

General introduction

Genotypic and genetic diversity in natural populations

Natural populations of animals and plants are rarely composed of randomly distributed alleles* but reflect a complex mosaic of frequent and infrequent genotypes** (Murawski and Hamrick, 1990 ; Aspinwall and Christian, 1992; Lokker et al., 1994; Lynch and Milligan, 1994; Hänfling and Brandl, 1998; Schläpfer and Fischer, 1998; Ayres and Ryan, 1999). The relative abundance of these genotypes is not fixed, but may vary over the life span of populations. Hence, natural populations of plants and animals are genetically structured in space and time (Ewing, 1979; Chevillon et al., 1995; Hossaert-McKey et al., 1996). Such evidence for spatial and temporal genetic structures clearly emerged during the last three decades with the development of molecular markers and the access to the genotype of individuals. Then, with the increasing body of genetic data, research began to focus on the identification of the ecological and evolutionary processes responsible for such genetic structures. In plant species, Loveless and Hamrick (1984) reviewed the effect of several species traits on population genetic structure. They looked among others at the effect of breeding systems, floral morphology, pollination mechanisms, dispersal modes, life cycles, and size of populations. The main result of this review was that the breeding system is the principal factor designing the genetic structure of plant populations.

Genotypic and genetic diversity in clonal plants

In clonal plants, which have a mixed breeding system (sexual-asexual), clonality may affect the genetic variation and structure of natural populations. As clonal growth does not produce any genetic variation, the question whether clonal species harbour the same genetic diversity as non-clonal species has been often discussed (Williams, 1975; Harper, 1977; Abrahamson, 1980). An increasing amount of literature on this topic has demonstrated that a wide range of genetic diversity can also be found in populations of clonal plants (Ellstrand and Roose, 1987; Hamrick and Godt, 1990; Eckert and Barrett, 1993; Widén et al., 1994; Herlihy and Eckert, 2002).

* **Allele:** one of the different forms of a gene or DNA sequence that can exist at a single locus

** **Genotype:** the actual alleles present in an individual.

Nevertheless, although the genetic variation and structure of clonal plant populations have been intensively studied, the maintenance, evolution, and factors influencing clonal diversity remain poorly understood (Eckert, 1999). It is obvious that only descriptions of the genetic patterns are not enough to understand the structuring of genetic variation within and between populations (McLellan *et al.*, 1997). In contrast, an investigation of genetic variation combined with an investigation of factors responsible for its creation and maintenance (i.e. processes that have led to these patterns) might be more relevant to relate the genetic diversity to the ecology of the studied organism.

Factors influencing genotypic and genetic diversity

An important factor that must be taken into account when one studies the genetic diversity of natural populations is the temporal heterogeneity. It has already been demonstrated that temporal heterogeneity can influence the genetic variation within and between populations (Ewing, 1979; Tilman, 1984; Hossaert-McKey *et al.*, 1996; Stanton *et al.*, 1997). However, it remains difficult to follow natural populations through long periods. A bypass to this difficulty can be to investigate natural populations having contrasting biotic and abiotic selective pressures. For example, ecological succession is a case often studied in ecology where biotic and abiotic selective pressures change with the age of populations (Quinn *et al.*, 1972; Beasleigh and Yarranton, 1974; Ross and Quinn, 1977; Escarré and Thompson, 1991; Piquot *et al.*, 1998). Looking at natural populations of different successional stages may help to understand the evolution of genetic or life-history characters over time.

Another important source of variation that acts on genetic diversity of natural populations comes from the herbivory selective pressures. It has already been demonstrated that herbivores and pathogens can affect the genetic diversity of plants (Mopper *et al.*, 1991; Krabel and Petercord, 2000; Koskela, 2002; Chen *et al.*, 2001). For example, in Douglas-fir (*Pseudotsuga menziesii*), Chen *et al.* (2001) demonstrated that phenotypically resistant trees to defoliation by the western spruce budworm (*Choristoneura occidentalis*) were less heterozygote but had more rare alleles compared with susceptible trees. However, it is not clear whether differences in genetic variation of the host are a consequence or a cause induced by the biotic selection pressures, and the impact that herbivores and pathogens have on the neutral genetic diversity of populations remains unknown.

