"Knobs and crossing over in maize"

Recombination nodules (RNs) are closely correlated with crossing over, and because they are observed by electron microscopy of synaptonemal complexes (SCs = pachytene chromosomes), RNs provide the highest-resolution cytological markers currently available for defining the frequency and distribution of crossovers along the length of chromosomes. Previously we prepared an SC karyotype for the maize inbred line KYS in which each SC was identified by its relative length and arm ratio and related to the proper linkage group using inversion heterozygotes. We mapped 4267 RNs on 2080 identified SCs to produce high-resolution maps of RN frequency and distribution on each SC. RN frequencies were closely correlated with chiasma frequencies and SC lengths. Each bivalent had a unique distribution of crossing over, but all bivalents shared a high frequency of distal RNs, a lower frequency of RNs in pericentric heterochromatin, and a severe reduction of RNs at and near kinetochores. Considering that knobs are constitutive heterochromatin where crossing over is thought to be inhibited, RNs should have been rare in knobs. However, although knobs are not visible on SC spreads, we saw no reduction in RN frequency in regions of the genome where knobs were expected to be (2003. Genetics 165:849-865). To investigate the physical relationship of knobs to SCs, we have now hybridized knob repeat sequences to SC spreads and found that long loops of knob chromatin are attached to SCs throughout the length of each knob. This data suggests that crossing over occurs regularly in knob heterochromatin. However, when we used MLH1 immunofluorescence to examine the relationship of class I (interference type) crossovers to knobs, we found only one example of an MLH1 focus within knob heterochromatin. We are now using electron microscopy to investigate the possibility that most RNs observed in knob locations represent crossovers mediated by the class II (non-interference) CO pathway.