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Identifying plant centromeres

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Abstract

Clever use of a mutation that allows tetrad analysis in a higher plant has enabled researchers to map the centromeres of *Arabidopsis* genetically with high precision.

Significance and context

The traditional use of cytogenetics as a tool for the examination of *Arabidopsis* chromosomes, in regard to their segregation, pairing and alterations in number or structure has been hampered by their extremely small size. Copenhaver *et al.* have taken advantage of a previously characterized mutation, *quartet1*, to allow them to define the centromere regions of the five *Arabidopsis* chromosomes genetically. The authors have also used the recently completed sequence of *Arabidopsis* chromosomes 2 and 4 to provide the first detailed sequence analysis of the centromeres of higher plants. As expected, the centromeric regions contain a large amount of repetitive DNA, and exhibit dramatic recombinational repression. The regions flanking the centromere also contain many repetitive elements but exhibit normal levels of recombination. Surprisingly, the centromere region is not only structural but also contains a number of expressed genes.

Key results

Copenhaver *et al.* describe two major research areas - the physical and genetic mapping of the centromeric regions and the sequence analysis of the defined centromeric regions of chromosome 2 and 4 (CEN2 and CEN4). Physical mapping of the centromeres was accomplished by using DNA markers to assign contiguous centromeric bacterial artificial chromosome (BAC) clones to specific *Arabidopsis* chromosomes. The resulting physical assignments were confirmed for chromosomes 2 and 4 by genomic sequencing.

Genetic mapping was then used to define the portions of the centromeric region that participate in centromere function. Genetic mapping of the centromere is easily done in certain fungi and single-celled algae in which the products of a single meiosis are found in a group of four cells called a tetrad. Because recombination is repressed at the centromeres, the segregation pattern of a given locus between meiotic products can indicate its position relative to the centromere. Copenhaver *et al.* have used the *quartet1* (*qrt1*) mutation of *Arabidopsis*, a mutation that causes the four products of the male meiosis to be

released as a single tetrad instead of four individual pollen grains, to mimic these simpler organisms genetically. By placing a single pollen grain from a genetically non-isogenic parent onto the stigma of an isogenic plant, it is possible to recover the unordered products of a single male meiosis and follow the segregation of DNA markers in the progeny. Because recombination rates decrease near the centromere, limiting the genetic resolution, the authors attempted to increase recombination rates in the centromere regions by treating with chemical agents known to cause DNA damage, modify chromatin structure or alter DNA modifications. In total, Copenhaver *et al.* examined the progeny of over 1,000 tetrads and refined the centromeric regions to 550, 880, 1,150, 1,260, and 1,070 kb for chromosomes 1 through 5, respectively.

Detailed sequence analysis of CEN2 and CEN4 shows that there is an abundance of repetitive elements in the centromeric regions, as seen with other eukaryotic chromosomes. They contain a large number of the *Arabidopsis* 180 bp repeat sequences, retrotransposons, and smaller number of transposons and middle repetitive elements. Low-complexity DNA, including microsatellites, homopolymer tracts and AT-rich regions are not enriched in *Arabidopsis* as they are in *Drosophila* or *Neurospora*. Most of the repetitive elements, except for the 180 bp repeat sequences, were less prevalent in the genetically defined centromere region than within the flanking regions. The authors conclude that the presence of these repetitive elements does not pinpoint areas that provide centromere function, a result that may be applicable to the study of other higher eukaryotic genomes.

Sequence analysis also revealed a number of actively transcribed genes in the centromeric region, somewhat contrary to expectations. Although there are examples of genes in the centromeres from other organisms, it is thought that they have special control elements that allow expression. That does not appear to be the case with CEN2 and CEN4. They contain a number of genes, predicted to have a variety of diverse functions not clearly linked to centromere function. Sequence comparisons between CEN2 and CEN4 have revealed a number of conserved, non-repetitive sequences but is too earlier to determine whether any of these sequence have a role in centromere function.

Links

More information can be found at The *Arabidopsis* Information Resource and the Preuss lab website. Sequence-based, genetic and physical maps of the *Arabidopsis* genome can be found at the Cold Spring Harbor Laboratory website.

Reporter's comments

The use of the *qrt1* mutation is a simple and elegant solution to the problem of mapping *Arabidopsis* centromeres. The nonspecialist may not realize how beautifully simple it is in conception, nor how tedious the hands-on work must have been. Repeatedly introducing a single pollen grain onto a stigma is a bit of a challenge, so the number of crosses performed is impressive. The sequence analysis reveals a couple of surprising results, most notably the presence of expressed genes in the centromere region.

Given that these genes do not appear to relate to centromere function, is there a reason for them to be within the centromeric region? Do they contain any special control elements that help govern their expression? It will be interesting to see whether the other centromeric regions share features common to CEN2 and CEN4. With a total sample size of five, it may be difficult to pinpoint areas associated with the attachment of the spindle fibers.

Table of links

Science

The *Arabidopsis* Information Resource

Preuss lab

Sequence-based, genetic and physical maps of the *Arabidopsis* genome

Cold Spring Harbor Laboratory

References

1. Copenhaver GP, Nickel K, Kuromori T, Benito MI, Kaul S, Lin X, Bevan M, Murphy G, Harris B, Parnell LD, et al: Genetic definition and sequence analysis of *Arabidopsis* centromeres. Science. 1999, 286: 2468-2474. 0036-8075