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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

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the eutetraploid, 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 distributions is the univalents move to either pole at random and are not lost. These events are rare. In the model it is assumed that disomic sporophytic sets produce all monosomic gametic sets.

Trisomic sets have two 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

Table 1. Disjunction patterns from sets of homologous chromosomes

No. of chromo-somes	Pairing config-uration	Univalent lost?		Patterns							
		T[a]	F[b]	2 – 2	1 – 1	2 – 1	3 – 1	3 – 2	3 – 3	4 – 1	4 – 2
2	II	–	–	–	all	–	–	–	–	–	–
3	II + I	no	–	–	–	all	–	–	–	–	–
		yes	–	–	all	–	–	–	–	–	–
	III	–	no	–	–	all	–	–	–	–	–
		–	yes	–	all	–	–	–	–	–	–
4	2 II	–	–	all	–	–	–	–	–	–	–
	III + I	no	no	1/2	–	–	1/2	–	–	–	–
		yes	no	–	–	all	–	–	–	–	–
		no	yes	–	–	all	–	–	–	–	–
		yes	yes		all	–	–	–	–	–	–
	IV	–	no	$1-y$[c]	–	–	y	–	–	–	–
		–	yes	–	–	all	–	–	–	–	–
5	2 II + I	no	–	–	–	–	–	all	–	–	–
		yes	–	all	–	–	–	–	–	–	–
	III + II	–	no	–	–	–	–	all	–	–	–
		–	yes	all	–	–	–	–	–	–	–
	IV + I	no	no	–	–	–	–	$1-y/2$	–	$y/2$	–
		yes	no	$1-y$	–	–	y	–	–	–	–
		yes	yes	–	–	all	–	–	–	–	–
	V	–	no	–	–	–	–	all	–	–	–
		–	yes	all	–	–	–	–	–	–	–
6	3 II	–	–	–	–	–	–	–	all	–	–
	IV + II	–	no	–	–	–	–	–	$1-y$	–	y
		–	yes	–	–	–	–	all	–	–	–
	VI	–	no	–	–	–	–	–	$1-z$[d]	–	z
		–	yes	–	–	–	–	all	–	–	–

[a] T = true univalent; [b] F = false univalent; [c] y = frequency of numerical non-disjunction from quadrivalent; [d] z = frequency of numerical non-disjunction from a sexivalent

2-2. A trivalent and bivalent will give a 3-2 disjunction barring the loss of a false univalent. If a false univalent is lost then the pattern is 2-2. A quadrivalent and a univalent will give a 3-2 pattern if there is no loss of true or false univalents and the disjunction of the quadrivalent is 2-2. If the disjunction of the quadrivalent is 3-1, this would give a 1 : 1 ratio of 3-2 and 4-1 disjunctions with the random movement of the univalent. If the univalent is lost a 3-1 disjunction of the quadrivalent would be expressed as such. A quinquevalent will give a 3-2 pattern barring losses of false univalents. The expected frequencies of functioning trisomic and disomic gametic sets will be represented by T and D_2, respectively. Here, as in the case with M, the value of T should be about 0.5.

Hexasomic sets have three chief pairing modes; three bivalents, a quadrivalent and a bivalent, or a sexivalent. Three bivalents will give a 3-3 pattern, barring non-disjunction of one or more of the bivalents. A quadrivalent and a bivalent will also give a 3-3 pattern. If the quadrivalent disjoins 3-1 then the pattern will be 4-2. The disjunction of the sexivalent will generally be 3-3, although a 4-2 separation is possible. The frequency of numerical non-disjunction from a sexivalent will be symbolized by z. In this model, z will be neglected, it will be assumed that all gametic sets from hexasomic sets will be trisomic.

This discussion is summarized in Table 1.

To determine the expected gametic output of a 4x plant we would expand the trinomial $(m+t+d)^x$. The results are shown in Table 2. Only terms where $m+t$ equals 4 or less are tabulated. It is assumed that more than four chromosomes plus or minus result in lethality. Experimentally, highly aneuploid individuals in autotetraploid populations are rare. In autotetraploid maize as reviewed by Doyle (1973) 99.7% of the population had chromosome numbers ranging from 36 to 44. Also, the model would become too unwieldy if more than 4 aneuploid producing events were considered. In nature, m and t would have low values and five or more events are very rare and may be neglected; note the low value labeled residual in Table 2.

