

ferent possible types of embryos, depend on whether the flower has been self- or cross-pollinated".

Apomixis will be discussed in greater detail in Chapter 11.

Theoretical genetic ratios

The ratios which might be expected in an allopolyploid depend on the behavior of the chromosomes that carry the genes responsible for the character being studied, and on the presence or absence of more alleles for that character than the two in a particular pair of homologous chromosomes. The extremes as to chromosome pairing in a $4n$ allo-tetraploid are: (1) complete synaptic homology between corresponding chromosomes in the different genomes and therefore association as multivalents or in some cases only bivalents but at random in all possible combinations, and (2) no synaptic homology between chromosomes in the different genomes and therefore autosyndetic pairing.

With reference to any point at which the chromosomes are paired, e.g. the centromeres, pairing as multivalents may be considered as consisting of allo- as well as auto-

Table 102. Genic constitutions of gametes formed by $A_1^A A_1^a B_1^A B_1^A$ with autosyndetic and with random pairing, first with no crossing over between the gene locus and the centromere*, then with a frequency of such crossing over that will result in maximum equational segregation. The expected ratios from backcrosses and in F_2 are included.

Crossing over and kind of pairing	Gametes	Back cross	F_2
1. No interstitial crossing over			
a. bivalents, autosyndesis	AA + Aa	$\infty:0$	$\infty:0$
" , random	AA + Aa	$\infty:0$	$\infty:0^{**}$
b. multivalents (random seg.)			
1 autosyndetic***	1 (AA + Aa)		
2 allosyndetic***	2 (AA + Aa)		
Total (1 auto- + 2 allo-)	AA + Aa	$\infty:0$	$\infty:0^{**}$
2. Maximum interstitial crossing over			
a. bivalents, autosyndesis	AA + Aa	$\infty:0$	$\infty:0$
" , random	AA + Aa	$\infty:0$	$\infty:0^{**}$
b. multivalents (random seg.)			
1 autosyndetic	1 (13AA + 10 Aa + 1aa)		
2 allosyndetic	2 (13AA + 10 Aa + 1aa)		
Total of 20	13AA + 10 Aa + 1aa	23:1	575:1

* The term "interstitial crossing over" is suggested, in the same sense as it is used for chromosomal interchanges.

** Certain F_3 lines will segregate, those that came from AAaa F_2 plants.

*** For multivalents "auto-" and "allosyndetic" refer to the chromosomes associated at the centromere, i.e.

$$\frac{A_1^A}{A_1^a} \quad \frac{B_1^A}{B_1^A} \quad \text{and} \quad \frac{A_1^A}{B_1^A} \quad \frac{A_1^a}{B_1^A} \quad \text{respectively.}$$

In multivalent cross-shaped configurations of the type shown in Figure 52, p. 187, the distal arms would be associated allo- and auto- syndetically respectively.

syndetic pairing (if associated at random, 1 auto-: 2 allo-). For the multivalents in an autotetraploid, chiasmata may be such that the three possible types of disjunction (alternate and two adjacents) occur with equal frequency. This may not be true for multivalents formed by an allopolyploid if the synaptic homology is limited to relatively few segments.

The kinds of gametes and the ratios that are theoretically possible from an allopolyploid will now be derived for one locus in one chromosome pair in the A genome and its allelic locus in the partially homologous pair in the second or B genome. These may be designated:

$$\frac{A_1^A}{A_1^a} \quad \text{and} \quad \frac{B_1^A}{B_1^a}$$

the superscripts indicating the genetic constitution for the one locus, A vs. a, and the bases indicating the genome (A or B) to which the chromosome belongs. The expected kinds of gametes (their A vs. a constitutions) for various possible associations with and without crossing over between the gene locus and the centromere are summarized in Table 102. For the multivalents with crossing over in the interstitial segments, a configuration such as that in Figure 52 in the previous Chapter may be used to derive the gametic types and frequencies.

