old populations of *C. arvense* were sampled in old fallows. The vegetation cover was totally closed and woody species were present. In this habitat *C. arvense* shoots were particularly tall and ligneous. Old populations had already been mapped in this advanced successional stage in

1994. Although, the date of foundation of old populations is unknown, they must exist for at least ten years.

Populations characteristics

Field observations and plant collection were done in early September 2000. In this paper, we define the population size as the number of shoots within populations. In 2000, the population size, percentage of flowering shoots and the sex ratio of all 13 populations was estimated. For populations having less than 100 shoots, the number of flowering and non-flowering shoots, and the number of males and females were counted as exact as possible. Then, counts were rounded to the nearest ten to estimate the population size and percentages were calculated to express sex ratio (proportion of females) and proportion of flowering shoots (Table 1). For bigger populations, average number of plants was counted within randomly placed square meters. Counts were extrapolated to the population area covered by *C. arvensis*. In these cases, the number of shoots was rounded to the nearest hundreds or thousands.

Table 1: Ecological characteristics of 13 natural populations of the perennial dioecious *C. arvensis*

Population name	Successional stage	Population size (number of shoots)	Sex ratio (% of females)	Percentage of flowering shoots	Number of plants sampled (N)
E1	Early	300	100	86	30
E2	Early	250	100	94	30
E3	Early	900	75	95	50
L1	Late	8000	100	60	72
L2	Late	100	0	31	9
L3	Late	500	100	49	37
L4	Late	100	73.3	27	9
L5	Late	30	0	25	5
L6	Late	3000	98	60	51
L7	Late	400	100	50	29
L8	Late	40	53.3	47	7
L9	Late	800	69	88	36
L10	Late	10	<i>No data</i>	0	0

To avoid possible “time sampling artefacts”, we recollected the same information in 2001 for three populations of each successional stage at the beginning, middle and end of the flowering time (mi-July; mi-August, mi-September). Because of the high disturbance in pioneer habitats, we lost two young populations due to mowing after the first survey. Thus, full data set 2000/2001 was available only for one of the young populations (E3), but for the

three old populations L1, L2, and L3 (Table 2). Additionally, in 2001 we measured directly in field the height of plants in these four populations (E3, L1, L2 and L3).

Reproductive and dispersal outputs

Populations differed markedly in their area, plant distribution and density, therefore sampling was adjusted in each population. Plants were collected on a ramet level. To avoid sampling the same genotype twice, we used adequate minimal distances between samples. Sampling effort was correlated to population size ($r = 0.96$; $P < 0.001$).

Plants were cut in the field and brought to the lab for measurements of reproductive and dispersal outputs. As we conducted a field survey, we could not estimate the reproductive effort according to Williams (1966). The reproductive effort was estimated independently from the investment into growth. Therefore in this paper, the reproductive effort represents the reproductive output we measured in the field for each plant.

For each plant collected ($n = 365$), we determinate its sex and counted its number of flower heads. Then we randomly selected four flower heads and counted the number of florets and fruits. In *C. arvensis*, there are three categories of achenes: non-pollinated, aborted (i.e. ovaries that displayed pericard development, but did not contain a healthy embryo), or successfully pollinated and developed (Lalonde and Roitberg, 1989). We checked the quality of each achene and we used the third category to define the fruit set. In addition, we calculated the average mass of an achene by dividing the mass of all filled achenes of a flower head by the fruit set of the same flower head.

Additionally, we tested for germination capacity in one population of each successional stage (21 and 24 families for early and of late successional stage respectively). Achenes were sowed in Petri dishes with 3 mm Whatman filter paper and 2.5 ml of distilled water. All Petri dishes were kept in a culture chamber at: 26°C with a 12 hours photoperiod (Moore, 1975; Heimann and Cussans, 1996). We recorded germination percentages after four weeks.

Pappus length was used as an indicator of the dispersal capacity. In *C. arvensis* the pappus derives from the corolla, and both males and females can develop a pappus after flowering. We limited our measures to females only. We measured the length of two random pappy per flower head.

