

Introduction

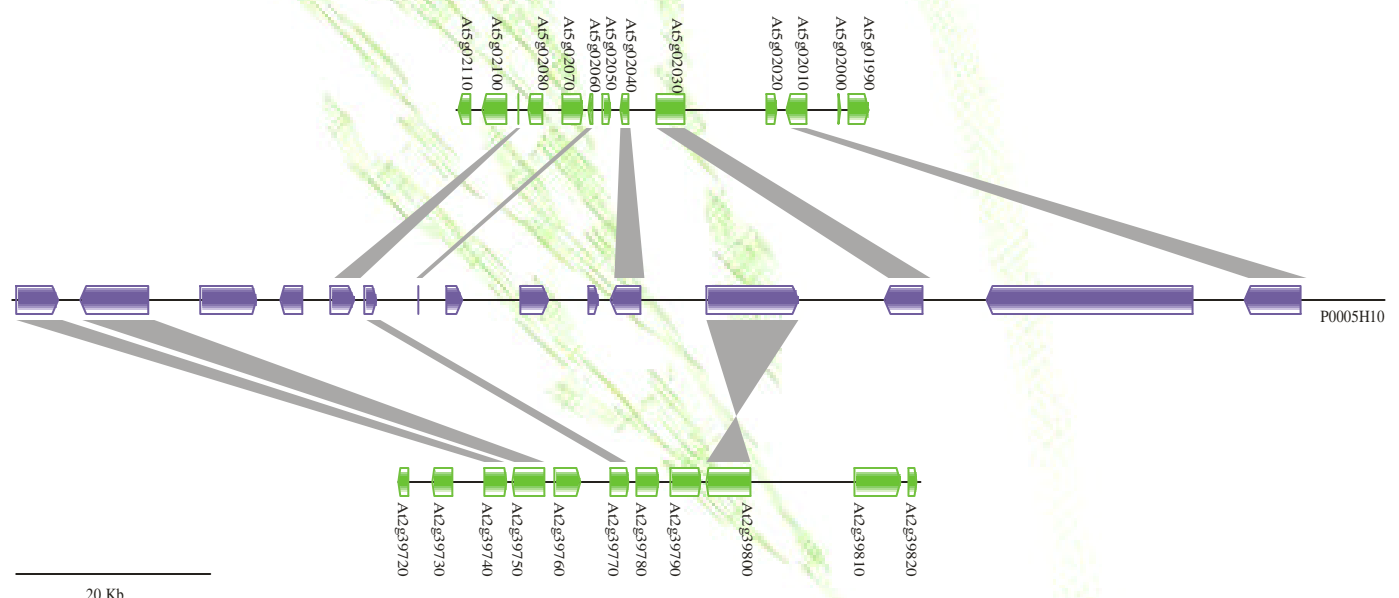
Genomic divergence due to tandem duplications, block duplications, inversions and gene loss is extensive in plant genomes, as well as the number of chromosomal rearrangements. Nevertheless, it is expected (and observed) that different plant species still exhibit a certain degree of conservation regarding gene content and gene order. Here, we demonstrate that a comparative approach by combining the genomes of rice and *Arabidopsis* can reveal unexpected additional information when studying in plant genome evolution.

Results

We applied the newly developed tool **ADHoRe** (Automatic Detection of Homologous Regions; Vandepoele et al. 2002a) to compare genomic sequences of rice and *Arabidopsis*, two model plant systems that have diverged about 200 Myr ago. Next to the identification of numerous examples of (short) genomic segments that shared conserved gene content and order (i.e. microcolinearity), in several cases multiple regions of the *Arabidopsis* genome showed clear homology with a single region in rice. Although this observation is in agreement with the duplication past of *Arabidopsis* (Vision et al., 2000; Simillion et al., 2002), some of these duplicated regions in *Arabidopsis* could not be detected as 'duplicated segments' in a within genome comparison of *Arabidopsis*.

BOX 1. 'Ghost' duplication in the *Arabidopsis* genome.