Although most of the variation expressed in genetic characters is neutral, variation expressed in life-history characters is usually non-neutral (i.e. induces changes in fitness). Life-history characters are assumed to undergo selection. Thus, the variation observed in life-history characters can be considered to result from heterogeneous selective pressures. For this reason, a mixed approach that combines the comparison of both characters (neutral genetic and selected) is important to localise selective pressures that act on natural populations (Bonnin et al., 1996).

Finally, most plant or animal species are organised as a set of local populations that interact via the dispersal of individuals. Such a spatial dynamic organisation of populations is called “metapopulation” (i.e. a population of populations which go extinct locally and recolonise; Levin, 1970). In a metapopulation organization, local populations do not obligatorily experience the same selective pressures. Therefore, certain characters of plants or animals might evolve differently in each local population (Hanski, 1998). For example, along a successional gradient, populations of early and late successional stage experience different local selection pressures. In clonal plants, which have a mixed reproduction system, these different local selection pressures might lead to different strategies of reproduction. In early stages of succession, the selection regime may favour individuals which display the best capacities for clonal reproduction (i.e. the best competitors, Ronce and Olivieri, 1997; Piquot et al., 1998). Sexual reproduction will be counter-selected at the population level. But because seeds are often the only mean of long distance dispersal for numerous clonal plants, sexual reproduction will be selected at the metapopulation level to assure the foundation of new populations in more favourable habitats.

In this case, the evolutionary equilibrium of characters related to the reproduction system (e.g. dispersal and reproductive effort) is not achieved at the population level, but at a higher level (the metapopulation level) while each local population is in disequilibrium (Olivieri et al., 1990; Olivieri and Gouyon, 1997).

Consequently, it is important to consider the metapopulation level while one studies traits that do not experience the same selective pressure during the different demographic stages of the population life span. Metapopulation approaches are also particularly relevant to study species in fragmented habitats (Hanski, 1998).

Cirsium arvense

This work is about the genetic diversity of a clonal plant, *Cirsium arvense*. *C. arvense* (Asteraceae), also called “Creeping thistle” in Europe or “Canada thistle” in North America, is one of the most frequent and most successful perennial weeds throughout Eurasia (Figure 1 from Meusel and Jäger, 1992).