When dealing with aneuploid genotypes the euploid sets and aneuploid sets are computed separately and

Table 2. Formulae for estimating the gamete production of euploid (4x) autotetraploids

Gamete type		General formulae	if x = 10	if d = 0.970, m and t = 0.015, and x = 10
a	$2x$	d^x	d^{10}	0.737424
b	$2x-1$	$xm\ d^{x-1}$	$10\ md^9$	0.114035
c	$2x+1$	$xt\ d^{x-1}$	$10\ td^9$	0.114035
d	$2x-1-1$	$xC2\ m^2\ d^{x-2}$	$45\ m^2\ d^8$	0.007935
e	$2x+1+1$	$xC2\ t^2\ d^{x-2}$	$45\ t^2\ d^8$	0.007935
f	$2x-1+1$	$xC1, 1\ mt\ d^{x-2}$	$90\ mt\ d^8$	0.015871
g	$2x-1-1-1$	$xC3\ m^3d^{x-3}$	$120\ m^3\ d^7$	0.000327
h	$2x+1+1+1$	$xC3t^3d^{x-3}$	$120\ t^3\ d^7$	0.000327
i	$2x-1-1+1$	$xC2, 1\ m^2\ td^{x-3}$	$360\ m^2\ td^7$	0.000982
j	$2x-1+1+1$	$xC2, 1\ mt^2\ d^{x-3}$	$360\ mt^2\ d^7$	0.000982
k	$2x-1-1-1-1$	$xC4\ m^4\ d^{x-4}$	$210\ m^4\ d^6$	0.000009
l	$2x+1+1+1+1$	$xC4\ t^4\ d^{x-4}$	$210\ t^4\ d^6$	0.000009
m	$2x-1-1-1+1$	$xC3, 1\ m^3\ td^{x-4}$	$840\ m^3\ td^6$	0.000035
n	$2x-1+1+1+1$	$xC3, 1\ mt^3\ d^{x-4}$	$840\ mt^3\ d^6$	0.000035
o	$2x-1-1+1+1$	$xC2, 2\ m^2\ t^2\ d^{x-4}$	$1260\ m^2\ t^2\ d^6$	0.000053
Residual				0.000006

Table 3. Formulae for gamete production for 30 possible chromosome constitutions

A	$4x$	$(m+t+d)^x$
B	$4x-1$	$(m+t+d)^{x-1}(M+D_1)$
C	$4x+1$	$(m+t+d)^{x-1}(T+D_2)$
D	$4x-1-1$	$(m+t+d)^{x-2}(M+D_1)^2$
E	$4x+1+1$	$(m+t+d)^{x-2}(T+D_2)^2$
F	$4x-1+1$	$(m+t+d)^{x-2}(M+D_1)(T+D_2)$
G	$4x-1-1-1$	$(m+t+d)^{x-3}(M+D_1)^3$
H	$4x+1+1+1$	$(m+t+d)^{x-3}(T+D_2)^3$
I	$4x-1-1+1$	$(m+t+d)^{x-3}(M+D_1)^2(T+D_2)$
J	$4x-1+1+1$	$(m+t+d)^{x-3}(M+D_1)(T+D_2)^2$
K	$4x-1-1-1-1$	$(m+t+d)^{x-4}(M+D_1)^4$
L	$4x+1+1+1+1$	$(m+t+d)^{x-4}(T+D_2)^4$
M	$4x-1-1-1+1$	$(m+t+d)^{x-4}(M+D_1)^3(T+D_2)$
N	$4x-1+1+1+1$	$(m+t+d)^{x-4}(M+D_1)(T+D_2)^3$
O	$4x-1-1+1+1$	$(m+t+d)^{x-4}(M+D_1)^2(T+D_2)^2$
P	$4x-2$	$(m+t+d)^{x-1}+(-1)$
Q	$4x+2$	$(m+t+d)^{x-1}+(+1)$
R	$4x-2-1$	$(m+t+d)^{x-2}(M+D_1)+(-1)$
S	$4x+2+1$	$(m+t+d)^{x-2}(T+D_2)+(+1)$
T	$4x-2+1$	$(m+t+d)^{x-2}(T+D_2)+(-1)$
U	$4x+2-1$	$(m+t+d)^{x-2}(M+D_1)+(+1)$
V	$4x-2-1-1$	$(m+t+d)^{x-3}(M+D_1)^2+(-1)$
W	$4x+2+1+1$	$(m+t+d)^{x-3}(T+D_2)^2+(+1)$
X	$4x-2+1+1$	$(m+t+d)^{x-3}(T+D_2)^2+(-1)$
Y	$4x+2-1-1$	$(m+t+d)^{x-3}(M+D_1)^2+(+1)$
Z	$4x-2-1+1$	$(m+t+d)^{x-3}(M+D_1)(T+D_2)+(-1)$
A′	$4x+2-1+1$	$(m+t+d)^{x-3}(M+D_1)(T+D_2)+(+1)$
B′	$4x-2-2$	$(m+t+d)^{x-2}+(-1-1)$
C′	$4x+2+2$	$(m+t+d)^{x-2}+(+1+1)$
D′	$4x-2+2$	$(m+t+d)^{x-2}+(-1+1)$

