



Genome wide association of high divergence, transmission ratio distortion and QTL for male fertility in hybrids between *Arabidopsis lyrata* subspecies

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Introduction

During allopatric isolation of populations, genic incompatibilities reducing hybrid fitness can evolve. In plants, hybrid sterility, especially hybrid male sterility, is the most common postmating reproductive barrier (Lowry *et al.* 2008). Another phenomenon associated with high divergence of genomes is transmission ratio distortion (TRD) of gametes in F1 hybrids observed also in *A. lyrata* (Kuittinen *et al.* 2004, Leppälä & Savolainen 2011). In several plant families, crosses within a population can also lead to cytoplasmic male sterility (CMS), because of conflict between maternally inherited mitochondrial and biparentally inherited nuclear genomes. Here we compare positions of TRD and loci associated with hybrid male sterility. In addition we looked at genome wide divergence data of the two *A. lyrata* populations.

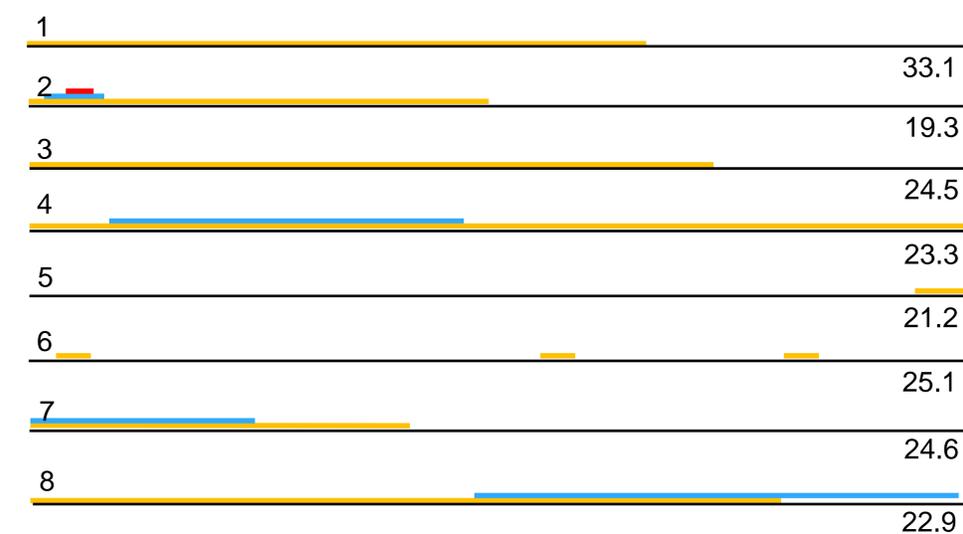


Figure 1. Positions of TRD areas and QTL found in the eight *A. lyrata* chromosomes. Sizes of each chromosome in Mb are indicated. Orange lines indicate areas of significant ($p < 0.01$) transmission ratio distortion and blue lines QTL areas for low hybrid pollen quality. Red line in the beginning of chromosome two indicates position of fertility restorer for cytoplasmic male sterility. F_{ST} was high across the whole genome, but we found no obvious association between divergence and the areas of TRD or pollen quality QTLs.

Methods

We made crosses between *A. lyrata* ssp. *lyrata* from North Carolina, USA and *A. lyrata* ssp. *petraea* from Spiterstulen Norway. 1880 F2 plants were genotyped for altogether 96 markers and QTL mapping was used to find loci associated with hybrid male sterility (Aalto *et al.* 2013). The genomes of six individuals of both parental populations were sequenced on Illumina platform and aligned to *A. lyrata* ssp. *lyrata* reference sequence (Hu *et al.* 2011). We calculated F_{ST} in 10 kb windows with 5 kb steps to compare it with locations of high TRD and the QTL for male sterility.

