Centromere Locations and Associated Chromosome Rearrangements in
Arabidopsis lyrata and A. thaliana

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ABSTRACT

We analyzed linkage and chromosomal positions of genes in A. lyrata ssp. petraea that are located near the centromere (CEN) regions of A. thaliana, using at least two genes from the short and long arms of each chromosome. In our map, genes from all 10 A. thaliana chromosome arms are also tightly linked in A. lyrata. Genes from the regions on the two sides of CEN5 have distant map localizations in A. lyrata (genes on the A. thaliana short-arm genes are on linkage group AL6, and long-arm genes are on AL7), but genes from the other four A. thaliana centromere regions remain closely linked in A. lyrata. The observation of complete linkage between short- and long-arm centromere genes, but not between genes in other genome regions that are separated by similar physical distances, suggests that crossing-over frequencies near the A. lyrata ssp. petraea centromere regions are low, as in A. thaliana. Thus, the centromere positions appear to be conserved between A. thaliana and A. lyrata, even though three centromeres have been lost in A. thaliana, and the core satellite sequences in the two species are very different. We can now definitively identify the three centromeres that were eliminated in the fusions that formed the A. thaliana chromosomes. However, we cannot tell whether genes were lost along with these centromeres, because such genes are absent from the A. thaliana genome, which is the sole source of markers for our mapping.

The chromosomes of Arabidopsis thaliana have undergone several rearrangements since this species’ common ancestor with related species. This is evident from the fact that A. thaliana has only five chromosomes vs. eight in outgroup species such as A. lyrata and Capsella rubella. Comparative genetic mapping (Boivin et al. 2004; Kuttinen et al. 2004; Koch and Kiefer 2005; Yogeeswaran et al. 2005) and molecular cytological analyses (Lysak et al. 2003) has revealed the major structural changes that occurred in the A. thaliana lineage (summarized in Figure 1).

As far as can be ascertained from the low-density genetic maps published so far, the changes during the evolution of the A. thaliana chromosomes are as follows (the order of events is unknown). There were two reciprocal translocations: one between the A. lyrata chromosomes AL3 and AL5 (corresponding to C. rubella chromosomes C and E, respectively), forming A. thaliana chromosome III and part of chromosome II, and the other between AL6 and AL7 (C. rubella chromosomes F and G, respectively), forming A. thaliana chromosome IV and part of chromosome V. In addition, three fusion events occurred: one between AL1 and AL2 (C. rubella chromosomes A and B, respectively), forming A. thaliana chromosome I, and two others involving the chromosomes with the reciprocal translocations. One of these fused AL4 (C. rubella chromosome D) to a chromosome resulting from the first translocation, forming the present A. thaliana chromosome II, and the other fused AL8 (C. rubella chromosome H) to a chromosome resulting from the second one, forming A. thaliana chromosome V. Two large inversions are also inferred: in the present A. thaliana chromosome I (inversion 1 of Koch and Kiefer 2005) and in chromosome IV (inversion 2 of Koch and Kiefer 2005) at one end of the part translocated from AL6. For three further inversions, the lineages in which they occurred cannot currently be determined, because markers are sparse in the relevant regions in either C. rubella or A. lyrata. Inversion 3, near the breakpoint of the fusion with AL8, has been detected only in C. rubella, and inversions 4 and 8 have been detected only in A. lyrata at the end of the translocated parts of AL7 and AL6, respectively (parts of A. thaliana chromosomes V and IV, respectively). To resolve the arrangements in these species and determine definitive the lineages in which they occurred, more markers were needed for mapping of these regions, or, alternatively, in situ hybridization studies.

An especially interesting question that can be studied by more detailed mapping is how these rearrangements affected the centromeres. How did the current A. thaliana
centromeres originate, and are the centromere positions conserved? If not, this is due to neo-centromere formation, as in examples such as the primate X chromosome (Ventura et al. 2001). This possibility is particularly interesting in these Arabidopsis species, because the centromere satellite families of A. arenosa, A. halleri, and A. lyrata, which are the closest relatives of A. thaliana, are very different from the A. thaliana centromere satellite sequences (Kamm et al. 1995; Kawabe and Nasuda 2005). It is thus important to test whether emergence of new satellite families involved formation of new centromeres. The alternative is that the new sequences emerged and replaced an existing centromere’s satellites and then became homogenized between different centromere regions in these species’ genomes.

