

Discussion and outline

This chapter discusses the results of this work on two levels - generally together with the ecology of clonal plants, and more specifically with the biology of *Cirsium arvense*.

Part I

Genotypic diversity has long been controversial issue in clonal plants. Whereas sexual reproduction allows recombination and production of new allele combinations, clonality propagates the same genotype (mutations excepted). This difference between the two means of reproduction has led people to hypothesise that clonality should lower the genetic variation in clonal plants in comparison to non-clonal plants. (Abrahamson and Gadgil, 1973; Williams, 1975; Harper, 1977; Abrahamson, 1980).

In *C. arvense*, the genotypic diversity was high (proportion of distinguishable genotypes equalled 0.73 ± 0.25 (mean \pm SD)). This result is in accord with the literature accumulated on this topic during the last three decades, which has led to reviews that demonstrate that clonal plants are as variable to non-clonal plants (Ellstrand and Roose, 1987; Hamrick and Godt, 1990; Widen et al., 1994). With regard to this surprising result, genotypic diversity in clonal plants became controversial and research strongly focused on factors responsible for this considerable level of variation (Silander, 1985; Klekowski and Godfrey, 1989; De Kroon and Van Groenendael, 1997; Klekowski, 1997).

In clonal plants, which have mostly a mixed reproduction system, occasional establishment of seedlings (if not inbred) is often proposed as a powerful mechanism generating genotypic variation (Soane and Watkinson, 1979; Marshall and Weir, 1979; Watkinson and Powell, 1993; Bengtsson, 2003).

In *C. arvense* seedling recruitment is not excluded in the first years following the establishment of populations, but must be improbable once populations have reached the carrying capacity (Bakker, 1960). Moreover, Eriksson (1989) reported no evidence for seedling recruitment in established populations in 60% of the 68 clonal species that he reviewed; a statement that moderates the power of seedling recruitment to explain the high genotypic variation in clonal plants. According to Bengtsson (2003), the fact that populations with limited or missing seedling recruitment nevertheless display a high genotypic variation, can be explained by the population effective “memory” of their earlier genetic history. In his

theoretical work, Bengtsson looked at the “Genotypic Identity” of populations (i.e. the probability that two randomly sampled adult individuals from a population have the same genotype) depending on population growth parameters, rate of sexuality and recruitment of sexually derived offspring. From his simulations, he concluded that: “a population which was started by a number of sexually derived propagules may thus retain its initial genotypic variation for a very long period of time, even if it later reproduces almost exclusively asexually”.

Coalescence theory (Kingman, 1982) can be used to illustrate the influence of clonality on population genetic variation. The coalescence theory aims to reconstruct the genealogy of a sample of observed gene copies, according to a specific mutation model of the molecular marker used to estimate the genotypic diversity, and according to the demographical history of populations. The coalescence time of a sample of observed gene copies is the time to the most recent common ancestor of these observed gene copies (expressed in number of generations). Whereas the normal coalescence time is $2N$ (for a large and constant population size N), Bengtsson (2003) obtained greater coalescence time in his model developed for partial asexuality (i.e. $4N$ for gene copies taken from the same individual, and $3N$ for gene copies taken from different individuals). This result means that clonality enlarges the coalescence time and thus allows genes copies to persist longer within populations.

From all these theoretical and experimental data, the general hypothesis that clonality should lower the genetic variation in clonal plants in comparison to non-clonal plants appears outdated. Predominantly asexual populations can display any pattern of genotypic and genetic variation, and can be as variable as non-clonal populations.

As already emphasized by McLellan et al. (1997), more relevant than the amount of variation is the distribution of the genotypic and genetic pattern within and among populations and the evolutionary processes responsible for it. Several reviews already attempted to determine which ecological variables are good predictors of genotypic and genetic structures (Hamrick et al., 1979; Loveless and Hamrick, 1984; Baur and Schmid, 1996; Hamrick and Godt, 1996; Bachmann, 2001). Nevertheless, conclusions drawn from these reviews are quite general and the distribution of the genotypic and genetic pattern within and among populations must still be analysed case by case. In *C. arvensis* genotypic diversity and population differentiation were extremely high (proportion of distinguishable genotypes = 0.73 ± 0.25 and $F_{ST} = 0.63$) and most similar genotypic and genetic patterns were found in the literature in species that

have similar ecology, e.g. *Rhus* species that are widespread, clonal, long-lived and dioecious (Sherman-Broyles et al., 1992).

Part II

Natural populations of *C. arvensis* were mostly multiclonal and almost all patterns of clonal diversity were combined with clonal evenness. Thus, genotypic diversity must be studied case by case in *C. arvensis*.