Table 4. Fitness factors for gametes

Gamete	Pattern				
	Std female	Std male	No. 1	No. 2	No. 3
a	1.00	1.00	1.00	1.00	1.00
b, c	0.90	0.80	1.00	0.80	0.95
d, e, f	0.70	0.60	1.00	0.60	0.85
g, h, i, j	0.50	0.40	1.00	0.40	0.65
k, l, m, n, o	0.30	0.20	1.00	0.20	0.25

then combined. The formulae for computing the gametes are shown in Table 3. The results from the expansions of these formulae are too lengthy to be given here. After obtaining the frequencies of the 15 types of gametes these value are multiplied by fitness factors. If the *a* (2x) gametes has a fitness of 1, the other gametes will have fitnesses of less than one, the more aneuploid the gamete the less will be its fitness. Various patterns of fitness factors are suggested in Table 4. The standard values show a progressive linear decrease from the *b* and *c* gametes which have one aneuploid chromosome set to the *k, l, m, n,* and *o* gametes which have four aneuploid chromosomes sets. The aneuploid male gametes are given lower fitnesses than are the corresponding female gametes. This is done to simulate the greater competition among male gametes. The standard values are used throughout this paper. These fitness factors are arbitrary. There is no adequate data available to assign fitness factors to different classes of aneuploid gametes. Three variations are examined and the results are given in Table 11; No. 1 where all gametes have a fitness of 1 unless there more than four chromosomes aneuploid, this is not the situation in nature, but is used to assess the effect of using fitness factors in the model. No. 2, which differs from the standard in that male and female gametes of the same type have equal fitnesses, and No. 3 where there is a non-linear decrease in fitness with increasing aneuploidy. This is probably the most likely model.

Zygote formation

The 15 gametes must be united in 120 different combinations to form the zygotes. Depending on whether the excess and deficient chromosomes are homologous or not, different zygotic products are possible. For example, a union of *b* (2x–1) and *c* (2x+1) gametes will produce A (4x) or F (4x–1+1) zygotes with frequencies of 1/x and x–1/x, respectively. A union of two *o* (2x–1–1+1+1) gametes will produce A, F, O, X, Y, and D′ zygotes. General formulae have been derived to give the relative frequencies of different zygotes where more than one are expected. These formulae require the number of combinations possible. For example, in *o* (2n–1–1+1+1) gametes there are 210 different possibilities with x=10. Thus the chance that two *o* gametes will have the same homologous chromosomes aneuploid with the opposite sign is 1/210, which will unite to form a A (4x) zygote. The formulae for figuring the zygotic output will not be given for the sake of brevity. It is assumed that zygotes with more than 4 chromosomes aneuploid are not viable.

