

Studying genetics of adaptive variation in model organisms: flowering time variation in *Arabidopsis lyrata*

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Abstract

Arabidopsis thaliana has emerged as a model organism for plant developmental genetics, but it is also now being widely used for population genetic studies. Outcrossing relatives of *A. thaliana* are likely to provide suitable additional or alternative species for studies of evolutionary and population genetics. We have examined patterns of adaptive flowering time variation in the outcrossing, perennial *A. lyrata*. In addition, we examine the distribution of variation at marker genes in populations from North America and Europe. The probability of flowering in this species differs between southern and northern populations. Northern populations are much less likely to flower in short than in long days. A significant daylength by region interaction shows that the northern and southern populations respond differently to the daylength. The timing of flowering also differs between populations, and is made shorter by long days, and in some populations, by vernalization. North American and European populations show consistent genetic differentiation over microsatellite and isozyme loci and alcohol dehydrogenase sequences. Thus, the patterns of variation are quite different from those in *A. thaliana*, where flowering time differences show little relationship to latitude of origin and the genealogical trees of accessions vary depending on the genomic region studied. The genetic architecture of adaptation can be compared in these species with different life histories.

Introduction

Arabidopsis thaliana is the best known plant species in terms of its genome and molecular biology (Arabidopsis Genome Initiative, 2000). Its small genome and readily available mutants have made it a favorite organism for developmental and molecular genetic studies. Recently, the interest in the population genetics of *A. thaliana* has increased (Hanfstingl et al., 1994; Innan et al., 1996;

Mitchell-Olds, 2001). At the same time, related species have begun to be seen also as potential model organisms. These relatives offer possibilities to study species with different life histories and the molecular genetic tools of *A. thaliana* can be often readily applied in the relatives (e.g., Kuittinen et al., 2002a). *A. lyrata* is a self-incompatible outcrossing species (Schierup, 1998; Kärkkäinen et al., 1999), to which the extensive population genetics theory of random mating populations can

Table 1. Comparison of *A. lyrata* and *A. thaliana* features

| Trait | <i>A. lyrata</i> | <i>A. thaliana</i> | Reference |
|---------------------|---------------------|--------------------|---|
| Outcrossing rate | 1.0 | 0.02 | Abbot and Gomes (1989) Kärkkäinen et al. (1999) and Schierup (1998) |
| Life cycle | Perennial | Annual | |
| Diploid genome size | 0.46–0.51 pg | 0.23–0.29 | <i>Arabidopsis</i> Genome Initiative (2000), Earle (unpublished) |
| Chromosome # | 8 | 5 | Jones (1963) |
| Distribution | Paleartic, nearctic | Worldwide | |

be applied. In outcrossing species, the different genes evolve more independently than in selfing species, where extensive linkage disequilibrium (LD) of genomes is maintained (Nordborg et al., 2002). The more independent variation of genes may make it easier to examine the evolution and its causes of individual genes. Further, *A. thaliana* is a weedy species, and outcrossing relatives may offer a possibility of studying populations where the effects of recent population expansions are not as much confounding in analyses of sequence variation. Third, for studies of local adaption, it may well be profitable to also use species that are not global generalist weeds.

In this paper, we examine the patterns of variation in one potentially adaptive trait, flowering time. Based on the life history differences between *A. thaliana* and *A. lyrata*, we can ask several questions. First, do the more stable, less weedy populations of *A. lyrata* show signs of local adaptation e.g. in flowering time, related to the environmental conditions. Do the populations of the outcrossing species have much variation within the populations, in comparison to the selfing *A. thaliana*. (e.g. Charlesworth & Charlesworth, 1995). Third, is the current distribution reflected in the genetic structure of *A. lyrata* populations? Do we find consistent patterns of genetic relationships between populations, using data from different parts of the genome. We address these questions with new data on the variation of flowering time, and with some new data and new analysis of earlier genetic markers and sequences. We discuss the implications of the differences between the species for the study of genetics of adaptation.

Materials and methods

Natural history of Arabidopsis lyrata

Arabidopsis lyrata is among the closest relatives to *A. thaliana* based on restriction fragment length polymorphism (RFLP) studies of cpDNA, and sequences of *rbcL* (Price, Palmer & Al-Shehbaz, 1994). Until recently, the two subspecies of *A. lyrata* (ssp. *lyrata* and ssp. *petraea*) were called *Arabis lyrata* and *Cardaminopsis petraea*, but O’Kane and Al-Shehbaz (1997) placed the species (and several others) in the genus *Arabidopsis*. This view of the systematics has been confirmed in many later studies of the Brassicaceae, using both cpDNA and nuclear sequences (Koch, Bishop & Mitchell-Olds, 1999; Koch, Haubold & Mitchell-Olds, 2000, 2001). The proportion of synonymous substitutions between the two species ranges between 10 and 15%, and for aminoacid changing nonsynonymous substitutions the divergence level is about 1–2%. Koch, Haubold and Mitchell-Olds (2000) have estimated a divergence time of about 5 MY for these two species based on *Adh* and *Chs* sequences.

The diploid genome size of *A. lyrata* (Swedish Mjällom and US Michigan populations) measured with flow cytometry is 0.46–0.51 pg, compared with the estimates for *A. thaliana* of 0.23–0.29 pg in the same set of measurements (Earle, pers. comm.). *A. lyrata* and other close relatives have eight chromosomes, against the five of *A. thaliana* (Jones, 1963). The two species can be crossed (Mesicek, 1967; Redei, 1974). Nasrallah et al. (2000) produced viable vigorous offspring from the