Statistical analysis

All variables representing a proportion or a percentage (sex ratio, flowering, fruit set and germination) were analysed with generalised linear models with the program GLIM (Crawley, 1993). In this model, we fitted our data to a binomial distribution. The variables sex ratio (counts of females) and flowering (counts of flowering shoots) were fitted to the total number of plants observed in the populations. For the fruit set, we took into account only the flower heads that have produced at least one achene. The number of achenes produced by flower head was fitted to the number of florets. For the germination test, the number of seedling obtained per achene family was fitted to the number of achenes sown for this family.

We conducted a variance analyse for variables that measured the reproductive and dispersal outputs (number of flower heads per plant, number of florets per flower head, pappus length and average mass of an achene). Analyse was done with the General Linear Models module of the program SAS (SAS Institute, Cary, NC). In clonal plants, it has already been proved that resources acquired by a genet can be but are not necessary equitably allocated between all ramets (clonal integration, Marshall, 1990; Marshall and Price, 1997). Therefore, as we sampled plants on a ramet level, we strongly increased the variation inter-individuals. Hence, we suppressed the individual level from our statistical analysis. We analysed our data on a two-level nested ANOVA with population nested within successional stage. Because of strongly unbalanced design between male and female sample sizes, males and females were analysed separately. Finally, differences in plant height between young and old populations were tested with a t-test

Results

The sex ratio was biased in favour of females (Figure 1A) but did not significantly differ between the two successional stages ($F = 0.00041, P > 0.98$). Temporal surveys of sex ratio did not show any differences in the proportion of females during the flowering time (Figure 2).