To run through several generations of random mating using this model requires a great number of calculations. If we start with all A genotypes, then the gametic output is determined by using the formulae in Table 2. These gametic frequencies are multiplied by fitness factors which are range from 1 to 0. After these multiplications the sum of the frequencies of the gametes is less than one. These frequencies are restored to unity by dividing each of them by this sum. The gametes are then combined to form the zygotes. These zygotes are multiplied by their fitness factors. Patterns of fitness factors are given in Table 5. The standard values are used throughout this study, except for the results shown in Table 11. The zygotic fitness factors are arbitrary like the gametic fitness factors. The standard values show a non-linear decrease in fitness as the aneuploidy increases. Also, it is assumed that zygotes P–D′ which have one or two disomic or hexasomic sets are less fit than zygotes in A–O which have the same amount of aneuploidy but have just trisomic or pentasomic sets. Pattern No. 1 shows no lose of fitness until the number of chromosomes aneuploid exceeds 4. This is, of course not the case in nature, but was used to find the effects of zygotic selection in this model. Pattern 2 shows a linear decrease in fitness with increasing aneuploidy and is based only on the number of chromosome aneuploid. Thus the fitness of P (4x–2) is equal to D (4x–1–1). Pattern No. 3 has a non-linear decline in fitness and is based on the number of chromosomes aneuploid.

Table 5. Fitness factors for zygotes

Zygotes	Pattern			
	Std	No. 1	No. 2	No. 3
A	1.00	1.00	1.00	1.00
B, C	0.90	1.00	0.80	0.95
D, E, F	0.70	1.00	0.60	0.85
G, H, I, J	0.50	1.00	0.40	0.65
K, L, M, N, O	0.20	1.00	0.20	0.25
P, Q	0.60	1.00	0.60	0.85
R, S, T, U	0.40	1.00	0.40	0.65
V, W, X, Y, Z, A′	0.20	1.00	0.20	0.25
B′, C′, D′	0.10	1.00	0.20	0.25

The sum of the products of the zygotes times their fitness factors is ZF (zygotic fitness). The deviation of this value from unity represents the loss of progeny due to lethality or lower fertility resulting from aneuploidy. To restore the zygotic population to unity the frequencies of each types of zygotes is divided by ZF. Now the gametic output of the 30 zygotic genotypes must be determined using the formulae in Table 3. This gametic output is added together, multiplied by their fitness factors, restored to unity and combined again for the next generation.

Self-fertilization is a little simpler but just as tedious. The progeny of each of the 30 zygotic genotypes is determined and a matrix is set up with the zygotic genotypes of the parental generation on the vertical axis and the their zygotic products on the horizontal axis. The sum of the columns gives the frequencies of each zygotic genotype in the next generation.

To do these computations with a calculator, even using all sorts of shortcuts, requires about a 8 h day for a single generation. Consequently, Edward J. Doyle wrote microcomputer programs to simulate the population genetics of aneuploidy in autotetraploids. These programs run through a generation in about 20 s.

The programs for random mating and self-fertilization were written in BASIC09. They were constructed using modules for different tasks; combinations, gametic matrix, zygotic matrix, and others. These modules were written separately and then combined. There are 76 inputs: m, t, d, M, T, D_1, and D_2, for male and female gametes, 15 GF (gametic fitness) factors for each set of female and male gametes, and 30 ZF factors for the zygotes. These variables can vary from 0 to 1. Since $d+m+t=1$, $M+D_1=1$, and $T+D_2=1$, it is only necessary to input m, t, M, and T from these groups. Another input is the number of chromosomes per genome (x) which can vary from 8 to 32. Because the program deals with 4x±4 sporophytes which can produce 2n±4 gametes, eight is the lower limit. When x is over 32 the number of combinations becomes too large for the computer to handle. The last input is the number of generations (g) desired. Copies of these programs will be sent on request.

Results

Table 6 gives the results of random mating in an autotetraploid population with the conditions $x=10$, $d=0.970$, m and $t=0.015$, M and $T=0.5$, and FF = Std). These values are arbitrary, but are close to the frequencies found by Doyle (1973) in autotetraploid maize. If $m=t$ and $M=T$, then the population is symmetrical and B (4x–1) will equal C (4x+1); D (4x–1–1) will equal E (4x+1+1), and so forth. There are other close symmetries in the relative frequencies of pairs or tetrads of genotypes. R, S, T, and U are equal as are V, W, X, and Y. F is twice the frequency of D or E. I or J are three times the frequency of G or H. There are other apparent regularities in the relative frequencies between other classes of zygotes.

There are two classes of zygotes, one without –2 or +2 sets (A–O), and the other with –2 or +2 sets (P–D′).

