Aneuploidy and inbreeding depression in random mating and self-fertilizing autotetraploid populations*

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Summary. Almost all autotetraploids produce aneuploid progeny because of irregularities at meiosis. Aneuploid plants produce high frequencies of aneuploids. If it were not for selection against aneuploid gametes and sporophytes the amount of aneuploidy would increase every generation. Most experimental and theoretical studies on population genetics and heterosis in autotetraploids have neglected aneuploidy as a factor. To take aneuploidy into account experimentally requires the cytological identification of all chromosomes and to consider it theoretically requires a huge amount of computations. Consequently, microcomputer programs have been devised to show the effects of random mating and self-fertilization in autotetraploid populations. According to the model aneuploidy rapidly increases in randomly mated and self-fertilized autotetraploid populations until they achieve an equilibrium where the amount of aneuploidy introduced into the population is balanced by the amount of aneuploidy removed from the population by selection. The model suggests that self-fertilized populations have greater frequencies of aneuploid gametes and zygotes than do randomly mated populations and therefore aneuploidy may be a significant cause of the great inbreeding depressions found in autotetraploids.

Key words: Autotetraploidy - Quadrivalents - Aneuploidy - Heterosis

Introduction
Autotetraploid plants have four identical genomes. Because of irregularities at meiosis, primarily the 3-1 disjunction of the chromosomes of quadrivalents (numerical non-disjunction), autotetraploid populations consist of a mixture of many kinds of aneuploids (4x-1, 4x+1, 4x-1-1, 4x-1+1, 4x-2, etc.) along with true tetraploids or eutetraploids (4x). Aneuploid plants produce a high frequency of aneuploid gametes which produce more aneuploid plants in the next generation. If it were not for selection against aneuploid gametes and sporophytes, the amount of aneuploidy would increase every generation.

Aneuploidy in autotetraploids has been studied by Bingham (1968) in alfalfa, by Morrison (1956) and Hagberg and Ellerstrom (1959) in rye, by Lamm (1945) in potatoes, and by Shaver (1963) and Doyle (1973) in corn. Many other papers could be cited showing the prevalence of aneuploids in autotetraploid populations.

However, most experimental and theoretical studies on autotetraploidy in regard to gene segregation, population genetics, and heterosis neglect aneuploidy. It has been demonstrated by Catcheside (1956, 1959) and Doyle (1973) that aneuploidy greatly affects genetic ratios. Several authors have investigated heterosis or inbreeding depression in autotetraploid populations without considering aneuploidy. Dewey (1969) believed that the great amount of inbreeding depression found in autotetraploid crested wheatgrass is the result of the induced homozygosity of deleterious mutants and deficiencies that have accumulated in this outcrossing species. Busbice and Wilsie (1966) and Gallais (1967) developed models for inbreeding depression that involve interactions between the four alleles present in autotetraploids. Hill (1976) devised a model using two alleles. Rice and Dudley (1983) have applied these models to inbreeding data in corn and found that Hill's model fits the best.

The validity of these hypotheses is not questioned. However, the presence of aneuploidy will affect the expression of these phenomena. Also, if it can be demonstrated that aneuploidy is different in randomly mated and self-fertilized populations, then aneuploidy by itself may be an important factor in heterosis and inbreeding depression.

In a randomly mated population, gametes such as 2x-1 and 2x+1 (from 4x-1 and 4x+1) plants may unite to restore
the cutetraploid, 4x, if they have the same homologue aneuploid. However, in a self-fertilized population there is no chance of compensation between hypoploids and hyperploids. A selfed (4x-1) plant will yield 1/4 (4x), 1/2 (4x-1), and 1/4 (4x-2). This assumes that no aneuploidy arises in the rest of the sets of homologous chromosomes and that 2x and 2x-1 gametes function with equal frequency. The disomic tetraploid (4x-2) should be uncommon in randomly mated populations but should be common in self-fertilized ones. If 4x-2 plants are not viable, then the fertility of a 4x-1 plant is reduced by 1/4. If they are viable they may be less fit than the equivalent 4x-1-1 (double trisomic tetraploid) found in a randomly mated population. If this is true we would expect a self-fertilized population to be less fit than a randomly mated one. A reduction in vigor and fertility has been shown to be the result of aneuploidy in rye by Hagberg and Ellerstrom (1959) and in corn by Shaver (1963).