Table 102 shows that with autosyndetic pairing, $A_1^A A_1^a B_1^A B_1^A$ will not segregate any recessives due to the covering effect of the A alleles present on the $B_1 B_1$ chromosome pair. Crossing over will not change this. The recessive would not appear until the same mutation had occurred in a B_1 chromosome. If allosyndetic pairing occurs, but there is no interstitial crossing over, no recessives will appear in F_2 but certain of the F_2 genotypes will be duplex $AAaa$ and will segregate in F_3 . Only if interstitial crossing over occurs as well as allosyndetic pairing will $A_1^A A_1^a B_1^A B_1^a$ segregate recessives in F_2 . One further point is that double reduction giving $A_1^A A_1^A$ or $A_1^a A_1^a$ occurs only if there is multivalent formation at the time of crossing over. Otherwise the pairs of chromatids,

Table 103. Genic constitutions of gametes formed by $A_1^A A_1^a B_1^A B_1^a$ with autosyndetic (bivalent pairing) and with random pairing (multivalent associations).

		Ratio of back- cross	A:a in F ₂
<u>Crossing over & kind of pairing</u>	<u>Gametes</u>		
1. No interstitial crossing over			
a. bivalents, autosyndesis	AA + 2Aa + aa	3:1	15:1
" , random	AA + 4Aa + aa	5:1	35:1
b. multivalents (random seg.)			
1 autosyndetic	1 (AA + 4Aa + aa)		
2 allosyndetic	<u>2 (AA + 4Aa + aa)</u>		
Total (1 auto- + 2 allo-)	AA + 4Aa + aa	5:1	35:1
2. Maximum interstitial crossing over			
a. bivalents, autosyndetic	AA + 2Aa + aa	3:1	15:1
" , random	AA + 4Aa + aa	5:1	35:1
b. multivalents (random seg.)			
1 autosyndetic	4AA + 16Aa + 4aa		
2 allosyndetic	<u>2 (6AA + 12Aa + 6aa)</u>		
Total (1 auto- + 2 allo-)	2AA + 5Aa + 2aa	7:2	77:4

two of which have crossed over will not have a chance to pass to the same pole. Hence for $A_1^A A_1^a B_1^A B_1^a$ one extreme is autosyndesis and no segregation in F_2 or F_3 ; the other is random pairing and maximum equational segregation. This last extreme is the same as in an autopolyploid. The actual ratios observed in allopolyploids will be between these two extremes; and may not be the same for different chromosomes. Also they might not be the same in every line or in different generations. The new combinations produced as a result of crossing over during allosyndetic pairing may result in aberrant phenotypes. For example, some of the speltoid types that occur naturally in wheat are monosomic for the entire chromosome 5A(9), others for only part of this chromosome. Crossing over between partially homologous chromosomes should produce lines with modified homologies between genomes. If these became established, lines would differ by one or more interchanges.

The theoretical ratios from $A_1^A A_1^a B_1^A B_1^a$, i.e. heterozygous for a in the B_1B_1 pair as well as in the partially homologous A_1A_1 pairs, have been calculated in the same manner as for $A_1^A A_1^a B_1^A B_1^A$. The ratios are summarized in Table 103.

As shown in Table 103, the differences between the extreme types of segregation are not great.

The greatest differences are expected when species A carrying recessive markers is crossed with species B carrying the dominants, and the F_1 is doubled. Here, as before, the two extremes are autosyndesis with pairing as bivalents; and random association in multivalents. The theoretical results are shown in Table 104.

Table 104. Theoretical results from $A_1^a A_1^a B_1^A B_1^A$; with autosyndetic pairing (bivalents) and random association (multivalents).

Crossing over and kind of pairing	Gametes	Ratios, dom. : rec. in	
		back-cross	F_2
1. No interstitial crossing over			
a. bivalents, autosyndesis	Aa	$\infty:0$	$\infty:0$
" , random	AA + 4Aa + aa	5:1	35:1
b. multivalents (random seg.)			
1 autosyndetic			
2 allosyndetic			
Total (1 auto- + 2 allo-)	AA + 4Aa + aa	5:1	35:1
2. Maximum interstitial crossing over			
a. bivalents, autosyndesis	Aa	$\infty:0$	$\infty:0$
" , random	AA + 4Aa + aa	5:1	35:1
b. multivalents (random seg.)			
1 autosyndetic	3AA + 6Aa + 3aa		
2 allosyndetic	5AA + 14Aa + 5aa		
Total (1 auto- + 2 allo-)	2AA + 5Aa + 2aa	7:2	77:4

As shown in Table 104, the differences here are considerably greater, since no recessives are expected if bivalent pairing and autosyndesis occur. Interspecific crosses

between autotetraploid races might be used in planning experiments of this type.