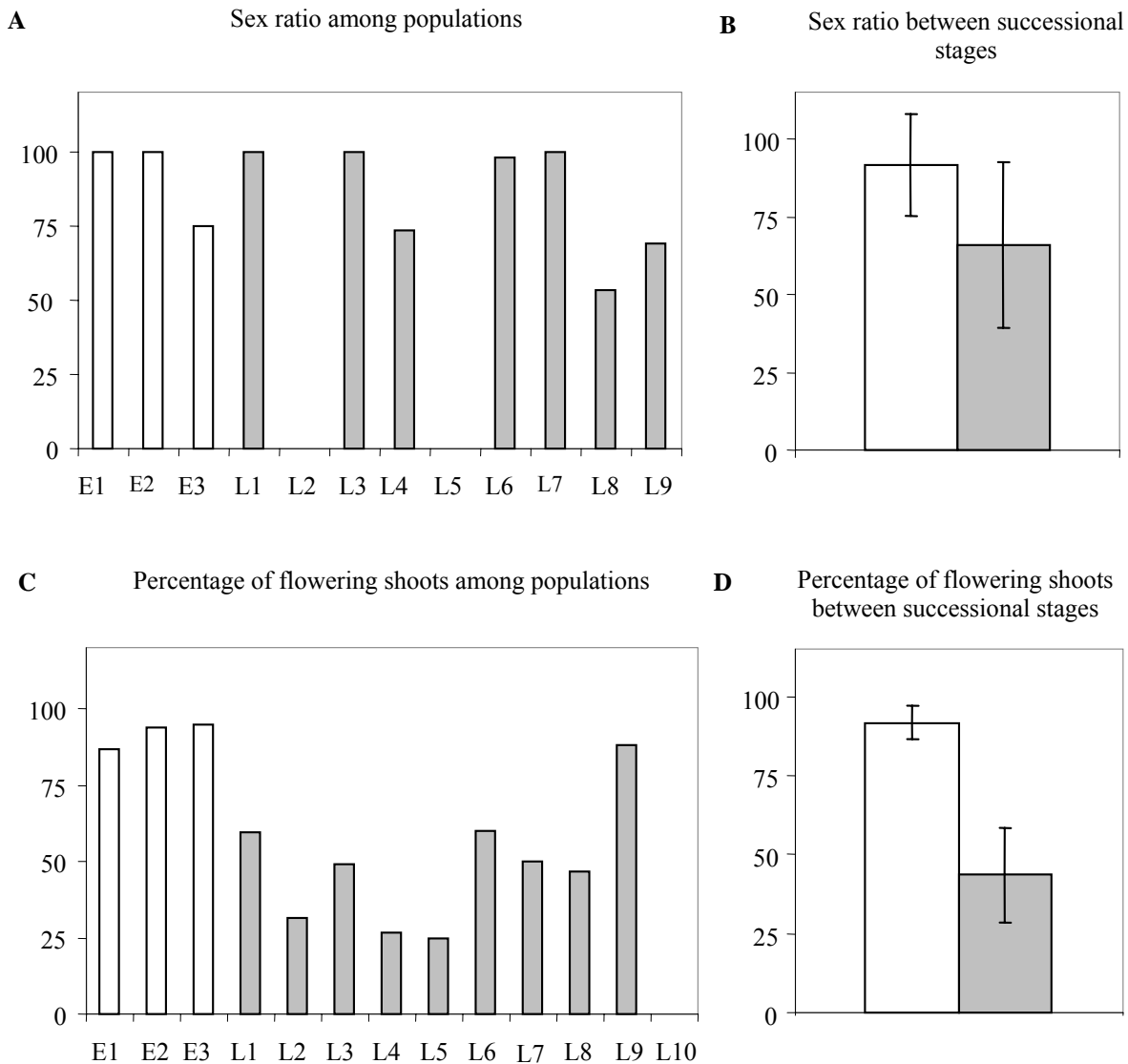


Figure 1: (A) Sex ratio (proportion of females) and percentage of flowering shoots (C) observed in the field among respectively 12 and 13 populations of *C. arvensis*. Sex ratio (proportion of females) (B) and percentage of flowering (D) expressed in relation to the successional stage of populations. Open and shaded bars represent respectively young and old populations. Error bars represent the 95% confidence interval. Average sex ratio between young and old populations did not differ significantly ($F = 0.00041; P > 0.98$), whereas the two successional stages significantly differ in their importance of flowering ($F = 10.60; P < 0.008$).

The proportion of flowering shoots was significantly different between the two successional stages ($F = 10.60$, $P < 0.01$). Old populations had a lower (43.7%) proportion of flowering shoots than young populations (91.67 %, Figure 1B).

