The genetic basis of adaptation in Arabidopsis lyrata

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Helmi Kuittinen[1], Bénédicte Quilot[2], Päivi H. Leinonen[1], Johanna Leppälä[1] and Outi Savolainen[1]

[1]University of Oulu, Department of Biology, [2]INRA, Avignon, Department of Ecology and Environmental Science

Introduction

The genetic basis of adaptation is a central question in evolutionary genetics (Orr 1998). It is not known if adaptations are due to changes in regulatory or protein coding parts of the genes, if they occur though many small of few large mutations, or what is the role of interaction between genes and environment. An interesting question is whether similar adaptations occur using similar mutations and same genes in different populations and species (Hoekstra and Coyne 2007).

Arabidopsis lyrata is an outcrossing perennial relative of selfing *Arabidopsis thaliana*. It occurs in isolated populations scattered in Europe and North-America. Transplant studies have shown that populations are locally adapted (Leinonen et al. 2008).

We focus here on two populations, one from a northern, high altitude site (Spiterstulen, Norway) and the second originating from Central Europe (Plech, Germany) (**Fig. 1**). We study the response of the reproductive and morphological characters to environmental cues that are known to affect flowering, and the genetic basis for these differences.

Material and methods

We made an F2 cross between Pech and Spiterstulen *A. lyrata* populations using two independent grandparents from each population.

Growth conditions

We grew F2 plants together with parental populations and F1 plants in growth chambers with three different combinations of photoperiod, vernalization and nutrient treatments. When vernalized, 5 week old rosettes were exposed to 4°C at 8 h photoperiod, for 9 weeks time, and then returned to normal growth conditions.

Experiment	GC01	GC05	GC05
Photoperiod	20 h	14 h	14 h
Fertilization	at day 178	continuous	continuous
Vernalization	no	no	yes
F_2 sample size	181	118	168
Abreviation	LD	14hD	14hDV

Traits scored

Probability and timing of flowering, and traits related to reproductive effort, morphology and size were scored in parents, F1 and F2.

Experiment	Probability	Timing	Reproductive effort	Morphology and size
GC01	Flowering probability at day 99, at day178(fertilization), at day 258	Days to flowering		
GC05	Flowering probability	Days to flower shoot emergence [a]	Nb of inflorescence shoots [a]	Length of main inflorescence shoot [a]
		Days to flowering [a]	Nb of secondary inflorescence shoots [a]	Rosette height [a]
		Days from shoot emergence to flowering [a]	Nb of inflorescence shoots [b]	Length of longest leaf [a]
			Total nb of flowers [b]	Width of longest leaf [a]
				Leaf ratio [a]
				Rosette area [b]

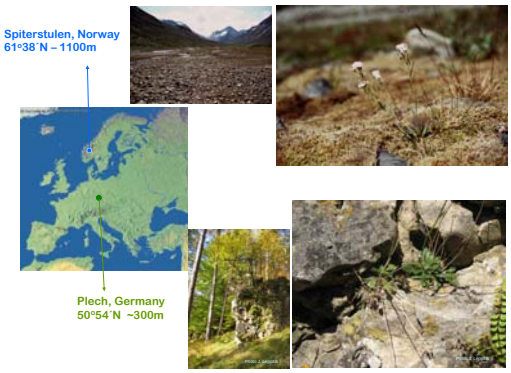

Figure 1. ***A. lyrata*** **plants in Spiterstulen grow on alpine river banks exposed to flood and hard winter conditions; in Plech they grow on rocky outcrops.**

QTL-mapping

We constructed a genetic map with 40 markers using 530 F2 seeds, resulting in a map with 18 cM mean intervals between markers. We did QTL-mapping with the program R/qtl version 1.02-2 (Broman et al. 2003).

Results and discussion

Populations showed significant differences in most traits in the three growth conditions. Plech generally flowered more probably, earlier, and more vigorously than Spiterstulen; further, Plech rosettes were smaller and flatter.

Flowering probability and timing were plastic, responding positively to fertilization and vernalization in both parentals, F1 and F2 (**Fig. 2**). Reproductive effort, on the other hand, was plastic only in Plech; inflorescence shoot number, flower number, and inflorescence height were strongly canalized in Spiterstulen. Respectively, only Spiterstulen showed plastic response of rosette height to vernalization, while the rosette was always very flat in Plech.

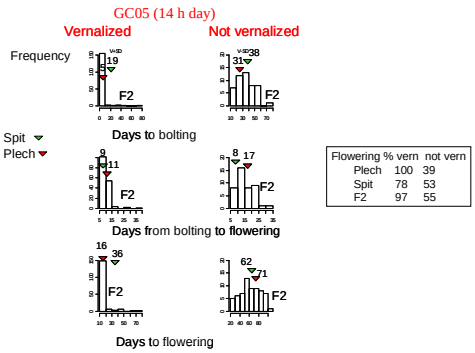

Figure 2. Timing of floweirng in parental populations and F2 plants in GC05 experiment.

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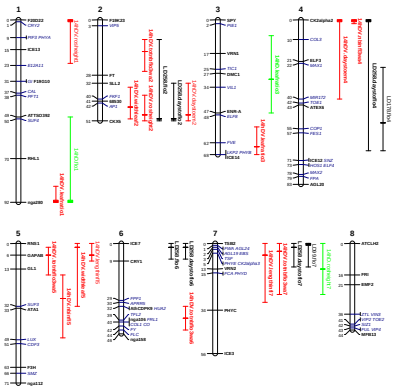
We detected a modest number of QTLs for flowering, reproductive investment and morphology (**Fig. 3**), each of the QTLs explaining 5 to 25% of the total variance in F2. Plech alleles generally promoted flowering and reproductive investment as expected. Some QTLs (e.g. bottom of chromosome 2 and beginning of chromosomes 4 and 7) were detected in many environments, and the same areas had QTLs for both flowering and morphological/reproductive traits, suggesting possible pleiotropic effects of genes in developmental pathways.

Our experimental design did allow detection of only large effect QTLs, so many smaller QTLs could additionally segregate in this cross.

In *A. thaliana*, two major genes, FLC and FRI are known to govern a large part of the naturally occurring variation in flowering time (e.g. LeCorre et al. 2002, Gazzani et al. 2003). In the current cross, there was a QTL for number of flowers close to the FLC, but no evidence for a QTL in the FRI region. The FRI indel polymorphism that was earlier found to govern flowering time variation (Kuittinen et al. 2008) did not segregate in the current cross.



Candidate genes
LOD > threshold 5% ; LOD > threshold 10%
Interval is drop of 1 LOD around optimal position
Red: GC05, 14 hours day vernalized, green: GC05, 14 hours day non vernalized, black: GC01, long day non vernalized

Figure 3. QTLs detected in three experminents.

Conclusions

The two populations showed contrasting responses to environmental cues, suggesting canalization of crucial traits due to adaption to local environments.

The genetic architectures of natural variation in flowering in *A. lyrata* and *A. thaliana* seem to be different. While the variation in *A. thaliana* is mainly governed by FRI and FLC, our results suggest that differences between *A. lyrata* populations in flowering time are due to more subtle mutations mainly at other loci.

We are currently studying additional crosses, and carrying out association studies and analyses of sequence variation at flowering time candidate genes.