A comprehensive theoretical or experimental study on the behavior of aneuploidy in autotetraploid populations has not been made. This paper is an attempt to show the effects of random mating and self-fertilization in autotetraploids by using a theoretical model. While the model is not complicated, it requires a great amount of calculations so microcomputer programs have been devised.

**Gamete production from euploid and aneuploid autotetraploids**

An autotetraploid has x sets of 4 homologous chromosomes (x is the number of chromosomes in the genome). A 4x-1 aneuploid has x-1 sets of four homologues and one set of 3 homologues. The number of homologues in an aneuploid set may be 2, 3, 5, or 6: as found in 4x-2, 4x-1, 4x + 1, and 4x + 2 plants, respectively.

It is assumed that sets of homologues pair and disjoin independently of each other. Thus, to determine the gametic output of a plant, sets are regarded separately and then the results are combined to give the expected gametic constitutions.

Also, because this model is concerned with true autotetraploids it is assumed that homologous chromosomes pair at random with each other, i.e., the inheritance is tetrasomic. It is possible that pairing code mutants or structural aberrations could arise that would cause preferential pairing with homogenetic bivalents and consequently disomic inheritance. Whether disomic inheritance patterns could become more easily established in self-fertilized or randomly mated populations is an interesting question, but it is beyond the scope of this paper. Experimentally, the decline in quadrivalent frequencies in autotetraploid populations selected for fertility which might indicate progress toward disomic inheritance as observed by Gillies and Randolph (1951); Mastenbrock et al. (1982), and others is very slow and therefore is probably not a major factor in affecting aneuploid frequencies in autotetraploid populations.

There are three chief pairing modes possible with a set of four homologues: two bivalents, a trivalent and a univalent, and a quadrivalent. The disjunction pattern of two bivalents is almost always 2-2 with two chromosomes going to each pole at the first division of meiosis. Very rarely there may be non-disjunction of a bivalent with both chromosomes going to the same pole.

Trivalent and univalent formation are rare in an autotetraploid because pairing is generally complete; in a trivalent and a univalent there is the equivalent of two chromosomes unpaired. Generally, the trivalent will disjoin 2-1 leaving the univalent to go to either pole, and this results in a 1:1 ratio of 2-2 and 3-1 disjunctions. Frequently the univalent is lost, this gives a 2-1 disjunction. Also the trivalent may be oriented in a linear configuration and may leave one chromosome on the metaphase plate, which is called a false univalent. This event also gives a 2-1 pattern. If the true and a false univalent are both lost then the disjunction is 1-1.

Quadrivalents generally disjoin 2-2. However, if the orientation of the quadrivalent on the metaphase plate is indifferent or linear, the disjunction may be 3-1. This event is called numerical non-disjunction (Catcheside 1956) and its frequency will be expressed as y. Also false univalents may be formed causing a 2-1 or 1-1 disjunction (if there are two false univalents). The expected frequency of functioning disomic, monosomic, and trisomic gametic sets from a tetrasomic is expressed as d, m, and t, respectively.

Disomic sets will form a bivalent that will disjoin to give a 1-1 disjunction. Non-disjunction of the bivalent would give a 2-0 pattern. Bivalent failure (two univalents) would give one half 1-1 and one-half 2-0 disjunctions. The expected frequency of functioning monosomic and disomic gametes from a trisomic is expressed as d, m, and t, respectively.

Disomic sets have four pairing modes; a bivalent and a univalent, and a trivalent. A bivalent and a univalent will give a 2-1 disjunction is the univalent is not lost. If it is lost then the pattern is 1-1. A trivalent gives a 2-1 disjunction. If a false univalent is lost then it is 1-1. The expected frequency of functioning monosomic and disomic gametes from a trisomic sporophytic sets is $M$ and $D_1$. The expected value of $M$ should be about 0.5 or more if there is no selection against monosomic gametes.

Pentasomic sets have four pairing modes; two bivalents and a univalent, a trivalent and a bivalent, a quadrivalent and a univalent, or a quinquevalent. Two bivalents and a univalent will give a 3-2 disjunction if the univalent is not lost. If it is lost the pattern will be