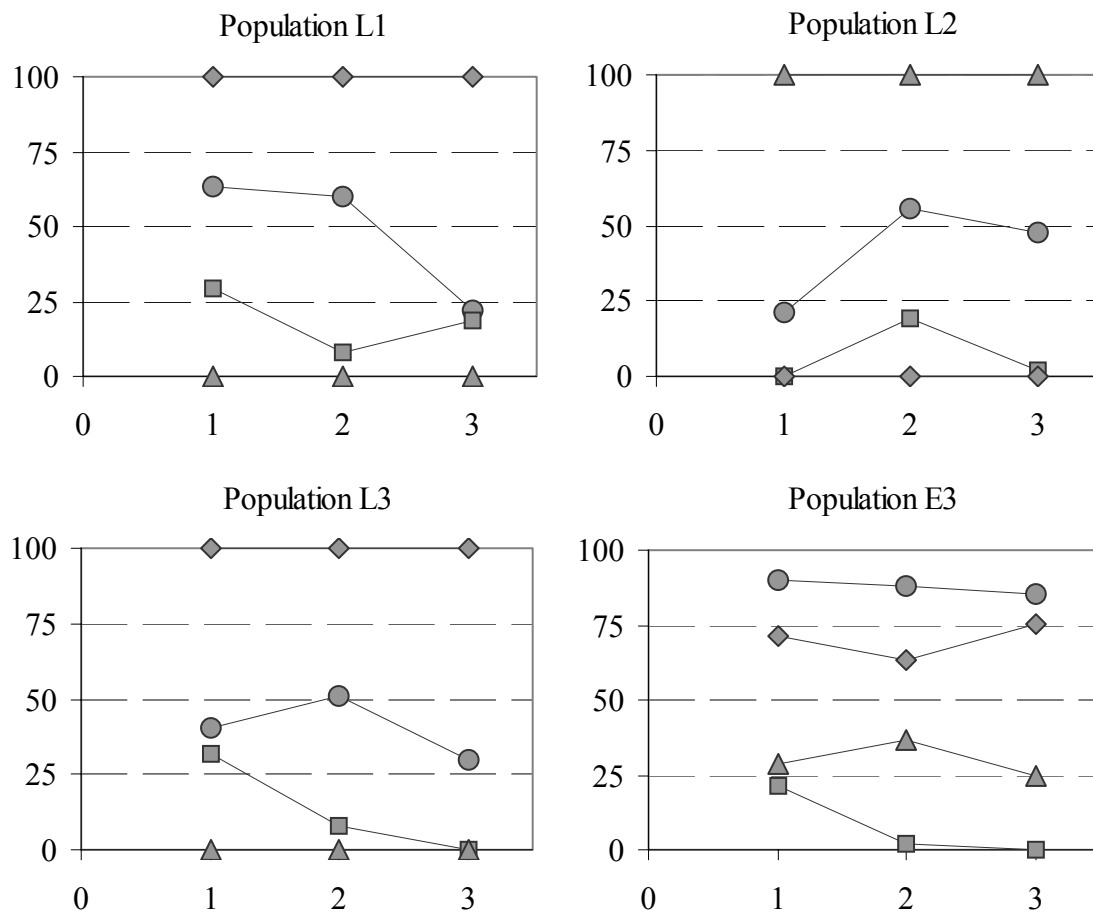


Figure 2: Proportion of males (▲), females (◆), buds (■) and flowering shoots (●) observed in four natural populations of *C. arvensis* during the flowering time. On the abscise axis 1, 2, 3 represent respectively the beginning, middle and the end of flowering. The proportion of males and females were calculated as the percentage of males and females observed within the flowering shoots. The percentage of buds and flowering shoots were calculated over the total number of plants observed within populations.

Comparison of reproductive outputs between males and females did not reveal significant differences for the number of flower heads (Table 2), but showed significant differences for number of florets per flower head in old populations ($t_{(838)} = 3.8$ $P < 0.01$).

Table 2: Descriptive statistics of variables measured in *C. arvensis* females (♀) and males (♂) in populations of early and late successional stages (respectively three and nine populations). In the table (N) represents the sample size and (Ci) the 95% confidence interval.

		Early successional stage			Late successional stage		
		Mean	N	Ci	Mean	N	Ci
Plant size (cm)		93.5	32	7.4	123	49	5.6
Reproductive output	Flower head ♀	23.5	102	2.8	15.8	230	1.1
	Flower head ♂	31.8	18	13.0	12.6	25	6.2
	Floret ♀	77.4	293	3.3	65.1	755	1.2
	Floret ♂	80.4	65	14.4	70.9	84	12.5
	Fruit set	34.2	231	8.8	24.5	407	3.8
	Achene mass (mg)	1.2	214	0.06	1.2	362	0.03
	Germination (%)	32	24	7.6	34.2	21	8.2
Dispersal	Pappus ♀	22.9	734	0.7	21.9	1433	0.3

Males in old populations had more florets per flower head than females. The analyse of variance did not reveal successional stage effect for characters measured in male plants (Table 3). However, in females the same analyse showed significant differences between the two successional stages for the number of flower heads per plant and number of florets per flower head (Table 3).

Table 3: Effect of successional stage on the reproductive and dispersal out put in male and female of *C. arvensis*. The table summarises the results of the nested analysis of variance showing the degree of freedom, the F-values and the level of significance (NS $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$). The number of flower heads per plant (Flower head) and the number of flowers per flower head (Floret) were measured in both males and females. The pappus length (Pappus) and the average mass of a seed (mass of a seed) were measured in females only. The analysis of variance was performed separately for male and female plants. Populations were nested into successional stage.

		Females			Males		
		df	F	P	df	F	P
Flower head	Successional stage	1; 8	9.95	**	1; 2	3.43	NS
	Population	8; 322	3.12	***	2; 39	12	***
Floret	Successional stage	1; 8	5.26	*	1; 2	0.38	NS
	Population	8; 1038	13.78	***	2; 145	22.02	***
Pappus	Successional stage	1; 8	1.97	NS	-	-	-
	Population	8; 2157	38.82	***	-	-	-
mass of a seed	Successional stage	1; 8	0.07	NS	-	-	-
	Population	8; 566	12.42	***	-	-	-

Plants in young populations produced more flower heads per plant and more florets per flower head than plants in old populations (Figure 3).