The percentage of eutetraploids (A) decreases rapidly. However, there is no change in the relative frequency of the different genotypes after the 20 generation. The population has reached equilibrium where the production of aneuploidy is matched by the removal of aneuploids by selection. The zygotic fitness (ZF) is given at the bottom of the table. To restore the population to unity, the frequency of all genotypes is divided by ZF every generation. Another measure of aneuploidy in the population is the average number of chromosomes aneuploid per plant. This is computed by multiplying the frequencies of genotypes B and C by 1; D, E, F, P, and Q by 2; G, H, I, J, R, S, T, and U by 3; and K, L, M, N, O, V, W, X, Y, Z, A′, B′, C′, and D′ by 4. The total of the these products is the average aneuploidy (AA). The ZF declines, and AA increases until about the 20th generation.

Table 7 gives the results of self-fertilization in an autotetraploid population with the same conditions used in the randomly mated population shown in Table 6. The self-fertilized population also achieves equilibrium, but ZF is lower. There is a higher frequency of P–D′ zygotes in the self-fertilized population as compared with the randomly mated populations. This is because the A–O genotypes will give rise to all the genotypes, while the P–D′ genotypes will only give rise to P–D′ genotypes. Therefore there is an accumulation of P–D′ genotypes.

Table 8 shows the effects of varying the chromosome number. Because there more chances for numerical non-disjunction to occur, the amount of aneuploidy increases as the chromosome number increases. However, the percentage of the A–O class increases with the chromosome number because there is less chance of aneuploid chromosomes to be homologous. The value

Table 6. Random mating in autotetraploid populations. Conditions: $d = 0.97$, m and $t = 0.015$, M and $T = 0.5$, $x = 10$, FF = Std

Zygotes	Generations in %							
	1	2	3	4	5	10	20	30
A	63.87	47.52	39.64	35.65	33.56	31.24	31.12	31.12
B, C	15.01	19.36	20.60	20.96	21.07	21.12	21.12	21.12
D, E	1.32	2.87	3.85	4.40	4.71	5.07	5.09	5.09
F	2.63	5.73	7.70	8.81	9.42	10.14	10.17	10.17
G, H	0.06	0.22	0.36	0.46	0.53	0.61	0.61	0.61
I, J	0.18	0.65	1.09	1.39	1.58	1.82	1.83	1.83
K, L	0.00	0.00	0.01	0.02	0.02	0.02	0.02	0.02
M, N	0.00	0.02	0.05	0.07	0.08	0.10	0.10	0.10
O	0.01	0.03	0.07	0.10	0.12	0.14	0.15	0.15
P, Q	0.07	0.15	0.20	0.23	0.24	0.26	0.26	0.26
R, S, T, U	0.01	0.03	0.06	0.08	0.09	0.10	0.10	0.10
V, W, X, Y	0.00	0.00	0.01	0.01	0.01	0.01	0.01	0.01
Z, A′	0.00	0.00	0.01	0.02	0.02	0.02	0.02	0.02
B′, C′	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
D′	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
A – O	99.83	99.55	99.33	99.18	99.09	98.99	98.98	98.98
P – D′	0.17	0.45	0.67	0.82	0.91	1.01	1.02	1.02
ZF	94.06	89.40	86.39	84.59	83.56	82.33	82.26	82.26
AA no.	0.43	0.68	0.83	0.91	0.96	1.01	1.02	1.02

Table 7. Self-fertilization in autotetraploid populations. Conditions: $d = 0.97$, m and $t = 0.015$, M and $T = 0.5$, $x = 10$, FF = Std, $g = 20$