Another possible type of behavior is included in Tables 102, 103 and 104. In certain allopolyploids, the chromosomes are never associated as multivalents, but as bivalents either of the autosyndetic type or a mixture of auto- and allosyndetic types. This is likely to be the case in species with very short chromosomes, and a low frequency of cytological crossing over. In those species multivalents are rare even in autopolyploids. Crossing over in the interstitial region, if it occurs when the chromosomes are associated as bivalents, does not change the expectations, as shown in Tables 102, 103 and 104. Again the extremes are autosyndesis and random pairing as bivalents.

The ratio is the same if multivalents are formed with no crossing over in the interstitial segments, followed by random segregation. If only bivalents are formed and pairing is at random, the ratios for the $A^aA^aB^aB^a$ and $A^aA^aB^aB^A$ genotypes are the same as for random segregation from $A^aA^aB^aB^A$, namely 35:1 in F_2 . As shown in Tables 102, 103 and 104, in allopolyploids showing autosyndesis, segregation for a recessive in one genome is not expected as long as the additional genome carries only the dominant alleles. If the dominant in the second genome mutates to the recessive allele, the recessive character should then segregate in a 15:1 or duplicate factor ratio in F_2 if both loci are heterozygous and pairing is autosyndetic. If in the meantime, the first locus has become homozygous recessive, the new mutant would segregate in a 3:1 ratio; that is, a ratio similar to that in a diploid. As mentioned earlier, this has been referred to as a diploidization process. It would not be until crosses were made with varieties or lines carrying the dominant alleles at both loci that the true duplicate factor nature of the character would be discovered. The point may be illustrated by a genetic study (Woodworth 1932) of cotyledon color in soybeans ($n = 20$), presumably a diploid species. Green cotyledon color is governed by duplicate factors, designated d_1 and d_2 (one other type of green is maternal). Of 38 yellow varieties tested, 33 carried both dominant genes for yellow ($D_1D_1D_2D_2$). Five carried only one of the genes for yellow, their genotypes being either $D_1D_1d_2d_2$ or $d_1d_1D_2D_2$ (Woodworth 1932). One genetic consequence is that in allopolyploids, the presence of a gene in one genome and its allele in a second genome results in a type of "heterozygosity", and possible factor interactions that may simulate heterosis and yet be true breeding. It should have applications in plant breeding, worthy of exploration (Beard 1959).

The $A^aA^aB^aB^A$ genotype is of some interest since it may be used in interspecific crosses to obtain information on the relative frequencies of auto- and allosyndetic pairing. Formulas for calculating a coefficient of autosyndetic pairing from such experiments, and data from one experiment are in the following section. The F_2 ratio of dominants:recessives is the same (5:1) for random association as multivalents or as bivalents (see Table 104). The ratio will be different if the association is non-random, also the proportions of heterozygous to homozygous gametes will be different. Hence such a study is not complete unless the genotypes are determined in a next-generation test. Also, genetic ratios indicating a certain kind of behavior apply only to the chromosomes carrying those genes. Not until experimental data are obtained for many different chromosomes in a species can general conclusions be drawn as to the type of ploidy. A different approach to this problem is the study of segregation for quantitative characters, the simultaneous segregation at numerous loci, as reported by Pergament and Davis (1961).