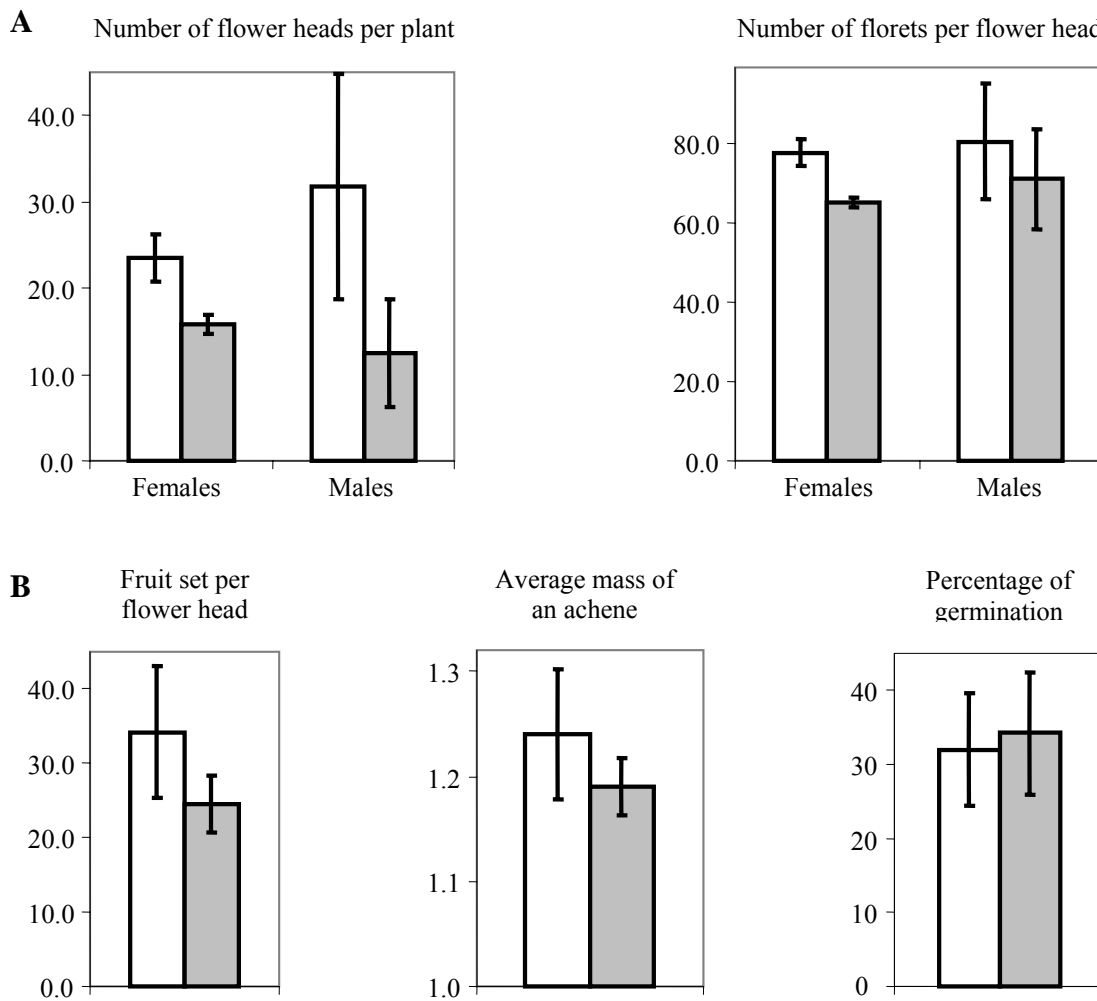


Figure 3: Reproductive output measured in the field in 12 populations of *C. arvensis*. Open and shaded bars represent respectively young and old populations. Error bars represent the 95% confidence interval. **(A)** Females in young populations have a significantly greater number of flower heads per plant and number of florets per flower head than females in old populations. The same characters do not present significant differences between the two successional stages in males. **(B)** All characters measured in achenes do not show any significant differences between young and old populations.

