Linkage and Recombination

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Linkage refers to the association and co-inheritance of two DNA segments because they reside close together on the same chromosome. Recombination is the process by which they become separated during crossing over, which occurs during **meiosis** . The existence of linkage and the frequency of recombination allow chromosomes to be mapped to determine the relative positions and distances of the genes and other DNA sequences on them. Linkage analysis is also a key tool for discovering the location and ultimate identity of genes for inherited diseases.

Basic Concepts

Each individual inherits a complete set of twenty-three chromosomes from each parent, and chromosomes are therefore present in **homologous** pairs. The members of a pair carry the same set of genes at the same positions, or **loci** . The two genes at a particular locus may be identical, or slightly different. The different forms of a gene are called alleles.

Genes or loci can be linked either physically or genetically. Genes that are physically linked are on the same chromosome and are thus syntenic. Only syntenic genes can be genetically linked. Genes that are linked genetically are physically close enough to one another that they do not segregate independently during meiosis.

Understanding independent segregation is crucial to understanding linkage. Independent segregation was first discovered by Gregor Mendel, who found that, in pea plants, the different forms of two traits found in the parents, such as color and height, could occur in all possible combinations in the offspring. Thus, a tall parent with green pods crossed with a short parent with yellow pods could give rise to offspring that were tall with yellow pods or short with green pods, as well as some of each parental type. Mendel concluded that the factors controlling height segregated independently from the factors controlling pod color. Later work showed that this was because these genes occurred on separate (nonhomologous) chromosomes, which themselves segregate independently during meiosis.

How is it possible for physically linked genes to nonetheless segregate independently? The answer lies in the events of crossing over. During crossing over, homologous chromosomes exchange segments at several sites along their length, in a process called recombination. Thus, two loci at distant ends of the chromosome are almost certain to have at least one exchange point occur between them. If only one exchange occurs, two alleles that began on the same chromosome will end up on different chromosomes. If there are two exchange points between them, they will end up together; if three, they end up apart, and so on. Over long distances, the likelihood of two **alleles** remaining together is only 50 percent, no better than chance, and, therefore, loci that are far apart on a large chromosome are not genetically linked. Conversely, loci that are close together will not segregate independently, and are therefore genetically linked. It is these that are most useful for mapping and discovering disease genes.

The loci examined in linkage analysis need not be genes of functional significance; indeed, anonymous segments of DNA (stretches of DNA with no known function) called genetic markers are often more useful in genetic linkage analysis. In order for a genetic marker to be of benefit in a linkage analysis, the chromosomal location of the marker must be known and, most importantly, there must be some variation in the sequence or length of these markers among individuals. Nongene markers used in linkage analysis are classified into four broad categories: restriction fragment length polymorphisms (RFLPs), variable number of tandem repeat (VNTRs), short tandem repeat polymorphisms (STRPs), and single nucleotide repeats (SNPs).