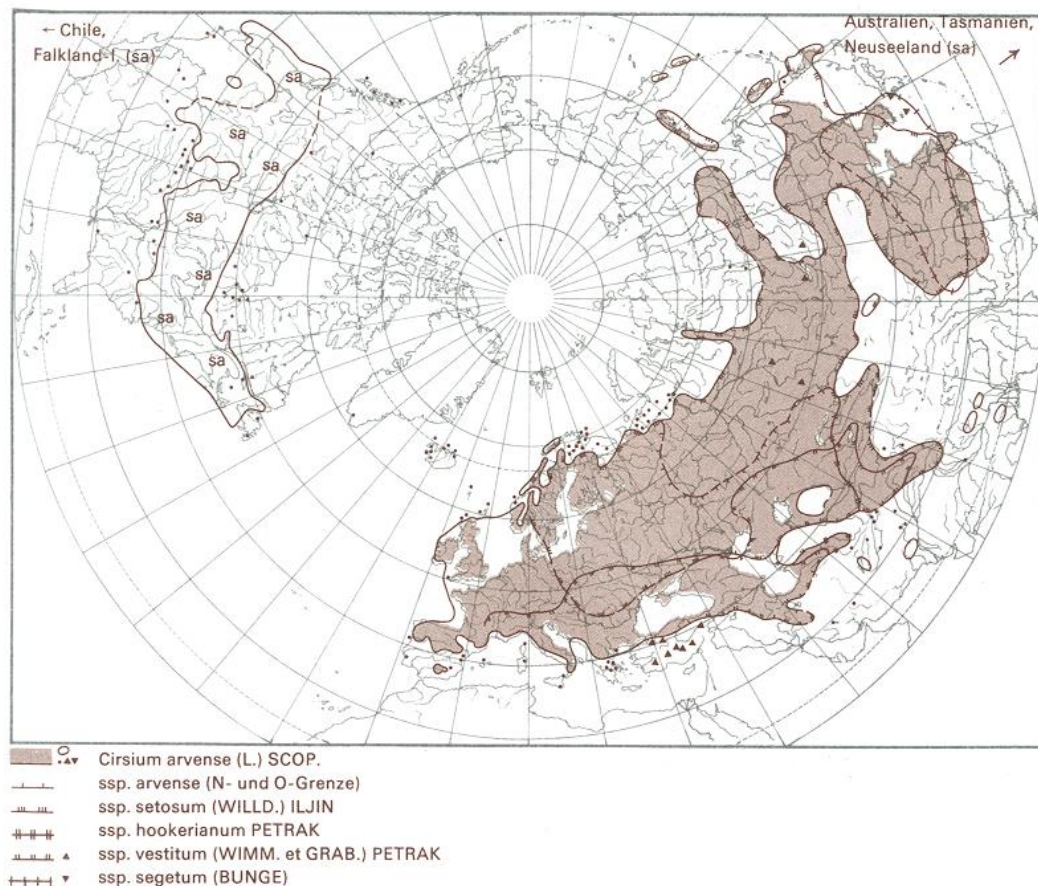


Figure 1: Geographical distribution of *Cirsium arvense* and subspecies within the northern hemisphere. Source: Meusel & Jäger (1992)

C. arvense occurs over a wide range of elevations from sea level (up to 2500m). The wide distribution of *C. arvense* suggests that the plant is adaptable to many soil types (Donald, 1994). *C. arvense* is an early successional species that emerges from seeds or root fragments shortly after disturbance. *C. arvense* grows best in open moist sunny sites. It usually grows in waste places, roadsides, fallows, or especially in arable fields and meadows or sites that have been impacted by disturbance (e.g. road building, fire, landslides...). Hence, the increasing intervention of humans in natural landscapes, which mostly opens the vegetation, multiplies suitable sites for *C. arvense*. The species is nowadays omnipresent in agricultural or semi-

natural landscapes. Furthermore, roads, streams and ditches offer new corridors for invasion. Thus, *C. arvense* invasion of native rangelands appears a problem especially for farmers who are worried about its invasion to arable fields.

Because of its economic importance (Moore, 1975; Donald, 1990) *C. arvense* has been intensively studied during the last century (Correns, 1916; Bakker, 1960; Lloyd and Myall, 1976; Hunter et al., 1985; Kay, 1985; Lalonde and Roitberg, 1989; Lalonde and Roitberg, 1994; Ang et al., 1995; Heimann and Cussans, 1996).

As most of perennial plants, *C. arvense* has a mixed reproduction system. Plants combine two modes of reproduction: sexual reproduction through seeds and clonal reproduction through vegetative propagation. *C. arvense* life cycle is presented in Figure 2.

Plants develop new roots and underground shoots in January and begin to elongate in February. New shoots of established *C. arvense* plants begin to emerge when average weekly temperature is at least equal to 8°C (Nuzzo, 2000). Plants remains short until a long day period activate stem elongation and flowering (Moore, 1975). The blooming period is bright, varies from place to place, but appears between May and October in Europe.

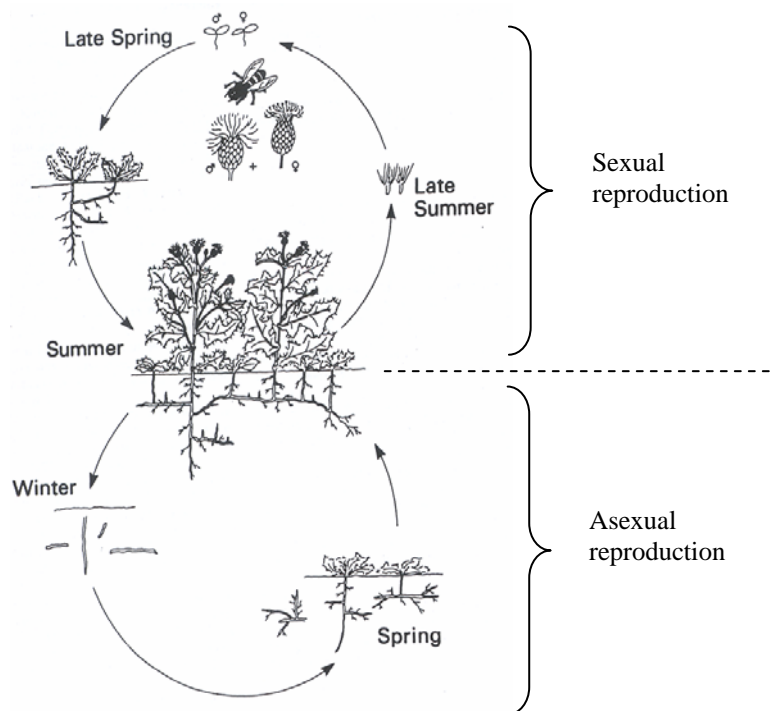


Figure 2: Life cycle of *Cirsium arvense* from Heimann & Cussans (1996)