The fruit set and the average mass of an achene did not significantly differ between young and old populations (respectively $F = 1.30$; $P > 0.28$ and $F = 0.07$; $P > 0.79$; Figure 3). The percentage of germination did not significantly differ among achenes families coming from young and old populations ($F = 0.14$; $P > 0.71$; Figure 3). However, we tested a single population for each successional stage; therefore, we could not directly test for a successional effect.

Fruit set class distribution revealed similar patterns of relative frequency between the two successional stages (Figure 4).

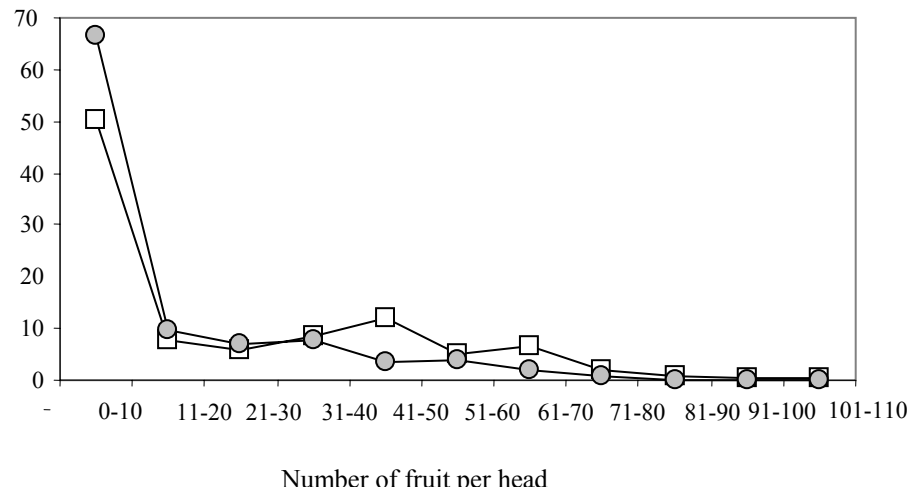


Figure 4: Frequency distribution of the average fruit set per flower head measured in young and old populations of *C. arvensis*. The plot with squared symbols represents young populations, whereas the plot with round symbols represents old populations.

For the dispersal capacities, the pappus length did not differ significantly between the two successional stages ($F = 1.97$; $P > 0.05$; Figure 5). Finally, the average height of plants was significantly different between the two successional stages ($t_{(79)} = -6.5$; $P < 0.001$). Plants in old populations were about 25% taller than plants in young populations (Figure 5).

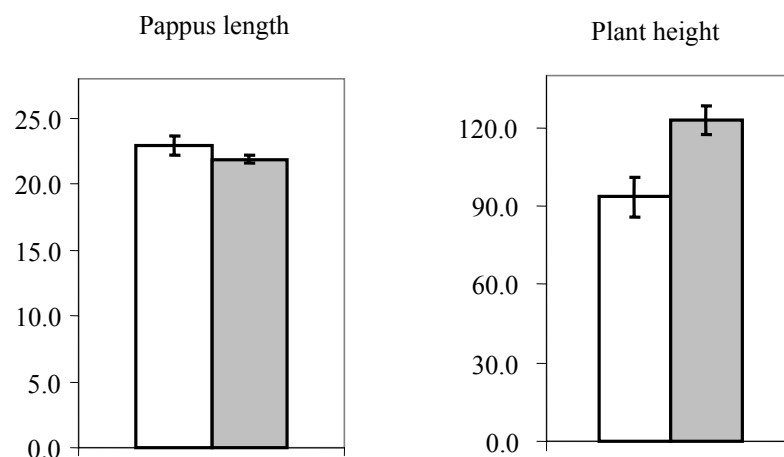


Figure 5: Dispersal capacity (pappus length) and plant height measured in the field in young and old populations of *C. arvensis*. Open and shaded bars represent young and old populations respectively. Error bars correspond to the 95% confidence interval. Pappus length and plant height are expressed in mm and cm respectively.