The evidence from the sparse maps already published evidently suggests that centromeres 2, 4, and 8 were the three centromeres that became lost during the evolution of the A. thaliana genome (in the fusions forming chromosomes I, II, and V; see Figure 1). These conclusions rest on the assumption that no large-scale centromere displacement or chromosome rearrangements occurred, which has not previously been tested. For A. thaliana chromosomes I and II, genes from both arms map to single A. lyrata chromosomes, AL1 and AL3, respectively (Kuttinnen et al. 2004), consistent with the above assumption, but the situation for chromosome V is not evident.

To test these assumptions explicitly, and to delimit the scale of any possible centromere displacements, we have attempted to identify the A. lyrata centromere locations by mapping more finely spaced markers in genes flanking the A. thaliana centromeres of each of the five A. thaliana centromere regions. This should also allow us to infer the centromere positions in at least some of the A. lyrata chromosomes and to develop reconstructions of the details of the rearrangement events that can be tested in future work (see Figure 1, which we will discuss at greater length below).

Because we start from known A. thaliana genes, we cannot map any genes lost in events such as the hypothetical loss of a centromere (see Figure 1). This means that we are unlikely to be able to discover the precise centromere locations of the three A. lyrata chromosomes involved in fusions. However, fusion events are expected to cause loss of a small numbers of genes, since large deletions are deleterious (Kush and Rick 1968). Moreover, there is no evidence in A. thaliana for non-duplicated genome tracts that might correspond to regions that were duplicates in the ancestral genome, but recently became single copy (Blanc et al. 2003). Thus the fusions often may have been between chromosomes with centromeres close to their ends. This implies either that the chromosomes in the ancestor in which the fusions occurred were telocentric or acrocentric or that inversions occurred before or during the fusion events to create this situation (see Figure 1). Because no A. lyrata or C. rubella chromosomes are telocentric (Al1 et al. 2005), the occurrence of inversions seems likely.

MATERIALS AND METHODS

Genes analyzed: We chose two genes from each chromosome arm of A. thaliana, in addition to nine markers on chromosome I analyzed previously (Hansson et al. 2006). From each chromosome arm, we chose one single-copy gene located as close as possible to the core centromere region, and one gene each at least 100 kb distal to the first gene (KumeKawa et al. 2000, 2001; Hosouchi et al. 2002). To ensure single-copy genes, we checked that there are no homologs with sequence identity >80% in the A. thaliana genome. The genes, with their
putative functions, are listed in supplemental Table 1 at http://www.genetics.org/supplemental/, which also gives the sequences of the primers used; these were designed on the basis of A. thaliana sequences.

**Typing and data analyses:** A mapping family of 99 F2 progeny plants made from crosses between plants from two different subpopulations of A. lyrata ssp. petraea (KUttTINEN et al. 2004) was used in the study. When variants heterozygous in only one parent can be scored, we can score only 99 meioses, but when scorable variants are heterozygous in both parents, 198 meioses were scored.

To detect polymorphisms and develop PCR-based markers in the genes selected, sequences of one parent F1 plant and three to seven F2 progeny plants were determined for each gene (supplemental Table 1 at http://www.genetics.org/supplemental/). For eight loci, single-nucleotide polymorphisms (SNPs) were typed by PCR–RFLP. Large-indel variants distinguishable on agarose gels were used to genotype one locus, small-indel variants that could be scored in an ABI 3730 capillary sequencer with fluorescent-labeled primers for three loci, and six loci with SNPs were scored with allele-specific primer-induced fragment length polymorphism, also detected by an ABI 3730 capillary sequencer (HANSson and KAWABe 2005). Including the nine markers close to the centromere of the A. thaliana chromosome I, we typed a total of 27 markers (from 24 genes). Details of the typing methods are given in HANSson et al. (2006).

To infer the history of genes found to be duplicates in A. lyrata, we used an outgroup species (Arabis glabra = Turritis glabra). Sequences of the duplicated genes from the A. lyrata ssp. petraea mapping family and T. glabra were deposited in GenBank. The accession numbers of the new sequences reported and analyzed here are as follows: DQ487163–DQ487167 for At1g43980, DQ487168–DQ487175 for At3g42050, and DQ487176–DQ487178 for At4g21150. The genes from A. thaliana centromeric regions are DQ487163–DQ487175.

