THE QUANTITATIVE ANALYSIS OF CHROMOSOME PAIRING AND CHIASMA FORMATION BASED ON THE RELATIVE FREQUENCIES OF M I CONFIGURATIONS

I. INTRODUCTION: NORMAL DIPLOIDS

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Whilst reliable estimates of chiasma frequencies can usually not be obtained, the probability \( b \) of a chromosome arm to be bound by at least one chiasma can often be determined. In the absence of interference this probability equals \( 1 - e^{-2\mu} \), where \( 2\mu \) is the average chiasma frequency of the chromosome arm and \( \mu \) the average crossover frequency or map length. In the presence of interference \( \mu \) is shown to retain its genetic meaning as an additive metric that may describe the chromosome arm or other distinctive chromosome segment in terms of genetic recombination. It is a form of potential map length, comparable to, but numerically different from the regular map length. It is termed provisionally \"crossing-over potential\".

A chromosome with arms \( m \) and \( n \) with \"crossing-over potentials\" \( \mu \) and \( \nu \) will form ring bivalents with a frequency \( (1 - e^{-2\mu})(1 - e^{-2\nu}) \); open bivalents with a frequency \( (1 - e^{-2\mu})e^{-2\nu} + (1 - e^{-2\nu})e^{-2\mu} \); univalent pairs with a frequency \( e^{-2\mu}e^{-2\nu} \). Estimates of these frequencies yield equations from which \( \mu \) and \( \nu \) may be solved. In rye (Secale cereale) their ratio \( q \) is approximately two and differs from the mitotic arm length ratio of 1.4, indicating localization of chiasmata in the long arms.

Graphs are given to show how, with constant \( q \), the relation between the probabilities \( b_m \) and \( b_n \) of the two arms being bound changes with changing average \( b \).

Data are presented on chiasma frequencies in M I, and compared with the frequencies expected in the absence of interference to give an impression of the degree of interference. Apparent fusion of chiasmata simulates interference.

The genetic composition of gametes is determined by the genetic composition of the organism on which the gametes are formed and by the behaviour of the chromosomes in meiosis. Because of the complexity of the processes involved, the large number of factors that may influence these processes and the large number of alternative situations that may occur, the behaviour of the chromosomes is usually treatep
as if its main processes were determined by chance. This inherently precludes exact predictability and any prediction may only be given with a certain known probability. In addition any estimate on which the prediction is based has its own error of estimation which introduces another uncertainty. The more is known about the processes that determine chromosome behaviour, especially when these can be represented quantitatively in addition to qualitatively, the smaller the role of "chance" and the better the prediction of the outcome. Although the qualitative aspects of chromosome behaviour have mainly been analysed in cytological studies, most of our knowledge of the quantitative aspects results from genetic experiments. Cytological studies, however, can also yield rather exact quantitative information on chromosome behaviour and the processes by which it is determined. The aim of the present studies is to work out methods for and to give examples of the use of cytological data in obtaining such information.

When the organism is "normal" with respect to the meiotic process, that part of the chromosome behaviour that is genetically of importance, is determined by:
1. pairing.
2. chiasma formation and crossing over.
3. orientation of configurations.

Only the first two points will be considered in detail.

While the genetic approach to the study of chromosome behaviour is clearly indirect, it is not true that the cytological approach is always much more direct. It appears that, except in very favorable material such as some grasshoppers, reliable observations are not possible before diakinesis or even metaphase I. Even there it can often not be decided whether a pair of chromosome arms has one, two or even more chiasmata, nor what the original position of the chiasmata has been. The distinction between no chiasma (pair of arms not bound) and one or more chiasmata (pair of arms bound) is much more reliable, although some uncertainty may arise due to "loss" of chiasmata as metaphase proceeds (Sybenga, 1958). On this basis three configurations can be distinguished in the diploid (see below). In more complex situations as in polyploids and with chromosomal aberrations, more types of configuration may be distinguished. It appears that observations on these configurations can lead to a genetically meaning-