Data on genetic segregation in allopolyploids

Maize

Among the hybrids between diploid maize and perennial teosinte which is tetraploid, an occasional fertile tetraploid occurs. One reported by Emerson (1929) and Emerson and

Beadle (1930) had only bivalent pairing at meiosis and normal pollen. It evidently had 20 maize chromosomes and 20 from perennial teosinte. The maize stock was homozygous for several recessives and teosinte carried the normal alleles. Data were obtained from backcrosses with pollen from the recessive maize stock. A similar fertile hybrid with perennial teosinte in which the maize parent was waxy was reported by Collins and Longley (1935). The results will be presented after considering the theoretical expectations.

The percentages of recessives theoretically expected from backcrosses and the frequencies of the Aa F₁ gametes as measured by the frequency of the Aaaa genotype among the backcross progeny have been calculated for different percentages of autosyndesis (Burnham, unpublished). They are in Table 105.

Table 105. Theoretical % of recessives in backcross progenies from an F₁ duplex for a recessive gene contributed by one parent if various percentages of autosyndetic pairing are assumed, and all pairing is as bivalents, i.e. AAaa x aaaa. In the last column are the expected percentages of all backcross progeny that had received a heterozygous gamete from the F₁.

	% <u>autosyndesis</u>	Backcross, % <u>recessives</u>	% of all backcross progeny that are <u>Aaaa</u>
all allosyndetic	0.0	25.0	50.00
	12.5	21.88	56.25
	25.0	18.75	62.50
<u>random pairing:</u>	33.33	16.67	66.67
	50.00	12.50	75.00
	66.66	8.33	83.33
	75.00	6.25	87.50
	87.50	3.125	93.75
all autosyndetic	100.0	0.000	100.00

From the foregoing table, the following relations are evident: for each 1% increase in autosyndesis there is a .25% decrease in recessives, and for each 1% increase in autosyndesis there is a .5% increase in the percentage of all backcross progeny that had received an Aa gamete from the F₁.

These relations may be expressed in the following formulas for t, the proportion of autosyndesis for backcross data:

$$t \text{ (for first backcross data)} = \frac{1}{3} + 4 \left(\frac{1}{6} - \frac{x}{n} \right) \text{ or,}$$

$$(1) \quad t \text{ (for first backcross data)} = 1 - 4 \frac{x}{n} \text{ where } x = \text{observed number of recessives and } n = \text{total number of backcross progeny.}^*$$

If the dominant phenotypes in the first backcross progeny are given a progeny test, the following formula may be used:

*The formula given by Collins and Longley (1935) for the first backcross is:

$$t = \frac{1 - 6x}{1 - 2x} \text{ where } x = \text{ratio of recessive gametes: all the gametes, and } \sigma t = \frac{t \cdot \sigma x}{16.7 - x}$$

The two formulas for t give essentially the same values.

$$t \text{ (for progeny test of first backcrosses)} = \frac{1}{3} + 2 \left(\frac{y}{n} - \frac{2}{3} \right) \text{ or,}$$

- (2) $t \text{ (for progeny test of first backcrosses)} = \frac{2y}{n} - 1$ where y = observed number of simplex genotypes, i. e. from an Aa F_1 gamete and n = total number of dominants and recessives in the first backcross progeny.

The data from backcrossing the tetraploid hybrid with pollen from the recessive maize stock (Emerson 1929) are shown in Table 106.

Table 106. Data from the tetraploid hybrid of recessive maize x perennial teosinte backcrossed to the recessive

Gene	Total seeds or plants	obs. % recessive	t_1 values (autosyndesis)
g	208	5.8	.77
lg	25	4.0	.84
su	58	8.6	.66
wx	<u>113</u>	<u>9.7</u>	<u>.61</u>
TOTAL	404	7.2	.71
expected if pairing is random:		16.7	.33
expected if pairing is all autosyndetic:		0.0	1.00

As shown in Table 106, the percentages of recessives and the co-efficients of autosyndesis are intermediate between $t = 1.00$ expected if the pairing were all autosyndetic, and $t = 0.33$ expected if it were at random. The coefficient (t) based on the total for all the loci tested was .71; that is, 71% of the bivalents were of the autosyndetic type, that is both members maize or both teosinte chromosomes.