**RESULTS**

**Conserved centromere positions in A. thaliana and A. lyrata:** Our markers in genes located near the centromere regions of the 10 chromosome arms of A. thaliana in all cases are linked in A. lyrata (Figure 2). These results support the previous results indicating the conservation of linkage groups representing most of the chromosome arms between these two species (KUttTINEN et al. 2004), but go beyond those results in that they show that even genes very closely linked to the centromere in A. thaliana are in the same locations in the A. lyrata map. They are also consistent with the conclusion that the A. thaliana CEN3 and CEN5 are in the same location as in C. rubella, A. arenosa, and Olimarabidosis pumila (HALL et al. 2006). Below, we discuss our evidence that these regions contain the centromeres of these A. lyrata chromosomes. For four A. thaliana chromosomes, we also find linkage between short- and long-arm genes in the A. lyrata map. These centromere regions (A. thaliana CEN1 and the putative centromere of AL1, A. thaliana CEN2 and the putative AL3 centromere, A. thaliana CEN3 and AL5, and A. thaliana CEN4 and AL6) are thus conserved between A. thaliana and A. lyrata, with no evidence of chromosome rearrangements in the immediately surrounding regions (see Figure 2).

CEN5 is more complex. The formation of chromosome V of A. thaliana involved a reciprocal translocation (see above and Figure 1), and an understanding of this event is critical for interpreting the origin of CEN5. Previous comparative molecular cytogenetic analyses of A. thaliana and A. lyrata could not precisely locate the breakpoint of the reciprocal translocation creating the A. thaliana chromosomes IV and V (between AL6 and AL7). Chromosome IV BAC probes were used in FISH experiments (LYSAK et al. 2003), but no BAC clones containing large amounts of repetitive elements were used, so that the details of event regions close to this centromere may not be resolved. It was concluded that the translocation event probably occurred near the centromere region because the transposition breakpoint in the chromosome corresponding to AL7 in our terminology is close to the pericentromere heterochromatic region (Figure 3E of LYSAK et al. 2003). In our A. lyrata genetic map, genes from the short arm of the A. thaliana chromosome V are completely linked to genes from the A. thaliana CEN4 region (Figure 2), suggesting that one breakpoint of the translocation lies between the markers closest to the core centromere in the two arms of this chromosome. Assuming that the centromere position is conserved between A. thaliana chromosome IV and AL6, as our mapping results indicate (Figure 2 and KAWABE et al. 2006), the breakpoint is probably in the pericentromeric region of the ancestral species, although its position still cannot be determined precisely (Figure 2).

We examined our results to see whether any gene copy number differences are suggested, because it has been found that the centromeric regions of A. thaliana have significantly fewer tandemly duplicated genes than noncentromeric regions (ZHANG and GAUT 2003). We detected four events in total and estimated duplication time using the T. glabra sequence as an outgroup (HANSson et al. 2006; KAWABE et al. 2006), two involving centromere region genes. In one such case, on chromosome I, At1g43980, the results suggest a recent duplication in the A. lyrata lineage, rather than loss in A. thaliana (HANSson et al. 2006). The other is the apparent triplication in A. lyrata of At5g42050, but the events involved appear complex and cannot be inferred in detail. Given that a much smaller number of centromeric than noncentromeric genes have been studied, these results suggest more such events in the centromere regions, which is inconsistent with the results based on an initial annotation of the complete genome sequence (ZHANG and GAUT 2003). That study did not include comparisons with related species, so that the ancestral states are not known, leaving it unclear whether the difference is due to loss of tandem duplicates in A. thaliana centromeric regions or to the occurrence of more such duplications in noncentromeric than centromeric regions. However, neither of the above possibilities explains our results. Instead, our data suggest that both
of these cases are tandem duplications in *A. lyrata* since the split from the *A. thaliana* lineage (Kawabe et al. 2006).

**Frequencies of recombination between markers:** Many organisms, including *A. thaliana*, have very low crossing-over frequencies in the regions around the "core" centromere regions. In *A. thaliana*, this is true for all five chromosomes (Copenhaver et al. 1998, 1999). The markers used in this study are not always located within these regions, but are nevertheless closely linked to the *A. thaliana* centromeres. To test whether our putative *A. lyrata* centromeres are indeed centromeres, we tested whether markers from *A. thaliana* centromere region genes show evidence for restricted recombination in *A. lyrata* and then compared the estimated recombination rates with expected values on the basis of probable physical distances (in *A. thaliana*) between the markers.

The physical distance corresponding to a centimorgan is not yet known in *A. lyrata*, but our genetic mapping results for *A. lyrata* chromosomes 1, 2, and 7 yield some rough estimates of the physical length per centimorgan for noncentromere regions of *A. lyrata* chromosomes. For chromosome 1, assuming the same physical size as in *A. thaliana*, we estimate a value of \(240 \text{ kb/cm} \) (4.0 cm/Mb) and \(100 \text{ kb/cm} \) (8–9 cm/Mb) for the *A. lyrata* chromosome 2; if we assume that the DNA content of each of these chromosome arms is 50% larger than the *A. thaliana* value, the ratio as estimated for the entire genome, these values are increased (Hansson et al. 2006). Our estimate from AL7, which, unlike AL6 (which includes an inversion), is not
rearranged, yields an estimate of ~200 kb/cM (or 4-5 cM/Mb), assuming the same physical size as in *A. thaliana*.