Literature cited

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Results

Transmission of most of the markers was distorted indicating incompatibilities between the diverged genomes. We observed cytoplasmic male sterility in almost one fourth of F2 and half of backcross hybrids in one of the reciprocal crosses (crosses with Norwegian cytoplasm). This asymmetrical hybrid incompatibility is due to sterility factors in one cytoplasm, for which the other population lacks effective fertility restorers. However, genotyping and genetic mapping revealed that only 60 % of the plants having the male sterile cytoplasm and lacking the corresponding restorers were phenotypically male sterile. We found that there is only one male fertility restorer locus that mapped to a 600 kb interval at the top of chromosome 2 (fig 1) in a region containing a cluster of pentatricopeptide repeat genes. In addition, we found pollen quality variation in the hybrids (fig 2) for which QTL areas are also presented in figure 1.

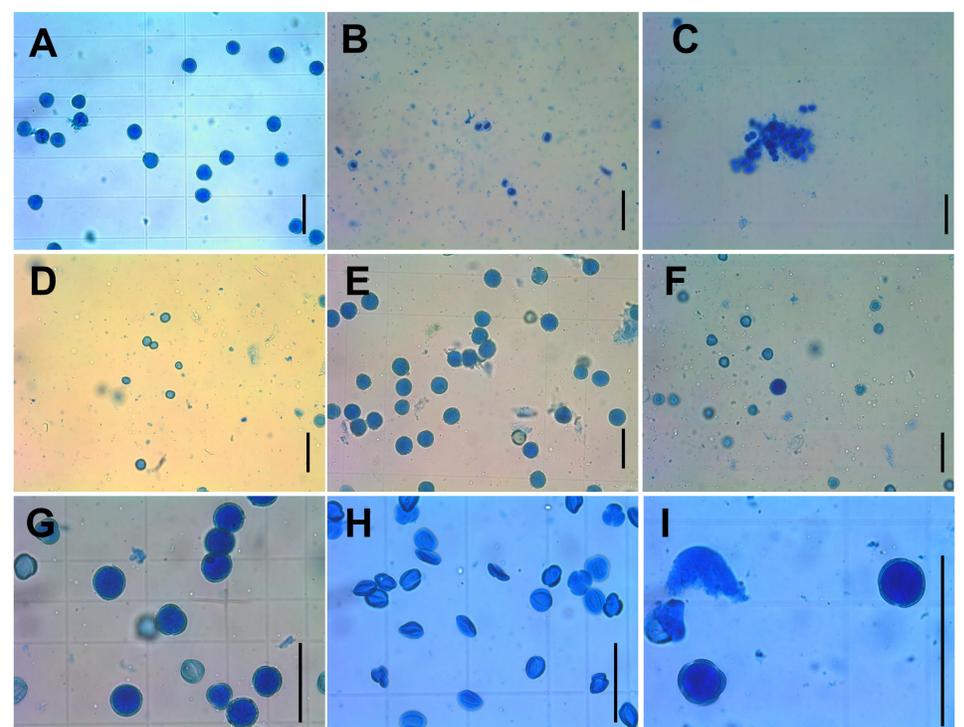


Figure 2. Aniline-blue stained pollen grains viewed under light microscope. The dye stains fertile pollen, while infertile pollen grains remain clear. Scale bars are 50 μ m. A) Pollen from Spiterstulen plant; B-C) Very small pollen grains produced by an (SpNC)NC-hybrid; D) Poor pollen from an F2-hybrid; E-G) Pollen samples from F2-hybrids with diverse fertilities; H) This F2-plant produced large amount of very small pollen which kept its shape under staining; I) Closer view to normally fertile pollen grains

Discussion

Demographic simulations show that the subspecies have diverged about 150 000 generations ago (Pyhäjärvi *et al.* 2012). Several different mechanisms causing incipient reproductive isolation have arisen during the period. The observed CMS lowering hybrid fitness is a transient effect with limited potential to form permanent reproductive barriers between diverged populations of hermaphrodite self-incompatible species (Aalto *et al.* 2013). F_{ST} between the two studied populations is high and the peaks in it are difficult to associate with the wide QTL and TRD areas, the causative loci of which are certainly much narrower.