In *C. arvensis*, blooming capability as well as others life-history characters might be altered by the tephritid fly *Urophora cardui* (Peschken and Harris, 1975; Peschken *et al.*, 1982; Heeb *et al.*, 1999). *Urophora cardui* is a gall-forming insect which attacks *C. arvensis* (Figure 3). In this plant-herbivore system, *U. cardui* is able to occur only within a narrow range of environmental conditions (Peschken *et al.*, 1997)

as the clonal *C. arvensis* as well as *C. setosum* are the only host plants of this species (Frenzel *et al.*, 2000). Adults of *U. cardui* emerge in early summer (June to July) and females lay eggs into suitable shoots of the host. With the development of the larvae the plant is forced to produce conspicuous multilocular stem galls (Peschken and Harris, 1975, Peschken *et al.*, 1982; Peschken and Derby, 1992).



Figure 3 :gall of *U. Cardui* on *C. arvensis*
(from Hegi, 1987)

C. arvensis has an open breeding system. The plant is reported to be subdioecious-dioecious. Male plants are morphologically hermaphrodites, with a vestigial ovary (Delannay, 1979). *C. arvensis* is insect pollinated, and pollinators mostly observed are bees (honey bees and wild bees), which can cover relatively important area (Walther-Hellwig and Frankl, 2000). Although *C. arvensis* is mostly known for its efficient vegetative reproduction, the species also produces high quantity of achenes. Mayer (2000) found that thistle stands produced between 7600 and 21000 well-developed achenes per m² in fallow sites. *C. arvensis* achenes are plumed, and can be easily dispersed by wind. Most achenes germinate in spring after the year in which they are produced (Bakker, 1960), but some achenes might germinate in the year, produce basal leaves before winter and then emerge to flower the next spring. The soil seed bank does not usually contain large numbers of *C. arvensis* achenes (Heimann and Cussans, 1996). No seedling establishment is usually observed in dense natural populations (Bakker, 1960; Bostock and Benton, 1983).

C. arvensis has a reputation to have a vigorous clonal propagation. *C. arvensis* does not form rhizomes. Vegetative reproduction (or clonal growth) is realised through efficient lateral roots (Figure 4). Horizontal roots are very productive (six and 12m per year in Moore (1975) and Bostock and Benton (1979) respectively) and give rise to numerous aerial shoots. *C. arvensis* allocates most of its resources to vegetative propagation. Total allocation of dry weight to sexual reproduction was only 7% for *C. arvensis* grown in pots (Bostock and Benton, 1979). New *C. arvensis* plants can also form from root fragments as short as 6 mm (Nadeau and Vanden Born, 1989). Therefore, *C. arvensis* can easily survive disturbance by resprouting from buried root and stems fragments. Long distance dispersal by vegetative propagules is not common in *C. arvensis*, as roots are deeply buried in the soil.



Figure 4: Two shoots of *C. arvensis* connected by horizontal roots.

Although a lot of information has been accumulated about the ecology and biology of *C. arvensis*, data about its genetic diversity are missing. The aim of this Ph-D was to conduct a mixed approach combining ecology and molecular biology to identify, on a landscape scale, the main factors acting and designing the genetic diversity of *C. arvensis* in natural populations.

Outline

The primary step of an ecological and genetic study of a clonal plant is the identification of clones. In clonal plants, each individual shoot (ramet) can produce offspring through sexual and/or asexual reproduction. Physiological individuals do not fit with genotypic ones, and the identification of clones in the field is often impossible. Hence, the first objective of this work was the identification of clones. For this purpose, we required to molecular biology. The choice of the molecular marker we used, as well as essential information about molecular markers in general are developed in the appendix.

Chapter I concerns the genotypic and genetic diversity of the common weed *Cirsium arvense*. In many clonal species, seedling establishment is restricted to early successional stages when recruitment is still possible. Then, one expects that adapted genotypes become dominant and genotypic and genetic diversity should decrease with time. In order to check this hypothesis, I compared genotypic and genetic diversity of *C. arvense* populations in early and late successional stage. I used highly polymorphic AFLP markers and found that contrary to the general expectation, genotypic diversity, clonal evenness and genetic diversity (i.e. molecular variance) did not differ significantly between founder and established populations (respectively: $U = 24, P > 0.3$; $U = 26.5, P > 0.3$; $U = 23; P > 0.44$).