Zygotes	Generations in %							
	1	2	3	4	5	10	20	30
A	63.87	50.09	44.10	41.24	39.79	38.18	38.08	38.08
B, C	15.01	17.13	17.08	16.75	16.47	16.20	15.98	15.98
D, E	1.32	2.19	2.46	2.53	2.53	2.49	2.49	2.49
F	2.63	4.37	4.92	5.06	5.06	4.98	4.97	4.97
G, H	0.06	0.14	0.19	0.20	0.20	0.20	0.20	0.20
I, J	0.18	0.44	0.56	0.60	0.60	0.60	0.60	0.60
K, L	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M, N	0.00	0.01	0.02	0.02	0.02	0.02	0.02	0.02
O	0.01	0.02	0.03	0.03	0.03	0.03	0.03	0.03
P, Q	0.07	1.89	3.31	4.25	4.84	5.69	5.75	5.75
R, S, T, U	0.01	0.41	0.78	1.04	1.19	1.41	1.42	1.42
V, W, X, Y	0.00	0.03	0.06	0.08	0.09	0.11	0.11	0.11
Z, A′	0.00	0.06	0.12	0.16	0.19	0.22	0.22	0.22
B′, C′	0.00	0.01	0.02	0.04	0.04	0.06	0.06	0.06
D′	0.00	0.01	0.04	0.07	0.09	0.11	0.11	0.11
A – O	99.83	94.33	89.66	86.54	84.59	81.88	81.69	81.69
P – D′	0.17	5.67	10.34	13.46	15.41	18.12	18.31	18.31
ZF	94.06	86.57	81.38	78.36	76.67	74.60	74.47	74.47
AA no.	0.43	0.69	0.84	0.91	0.96	1.01	1.02	1.02

Table 8. The effect of chromosome number. Conditions: d = 0.97, m and t = 0.015, M and T = 0.5, FF = Std, g = 20

No. of chr.	BS[a]	%				No.
		A	A − O	P − D′	ZF	AA
10	RM	31.12	98.98	1.02	82.86	1.02
10	SF	38.08	81.69	18.31	74.47	1.02
11	RM	28.53	98.95	1.05	82.57	1.05
11	SF	35.14	80.83	19.17	72.28	1.08
12	RM	26.25	98.92	1.08	78.90	1.15
12	SF	32.51	80.07	19.93	70.15	1.15
15	RM	20.78	98.87	1.13	74.06	1.32
15	SF	26.02	78.26	21.74	64.13	1.34
20	RM	14.75	98.82	1.18	66.58	1.57
20	SF	18.57	76.42	23.58	55.19	1.59
25	RM	10.94	98.82	1.18	59.83	1.76
25	SF	13.71	75.53	24.27	47.48	1.79
30	RM	8.38	98.84	1.16	57.39	1.92
30	SF	10.41	75.23	24.77	40.84	1.96

[a] BS = breeding system
RM (random mating) or SF (self fertilization)

Table 9. The effect of varying d, m, and t. Conditions: M and T = 0.5, FF = Std, x = 10, g = 20

d	m, t	BS	%				No.
			A	A − O	P − D′	ZF	AA
0.998	0.001	RM	88.57	99.99	0.01	98.58	0.11
0.998	0.001	SF	92.74	98.00	2.00	98.02	0.09
0.970	0.015	RM	31.12	98.98	1.02	82.26	1.02
0.970	0.015	SF	38.08	81.69	18.31	74.47	1.02
0.900	0.050	RM	8.10	96.27	3.73	55.80	1.91
0.900	0.050	SF	8.22	71.94	28.05	39.15	2.07
0.500	0.250	RM	0.52	88.30	11.70	11.55	3.02
0.500	0.250	SF	0.23	78.20	21.80	2.10	3.25

Table 10. The effect of varying M and T. Conditions: d = 0.97, m and t = 0.015, and x = 10, g = 20, FF = Std

M, T	BS	%				No.
		A	A − O	P − D′	ZF	AA
0.00	RM	64.87	99.84	0.16	94.30	0.41
0.00	SF	64.91	99.64	0.36	94.18	0.41
0.10	RM	60.69	99.79	0.21	93.30	0.47
0.10	SF	59.89	99.10	0.90	92.60	0.49
0.25	RM	52.46	99.66	0.34	91.01	0.60
0.25	SF	51.20	95.62	4.37	87.90	0.66
0.50	RM	31.12	98.98	1.02	82.86	1.02
0.50	SF	38.08	81.69	18.31	14.41	1.02

Table 11. Effect of different patterns of fitness factors. Conditions: x = 10, g = 20, d = 0.91, m and t = 0.015, M and T = 0.5