Discussion

The overall sex ratio in natural populations of *C. arvense* was heavily biased towards females (72 %) irrespectively of the population successional status. The sex ratio did not change over time during the flowering season in the four populations surveyed. Similar female to male ratios of 3 to 1 have already been reported for *C. arvense* in Lake Yssel in the Netherlands by Bakker (1960) and in England by Kay (1985). However, two old populations consisted almost entirely of males (L2 & L5) and a single small old population (L8) had an equilibrate 1:1 ratio.

The inheritance of sex in *C. arvense* is poorly known. The only investigation of this issue was done by Correns (1916), who proposed that males were heterogametic and the female homogametic. However, as the crosses were interspecific (*Cirsium arvense* ♀ + *Cirsium oleraceum* ♂), the results are hardly interpretable. Moreover, other studies that looked at the sex ratio of progeny clearly showed strong females biases (around 1 male for 80 females, Lalonde and Roitberg, 1994). These results strongly suggest a complicated inheritance of sex in *C. arvense*, with possible nuclear-cytoplasmic factors involved in the turn of offspring into females (like in *Thymus vulgaris*; Couvet et al., 1986).

The principal effect of a female biased sex ratio is the poor availability of pollen donors, which might lead to important changes in seeds quantity and quality. For example, Lalonde and Roitberg (1994) demonstrated that a reduction of pollination success increases the average achene mass. In our study, there were no significant differences in the average mass of an achene between young and old populations. Moreover, populations of both stages present a similar pattern in their frequency distribution of the number of fruits produced per flower head. Although seed abortion was high (more than 50% of flower heads did not produce a seed), it appears invariant with respect to the successional stage. These results, adding to the fact that seeds were produced even in populations composed by 100 percent of female plants, suggest that young and old populations experience similar pollination conditions. This can be explained by the high mobility of bumble bees (Walther-Hellwig and Frankl, 2000), which are the main pollinators of *C. arvense*.

Young and old populations of *C. arvense* differ in their reproductive output. Young populations have a higher percentage of flowering shoots. Plants in young populations produce more flower heads per shoot and more florets per flower head. These results were found only for female plants; however, we observed similar trends in males. The non-

significance of the variance analysis in males might result from the low size of the samples. Because of the highly female-biased sex ratio, male plants were difficult to find and to sample in natural populations.

Plant size, average mass of an achene and germination did not vary significantly with population age. This discards the hypothesis that the decrease of reproductive output is due to environmental factors (like a reduction of resources in old populations) or maternal effects. Moreover, in clonal species, a decrease of reproductive output occurring with an increase age of populations might be due to the accumulation of somatic mutations, which affect sexual reproduction (Barrett, 1980; Carson et al., 1982; Klekowski, 1988; Klekowski and Godfrey, 1989; Eckert et al., 1999). As the average mass of an achene and the germination rate are not affected by population age, reduction of reproductive output should result from a selective process.

In a metapopulation context, local populations of different successional stage may experience opposing selection pressures. In early successional habitats, where seedling recruitment is frequent relative to late successional habitats, plants that maximise their resource allocation to sexual reproduction and dispersal will be selected. In late successional habitats, plants that maximise allocation to vegetative growth and survival will be selected by density dependant selective pressures. Because achenes are the primary means of dispersal in *C. arvensis*, sexual selection will be selected at the metapopulation level for the foundation of new populations. Consequently, new populations are generally composed of genotypes with a high output for sexual reproduction. However, when the population reaches the habitat's carrying capacity, density dependant selection pressures will be maximal and genotypes that the best at clonality will be selected (Harper, 1977; Abrahamson, 1980; Gray, 1987; Eriksson, 1993). As clonal extension is favoured within populations, while sexual reproduction is counter-selected, a decrease of reproductive output over time is expected and should result from evolutionary changes in the genetic composition of populations. This is supported by several theoretical models (Ronce and Olivieri, 1997). Ronce and Olivieri assume that differences between populations are genetic (i.e. distinctive genotypes with different selective values for reproductive output have been selected in different local populations) and predict a decrease of the average reproductive effort when populations get older (Ronce and Olivieri, 1997). The model developed by Ronce and Olivieri was developed for species that have overlapping generations but no senescence and could be applied to *C. arvensis*.