However, the absence of isolation by distance was surprising and might bring some new information about seed dispersal in this species. In *C. arvensis* the fact that the pappus often breaks off the achene has led people to hypothesize that *C. arvensis* possesses a low or limited seed dispersal (Bakker, 1960; Bostock and Benton, 1979). Under this condition, in a metapopulation context where new populations are mostly founded by seeds coming from older ones, one could have expected to observe an increasing genetic divergence of populations with an increasing geographical distance. However, this pattern was not observed with nucleic molecular markers and suggests that genetic divergence among populations might occur, with these markers, at a bigger scale than the 4 km² of the study area. This, this absence of isolation by distance could defend the hypothesis of a long distance dispersal occurring in *C. arvensis*, which is not in accord with the few available data about field experiment seed traps (maximal dispersal distance measured = 139m in Mayer, 2000; less than 0.2% of achenes bore a seed 1 Km from the mother plant, references in Heimann and Cussans, 1996). However, recent models about wind dispersal based on landscape 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 distance dispersal is significantly increased relative to traditional models using terminal velocity. Still, these models need calibrations (e.g. landscapes parameters, falling velocity, seed release rate) and the measurement of real maximum dispersal distance for comparison is impossible. A solution to study seed dispersal in natural populations would be to investigate genetic differentiation and isolation by distance with maternally inherited molecular markers e.g. mitochondrial DNA or chloroplastic DNA more specifically in plants (McCauley, 1995; Ouborg et al., 1999). Indeed, the comparison of patterns of differentiation obtained with nuclear and cytoplasmic markers can inform about the ratio of pollen versus seed gene flow (Oddou-Muratorio et al., 2001; Lian et al., 2003) and might help to determine the seed

dispersal distance. For example, it has already been demonstrated that the ratio of pollen to seed ratio changes with the spatial scale (McCauley 1997 in Ouborg et al., 1999). In *Silene alba*, the author found an increase of pollen dispersal, in comparison to seed dispersal, with an increase of the study area (pollen to seed ratio equalled 3.4, 9.2, and 124.0 at large, intermediate and small scales respectively). In *C. arvensis*, the absence of isolation by distance observed with nuclear inherited molecular markers might be explained by the long distance dispersal of honey bees (up to kilometres; Walther-Hellwig and Frankl, 2000), which leads to an extensive dispersal of pollen. However, it is not excluded that isolation by distance occurs at the same scale according to maternal inherited molecular markers (i.e. in case of limited seed dispersal).

The absence of isolation by distance also questions the application of the metapopulation concept to *C. arvensis*. It is not as straightforward to decide whether populations are organised as a metapopulation. Levins (1970) originally defines the metapopulation as “a population of populations that go extinct and recolonise”. Since this first definition the concept of metapopulation rapidly evolved and become a paradigm in ecology (Hanski, 1998). Currently, the concept of metapopulation can be applied to situations of heterogeneous habitats (islands or patches). Due to isolation from other patches, individual patches have their own dynamics. On the other hand, patches are not completely isolated since they are still connected via gene flow (pollen or seed flow). Under this hypothesis, a genotypic isolation is often found within the metapopulation because of distance-dependant dispersal of propagules (Planes et al., 1996; Colas et al., 1997).

However, recent studies of the demography of *C. arvensis* conducted over five years in the same area have demonstrated a dynamic pattern in time and space with important changes in the number, distribution and size of plant stands (Eber and Brandl, 2003). Whereas large patches were more or less persistent, Eber and Brandl found important turnover rates in small patches with an increasing probability for a patch to become extinct as patch size decreases. This result suggests important extinction–recolonisation events, which fit to the metapopulation concept. In a metapopulation, both local extinction and recolonization events occur continuously. When the recolonization rate of patches is lower than the rate of local extinction, the metapopulation itself becomes extinct and the species disappears from the landscape, which is not the case for *C. arvensis*. Besides, this metapopulation dynamic of populations of *C. arvensis* is confirmed by our study looking at the neutral genetic diversity of populations of *C. arvensis* infested by the phytophagous insect *Urophora cardui*. No specific

influence of *U. cardui* on genotypic and genetic diversity of *C. arvensis* infested populations was found. The metapopulation dynamics of the host plant might play a role to escape the selection pressures imposed by *U. cardui*. Thus, selection imposed by *U. cardui* on natural populations of *C. arvensis* appeared weaker in than it was supposed in experimental studies.

Additionally, the results of the chapter III concerning the evolution of reproductive effort strongly suggest that local populations of *C. arvensis* of different successional stages undergo different selection pressures. Once a population is founded, the selection regime will favour clonality (because of its better strategy for colonisation) leading to a decrease of reproductive effort in female plants of *C. arvensis*. Consequently, the maintenance of sexual reproduction can not be explained at the population level, but at the metapopulation. Because of seed dispersal, which allows the colonisation of new favourable sites, sexual reproduction is selected and maintained at the metapopulation level.

Nevertheless, the genetic basis of the characters linked to the reproductive effort still need to be demonstrated as similar patterns could also result from phenotypic plasticity (Beasleigh and Yarranton, 1974; Hickman, 1975; Holler and Abrahamson, 1977; Ross and Quinn, 1977; Antos and Allen, 1999). The genetic basis of the trade-off between sexual and asexual reproduction in relation to the successional stage of populations has already been demonstrated in *Sparganium erectum* (Piquot et al., 1998). However, as the authors started from ramets instead of seeds, the demonstration was not complete as the decrease of reproductive effort could still result from senescence of plants.

To summarise, patterns of reproductive effort as well as those found in chapter II suggest a spatio-temporal dynamic of *C. arvensis* populations, as it is classically found in metapopulation context, with numerous extinction-recolonisation events. However, this still needs to be confirmed by cytoplasmic data (i.e. seed dispersal) to find out at which scale recolonisation events occur.

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