FF	BS	%				No.
		A	A − O	P − D′	ZF	AA
Std	RM	31.12	98.98	1.02	82.26	1.02
	SF	38.08	81.69	18.31	74.47	1.02
#1	RM	5.27	93.30	6.70	91.67	2.33
	SF	3.52	11.21	88.79	80.29	2.93
#2	RM	41.01	99.20	0.80	78.92	0.82
	SF	44.32	82.42	17.58	73.32	0.91
#3	RM	17.19	97.54	2.46	82.88	1.45
	SF	21.30	55.13	44.87	74.16	1.61

of ZF declines, and AA increases. The ZF values are always lower in the self-fertilized (SF) populations than in the randomly mated (RM) populations with the same chromosome number. The frequencies of the A (4x) genotype is greater in the self-fertilized populations than in the corresponding randomly mated populations. This result from the greater loss of aneuploids in the self-fertilized populations which leaves a proportionally higher amount of A genotypes after restoration of unity. This effect may be seen in some of the following tables.

Table 9 shows the effects of varying d, m, and t. With a decrease in the value of d there is an decrease in ZF and an increase in AA, which are greater in the SF populations than the RM populations with the same conditions.

Table 10 shows the effects of varying M and T. Decreases in M and T result in an increases in ZF and decreases in AA. Here again, the ZF values are lower in the SF populations than in the RM populations with the same conditions.

Table 11 shows the effects of different patterns of fitness factors. In pattern No. 1 where there is no selection against gametes or zygotes that are aneuploid for less than four chromosomes there is a large accumulation of P–D′ genotypes. The ZF value is high. The differences between the Std, No. 2, and No. 3 are apparent.

Discussion

The only real use of a theoretical model is to suggest hypotheses that can be tested in the real world. Clearly, what is needed are data on the genotypic constitutions of autotetraploid populations. Most of the published data consist of raw chromosome counts with no identification of the chromosomes. Recent advances in chromosome banding have greatly facilitated the determination of chromosomal genotypes. Also, it is possible to ascertain the genotye by using genetic markers and to study the inheritance of aneuploidy. The author has recently synthesized multiple-marked autotetraploid stocks in maize.

A critical assessment of the assumptions on which this model is based is needed.

1. Do the values of *m, t, M,* and *T* vary between the male and female? In the data reported by Doyle (1973) for chromosome 3 there seems to be considerable variability in these values; for the female, $m = 2.42\%$, and $t = 0.99\%$, and for the male $m = 0.36\%$ and $t = 1.36\%$. The total number of gametes tested was 808 for both female and male. For the sake of simplicity *m* and *t* were given equal values in the model as were *M* and *T*.

2. How much do the *m, t, M,* and *T* parameters vary among the sets of chromosomes? To refine the model we would have to give separate values of *m, t, M,* and *T* to each set.

3. Do sets of homologues pair and disjoin independently of each other? It is possible that the behavior of set may depend on the whole genotype. Because meiosis is under control of genes, it is possible that some aneuploid genotypes might have a more irregular meiosis with possibly higher general rates of numerical non-disjunction and perhaps non-disjunction of disomic sets due to bivalent failure.

4. What is the relative fitness of the various gametic and zygotic genotypes? What fitness factor pattern would mimic nature most accurately. Also, how would fitness factor fit individuals in a class of genotypes. For example there are x types of 4x-1 plants depending on what chromosome was in trisomic conditions. Each should have its own fitness factor. Also would these fitness values be independent of the environment. A stressful environment may lower the fitness of the more extreme aneuploids.

5. It was assumed in this model that disomic sets produce all monosomic gametic sets and that hexasomic sets produce all trisomic sets. While bivalent failure (two univalents) or non-disjunction of the bivalent may be rare, if there is a great selective advantage in the pollen of disomic gametes over monosomic gametes then the disomic trap may be avoided. The frequency of numerical non-disjunction in sexivalents and the loss of a chromosome as a false univalent maybe enough to yield a significant frequency of disomic subset gametes from a hexasomic set.

Conclusions

It seems to be futile to expand or elaborate this model until such time as actual data become available. Nonetheless, this model demonstrates the complex nature of aneuploidy in autotetraploid populations.

For all the hypothetical conditions tested the ZFs are lower and AAs are usually greater in SF populations than in RM populations. Hexasomic and disomic tetraploids which probably have relatively low fitnesses are common in self-fertilized populations and uncommon in randomly mated ones. It is suggested that part of the inbreeding depression of self-fertilized autotetraploid populations can be explained by this model.

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