Studies that followed the reproductive effort through time (Beasleigh and Yarranton, 1974; Antos and Allen, 1999) or compared populations in sites which differed in successional stage or disturbance (Gadgil and Solbrig, 1972; Quinn et al., 1972; Hickman, 1975; Holler and Abrahamson, 1977; Ross and Quinn, 1977; Grace and Wetzel, 1981; Escarré et al., 1985; Escarré and Thompson, 1991; Piquot et al., 1998) generally found a decrease of reproductive effort with an increasing maturity of the habitat.

However, variation in reproductive output maybe genotypic or may result from phenotypic plasticity. Not all studies cited above attempted to separate environmental and genetic components. In some cases, differences between habitats were found to be genetic (e.g. Gadgil and Solbrig, 1972; Escarré et al., 1985; Escarré et al., 1994; Grace and Wetzel, 1981). In others, they were attributed to an environmental plastic response of plants (Beasleigh and Yarranton, 1974; Hickman, 1975; Holler and Abrahamson, 1977; Ross and Quinn, 1977; Antos and Allen, 1999), or both (Reinartz, 1984).

Here, we recorded characters in natural populations of *C. arvensis*. The hypothesis that changes in reproductive output were due to phenotypic plasticity can not be excluded. However, in a molecular study of the same area we found an extremely high population differentiation (Solé et al., 2004) independent of geographical distance (even within each successional stage). This high population differentiation was partly due to founder effects, but the occurrence of a strong selection during the early successional stages can not be rejected.

Similarly to reproductive output, two opposing selection pressures act on dispersal when a habitat is maturing, selection for dispersal during recolonisation, and selection against dispersal once a population is founded. Therefore, changes in dispersal capacity over time might also be explained by evolutionary changes in the composition of populations in a metapopulation context (Olivieri et al., 1995). Assuming local extinctions to be the sole source of environmental variation, and dispersal capacities to have a genetic basis, the model of Olivieri et al. (1995) predicts a decrease of dispersal with an increase of habitat maturity. Environmental studies that looked at dispersal capacities during succession are rare. Some studies found genetic changes in populations composition (Olivieri et al., 1983; Peroni, 1994; Cody and Overton, 1996), whereas in others the variation in dispersal capacities was clearly due to phenotypic plasticity (Imbert and Ronce, 2001) or maternal effects (Donohue and Schmitt, 1998; Acosta et al., 1997).

Although the pappus is one of the most obvious characteristics of *C. arvensis* achenes, we did not detect differences in the pappus length of *C. arvensis* between young and old populations. This result calls for the suitability of this trait for estimating the dispersal potential in plants. Many methods (including falling velocity experiments, diaspore flight angle, releasing height...) have been developed to determine dispersal potential in anemochorous species (Sheldon and Burrows, 1973; Greene and Johnson, 1990; Hensen and Müller, 1997), but there is no consensus about which estimator is the best. Peroni (1994) noted that differences in dispersal potential appeared smaller when dispersal capacity was measured by a continuous variable (wing loading ratio in her case) than when dispersal capacity was measured by discontinuous variable (presence / absence of a pappus).

Furthermore, the pertinence of the length pappus for estimating the dispersal potential in *C. arvensis* may be arguable, since the pappus often breaks off the achene (Bakker, 1960; Bostock and Benton, 1979). Thus, an estimation of the percentage of achenes released might have been a better parameter than the length of the pappus to assess dispersal potential in *C. arvensis*. Recently, new models about wind dispersal and assessment of dispersal potential, which include topography, weather conditions, turbulence and thermal up-drafts, have been developed (Nathan et al., 2002; Tackenberg et al., 2003; Tackenberg, 2003). Tackenberg (2003) showed that wind dispersal potential was more sensitive to weather conditions than falling velocity. These new results should be taken into account in the future when choosing a variable to estimate dispersal potential of plant species

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