However, the most surprising result of this study was the extremely high genetic structure among populations ($\Phi_{sc} = 0.64$) which occurred without loss of diversity. It is proposed that genetic differentiation among populations might result from founder effects and early selection in the seedling stage, while because of the particular reproductive system of the species (dioecious) seeds that are produced must be highly variable and therefore their recruitment (even sporadically) might contribute to maintain a high genotypic and genetic diversity. In *C. arvense* genotypic and genetic diversity mainly seem to reflect the status built up during the early stage of succession.

Chapter II looks at the influence of the phytophage insect *Urophora cardui* on *Cirsium arvense* neutral genotypic and genetic diversity. Several studies in controlled conditions have demonstrated that *U. cardui* has profound negative effects on life history traits of its host (*C. arvense*). The purpose of this chapter is to test rather these negative effects observed on an individual scale influence the neutral genotypic and genetic diversity of natural populations of the host plant. To investigate the effect of *U. cardui* on *C. arvense* neutral genotypic and genetic diversity, I used AFLP markers eight populations of *C. arvense*

having different history of infestation by *U. cardui*. Half of the populations were in the last 5 years infested by *U. cardui*, whereas the other half was not. The results were the following: average genotypic diversity and clonal evenness did not differ between infested and not-infested populations ($U = 6; P > 0.56$; $U = 5.5; P > 0.46$) for clonal evenness). Molecular variance due to infestation state of populations was also not significant (1.81 ± 1.05 versus 2.22 ± 0.82 ; $P > 0.11$) and explained less than five percent of the total variance. Hence, the results suggest that selection imposed by *U. cardui* on *C. arvensis* was weaker on a population and/or metapopulation scale than it was supposed in experimental studies. This can be explained by the complex spatio-temporal population dynamics of the *C. arvensis-U. cardui* system.

Chapter III further analyses the impact of ecological succession on natural populations of *C. arvensis*. Whereas chapter I attempted to look at the impact of ecological succession on neutral molecular characters, chapter III is based on life-history characters, which are supposed to be selected. Certain life-history characters, especially those related to the breeding system, are generally considered to be able to evolve rapidly when affected by a change in the selection regime (Fisher, 1930; Reznick et al., 1990; Li and Margolies, 1994; Cody and Overton, 1996). Therefore, this chapter focuses on the reproductive effort and on the dispersal potential of *C. arvensis*. Female and male of *C. arvensis* plants were collected in three populations of early successional stage and in ten populations of late successional stage. Succession caused no change in the dispersal potential of *C. arvensis* (length of the pappus), but important phenotypic changes in characters related to the reproductive outputs. These changes included 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). Data on achene mass and germination rate show no relation to the successional stage of plants ($F = 0.07$; $P = NS$ and $F = 0.14$ $P > 0.71$). Based on recent theoretical investigations on the reproductive effort in metapopulation context (Ronce and Olivieri, 1997), it is suggested that the differences found in reproductive effort may result from evolutionary changes in the genotypic composition of populations because of increasing intraspecific selection pressures when the habitat is maturing. This idea of selection during early successional stage is supported by previous genotypic analysis of some populations with AFLP markers (Solé et al., 2004). However, we found no changes in the dispersal potential (length of the pappus) of *C. arvensis*. Chapter III also discuss the role of the length pappus to estimate the dispersal potential in this species.

Own contribution

Since the scientific papers are co-authored by several people, the own contribution (%) of Magali Solé is listed subsequently.

Chapter I: Genotypic and genetic diversity of the common weed *Cirsium arvense* (Asteraceae). Together with Walter Durka, Sabine Eber, Roland Brandl.

1. Sampling and data acquisition 80%
2. Data analysis 90%
3. Writing paper 70%

Chapter II: Does history of parasitism by *Urophora cardui* influence the genotypic and genetic diversity of *Cirsium arvense*? Together with Walter Durka, Sabine Eber, Roland Brandl.

1. Sampling and data acquisition 70%
2. Data analysis 90%
3. Writing paper 80%

Chapter III: Environmental study of reproductive and dispersal efforts of the common weed *Cirsium arvense* on a metapopulation level. Together with Yves Piquot, Walter Durka, Roland Brandl

1. Sampling and data acquisition 90%
2. Data analysis 90%
3. Writing paper 70%

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