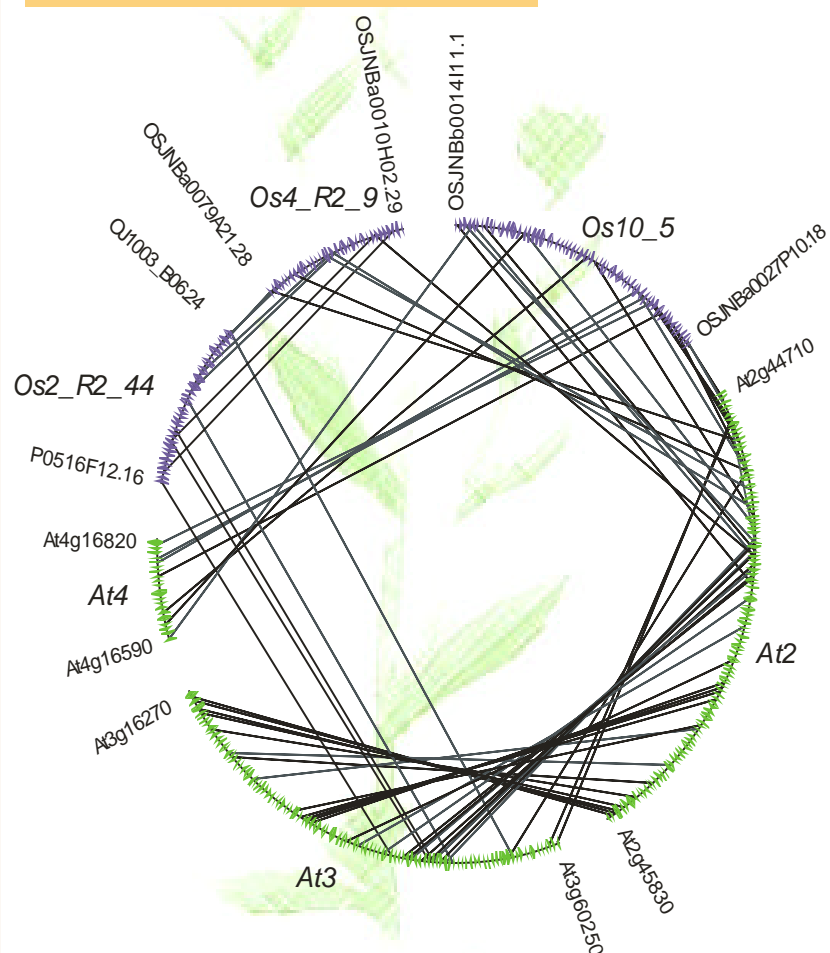
Homologous genes between *Arabidopsis* (green) and *Oryza sativa* (purple) are indicated by grey bands. Two genomic segments of *Arabidopsis*, on chromosomes 2 and 5 respectively, map to the same rice segment (P005H10). Therefore, these segments are paralogous and the result of a duplication event within the *Arabidopsis* genome. However, due to differential gene loss, the duplicated *Arabidopsis* segments no longer share any retained gene duplicates, which makes them undetectable through a within genome comparison.



More detailed analysis of ghost duplications shows that the phenomenon, which we refer to as 'differential gene loss' (Vandepoele et al., 2002b), turns the originally identical duplicated regions into two non-redundant sets of genes, divided over two distinct genome locations. Therefore, the use of inter-genomic comparisons can help to recover seemingly disappearing block duplications. By combining sets of homologous chromosomal segments (~multiplicons) of different organisms, complex networks of microcolinearity can be created (as discussed in Box 2), which can be used to detect different mechanisms and their corresponding rates rearranging plant genomes.

BOX 2. Mixed multipicon with homologous chromosomal segments of *Arabidopsis* and rice reveals ghost duplications in both organisms.

Arrows on the curved lines represent the genes on the chromosomal segments and lines connecting the arrows indicate the anchor points (i.e. homologous gene pairs). Next to the block duplication between rice segments Os2_R2_44 and Os4_R2_9, a rice ghost duplication (Os04_R2_9/Os10_5) can be inferred by combining the colinear segments between Arabidopsis and rice (Os04_R2_9/At2 and At2/Os10_5). Note that within this multipicon an additional Arabidopsis ghost duplication can be inferred by defining all transitive homology relations (i.e. At4/Os10_5 and Os10_5/At2), which links all three Arabidopsis segments (i.e. At4, At2 and At3) in a previously unidentified Arabidopsis multipicon with multiplication level 3. Similarly, all three segments of rice are also part of a multipicon with level 3, which indicates that multiple block duplication events occurred in the rice genome.



Conclusions

Apart from the partial recovery of seemingly disappearing block duplications through the construction of ghost duplications, in the future, when more plant genomic data becomes available, extensive networks of microcolinearity will allow the precise determination of mechanisms that shape a plant genome. The frequencies of these mechanisms within and between different organisms or in general the consequences of these processes should further enlight our understanding of plant genome evolution.