If recombination is not suppressed in the region covered by our centromere region markers, we should therefore observe recombinants across the distances between these markers, which, even in *A. thaliana*, are several megabases (Figure 2). The *A. thaliana* core centromere region consists of repetitive sequences, including short satellite sequences and transposable elements, and always exceeds 2 Mb (Hosouchi et al. 2002). Given its larger genome size (Johnston et al. 2005), at least similar amounts of DNAs may be expected at *A. lyrata* centromeres. If the core satellite regions are at the same locations in *A. thaliana* and *A. lyrata*, the physical distances between our markers should thus probably be >3 Mb and should correspond to several map units (Figure 2). With our family size, we expect to find recombinants between markers at distance of a few centimorgans, and we indeed almost always detect recombinants between markers from noncentromere regions of the *A. thaliana* genome across comparable physical distances (Hansson et al. 2006). Therefore we should be able to detect the presence of nonrecombinating regions in the *A. lyrata* chromosomes, if these indeed exist near the putative centromere regions identified by our markers, and if they indeed are regions of low recombination.

We scored multiple markers from each *A. thaliana* centromere and found that almost all the centromere markers are very closely linked in *A. lyrata* (Figure 2), except for the lack of linkage of genes from the two arms of the chromosome V centromere region (see above). All four markers from the *A. thaliana* chromosome II centromere region are completely linked in our family, although we observed occasional recombinants between the two distally located pairs of genes on the other chromosomes (Figure 2). For the two genes on the long arm of chromosome V, we observed nine recombinants in the 99 mapping family progeny, while the short-arm genes are completely linked to chromosome IV centromere region genes. Thus these centromeres have apparently remained in the same regions, flanked by the same set of closest loci, in both species.

**DISCUSSION**

**Conserved centromere positions in *A. thaliana* and *A. lyrata***: The genes from each *A. thaliana* centromere region showed almost complete linkage in *A. lyrata*, suggesting both that the centromere locations have not changed in the evolution of the *A. thaliana* chromosomes and that there are regions with very low crossing-over frequencies around the *A. lyrata* centromere regions. Our results do not establish definitively that the centromere locations are completely unchanged in *A. thaliana*, i.e., that long- and short-arm genes are also on different sides of *A. lyrata* centromere satellite arrays, but this seems likely. Our observation that linkages of short- and long-arm genes are maintained between *A. thaliana* and *A. lyrata* narrows down the possibility for centromere movements to within the region spanned by the nonrecombining genes, whose order cannot be determined by genetic mapping alone. This conclusion is consistent with the finding that the *A. arenosa* BAC clone containing genes orthologous to those close to the *A. thaliana* CEN3 also contains *A. arenosa* centromeric satellite sequences (Hall et al. 2006).

*A. lyrata* and *A. thaliana* have different centromere satellite sequences in their core centromere regions (Kawabe and Nasuda 2005). The conclusion that the centromeres are in all cases at least close to the same map locations suggests that the loss of old satellite sequences and the increase of new ones probably occurred within established centromeres, i.e., that the satellite sequences changed without centromere movement or rearrangement of the surrounding chromosome structure, even when the orientation of some short- or long-arm genes differed between the species. In turn, this implies that homogenization of centromere satellite sequences throughout the entire set of chromosomes must have involved interchromosomal transposition by some form of sequence exchange between nonhomologous chromosomes, such as gene conversion, but does not require reciprocal translocations involving the core centromere regions. In some primates, different centromere sequences have also been observed in species without changes in chromosome structure, although small sequential pericentromeric inversion events followed by emergence of neo-centromere sequences at the initial position cannot be excluded (Ventura et al. 2001).

Are chromosome rearrangements associated with centromere regions? Our new map results suggest the occurrence of one reciprocal translocation between the centromere regions of the two chromosomes AL6 and 7 without loss of genes. The chromosome fusion events that reduced the chromosome number from eight to five in *A. thaliana* involved loss of three centromeres, possibly involving loss of large amounts of the genome. This could partially account for *A. thaliana*’s genome size being considerably smaller than *A. lyrata*’s (Johnston et al. 2005). If the centromere regions in the ancestral species contained large amounts of repetitive sequences, it is possible that these regions might have contained few genes and could be lost. However, some evidence suggests that pervasive small changes have also occurred throughout the genome. Intron sizes tend to be smaller than in *A. lyrata* orthologs on the basis of a sample of 19 genes (Wright et al. 2002), and a survey suggests consistently larger intergenic physical distances in *A. lyrata* in the FLC gene region (Sanyal and Jackson 2005).
There are two possibilities for chromosome fusion and centromere loss without loss of many genes. A simple Robertsonian translocation could cause loss of one small chromosome arm along with the chromosome’s centromere region. However, the inferred morphology in the ancestral species of the chromosomes involved in fusions does not suggest that they were telocentric. Alternatively, an inversion could occur before or together with the chromosome fusion, preserving most of the chromosome arm. Interestingly, two of the three chromosomes that are inferred to have lost their centromere regions in fusion events, AL2 and AL8, do indeed have large inversions near the locations of the fusions in the A. thaliana chromosomes (Kocic and Keifer 2005). We find that inversion 1 (in AL2) is present in A. lyrata (Hansson et al. 2006), as well as in C. rubella (Boivin et al. 2004). Thus this inversion should be attributed to the A. thaliana lineage. An inversion has also been detected cytologically in the relevant part of AL4, another chromosome involved in a fusion event, but whose centromere is not at the distal end of the chromosome (Lysak et al. 2006; note that this is not shown in Figure 1, which reviews previously established rearrangements by genetic mapping).

Overall, it thus appears likely that of the eight major chromosome rearrangements previously inferred, seven occurred at or near the centromere regions inferred in the ancestral species. The rearrangement confirmed in this study (a translocation between AL6 and AL7 and an inversion in AL6) probably involved pericentromeric regions. The reciprocal translocation between AL3 and AL5 is thus the only rearrangement that did not involve a centromere region. The involvement of centromere regions in the rearrangements may be due to the presence of repetitive sequences in such regions, which can induce ectopic exchanges leading to chromosome breaks; thus independent events might occur in the same region at separate times. Pericentromeric regions of chromosomes contain abundant transposable elements and some of these retain their mobility (Frank et al. 1997; Miura et al. 2001; Singer et al. 2001). Activation of transposable elements, especially the cut-and-paste type, can cause chromosome breaks and create sticky ends, which can lead to rearrangements.

Alternatively, some of these events may have occurred simultaneously as single complex events sharing the same breakpoints. The numbers of events previously proposed would then be reduced from eight to a minimum of five: fusion/breakage 1 and inversion 3 in A. thaliana chromosome V (events E and G in Yogeeswaran et al. 2005), fusion/breakage 3 and inversion 1 in A. thaliana chromosome I (events A, X, and Y in Yogeeswaran et al. 2005), and translocation 1 and inversion 2 in A. thaliana chromosomes IV and V (events D and F in Yogeeswaran et al. 2005).

In other Arabidopsis relatives (Lysak et al. 2003), however, chromosome structure is highly conserved, even between C. rubella and A. lyrata. These species diverged about twice as long ago as A. lyrata and A. thaliana (Kocic et al. 2000), suggesting that chromosome rearrangement is considerably accelerated in the A. thaliana lineage. This is consistent with theoretical models predicting a tendency toward higher chromosome rearrangement rates in inbreeding than in outcrossing species and observations of this tendency in plant karyotypes (Lande 1984; Charlesworth 1992). The C. rubella map, however, provides an exception. This map was made using the self-compatible annual C. rubella crossed with the self-incompatible perennial, C. grandiflora, and shows no evidence for chromosome rearrangements having accumulated in the former. The divergence time between these taxa has not yet been estimated and could be too recent for chromosome rearrangements to have occurred.

With our probable interpretations of the rearrangements in the genetic map in A. thaliana, we can suggest possible locations of the A. lyrata centromeres that cannot be mapped, which can be tested in future work. No centromeres were apparently lost in the formation of A. thaliana chromosome IV by a reciprocal translocation between A. lyrata chromosomes 6 and 7. In the cases where centromeres were lost in fusions, it is likely that, in the ancestral species, they were located close to the inversion breakpoints (on the basis of the consideration that deletions involving many genes are unlikely). Since the A. lyrata map is similar to that of the outgroup species, C. rubella, the ancestral state for each chromosome was probably similar to that of A. lyrata. In the case of A. thaliana chromosome 1, the centromere of A. lyrata chromosome 2 was thus lost, and its location is evidently within the large gap in the current genetic map (Hansson et al. 2006). It will be interesting in the future to map A. lyrata chromosomes 4 and 8 more precisely, to determine whether gaps are also present on these chromosomes in the regions that were lost in forming A. thaliana chromosomes II and V. It may be informative to search for A. lyrata genes that are absent in A. thaliana (in EST sequences or in the forthcoming genome sequence) and to map them. If this eliminates the gaps, it would imply that many genes were lost in these fusions.

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