The fertile tetraploid hybrid between wx maize and perennial teosinte had $4.6 \pm 0.94\%$ of waxy pollen (Collins and Longley 1935), giving a t value of 0.80 ± 0.06 based on their formula and 0.816 based on the one presented here. In subsequent studies of F_2 and F_3 progenies, they observed segregation on the ears as well as in the pollen. The F_2 plants included 1 Wx^4 , 2 $Wx^3 wx$, 48 $Wx^2 wx^2$, and 5 $Wx wx^3$. The variation in percentage of waxy pollen in $Wx^2 wx^2$ plants, from 1.1 to 16.6, was four to nine times that in $Wx wx^3$ plants. The mean t values for all the $Wx^2 wx^2$ plants in F_2 and for those in F_3 were slightly lower than for the F_1 , but not significantly so. This might be a result of cross-overs which re-shuffled segments of the chromosomes. From a study of parent-offspring and inter-progeny correlations for percentages of waxy in pollen and seed, they concluded that the tendency toward autosyndesis was inherited.

Lycopersicon

Data have been reported from an experiment in which the diploid species of tomatoes Lycopersicon pimpinellifolium was crossed with L. esculentum carrying five genetic markers and the chromosome number of the F_1 doubled. The F_2 segregations from these plants, duplex for each recessive as reported by Lindstrom and Humphrey (1933) and Lindstrom (1936), are given in Table 107, along with F. W. Sansome's 1933 data from autotetraploid L. esculentum.

The percentages of recessives shown in Table 107 are in general intermediate between those expected for maximum equational segregation and random association as bivalents. The segregation for Rr in the allotetraploid suggests maximum equational

Table 107. F₂ data from allo- and autotetraploid tomatoes duplex for certain genetic markers. Allotetraploid data: Lindstrom, 1936, from Table 4, p. 205, Bot. Rev. Vol. 2. Autotetraploid data: F. W. Sansome, 1933, from Table 1, p. 107, Journal of Genetics Vol. 27.

	D-d	R-r	Y-y	C-c	A-a	B-b	Total of ratios Omitting Cc, Bb	Ratio	% rec.
allotetraploid:	1655-65	541-29	382-13	1314-92	992-37		3570-144	24.8:1	3.9
Observed % recessives	3.8	5.1	3.3	6.5	3.6		3.9		
autotetraploid:	995-43	647-26	554-17		172-4	207-8	2368:90	27.3:1	3.5
Observed % recessives	4.1	4.0	3.0		3.7	3.7	3.7		
expected, only autosyndetic pairing								∞:0	0
"	random assoc. (multivalents), genes close to centromere*							35:1	2.8
"	random assoc. (multivalents), maximum equational seg.							19.25:1	5.19
"	random assoc. (bivalents)							35:1	2.8

* When there is no crossing over in the interstitial region, the ratio is the same whether the association is as bivalents or as multivalents.

segregation. The percentages of potato leaf(c) are also high, but they mentioned difficulties in classifying the character as seedlings. Based on the totals of the comparable data the ratios for both types of tetraploids, 25:1 and 27:1 are almost exactly intermediate between maximum equational and random association as bivalents. In the allotetraploid F₁ there were bivalents and quadrivalents at diakinesis, but the associations were loose, with some disparity in size. At metaphase there were 24 bivalents. The behavior was not greatly different from that of autotetraploid *esculentum*. The genetic data agree well with the expectations on this basis. Backcross data are more desirable in such an experiment since there is a bigger difference between the expectations for the two extremes.

Examples of natural polyploids which have been studied to determine if they behave as auto- or allopolyploids are orchard grass, *Dactylis glomerata* (2n = 28), studied by Brix and Quadt (1953), Myers (1944), Timothy, *Phleum pratense* (2n = 42) by Norden-skiöld (1949, 1953, 1957); alfalfa, *Medicago sativa* (2n = 32) by Stanford (1951), Twamley (1955) and Davis (1956); and the potato, *Solanum tuberosum* (2n = 48) by Peloquin and Hougas (1958), and many others.

Dactylis

In *Dactylis*, chlorotic plants were found among the offspring of plants being used in the breeding program. White seedlings were believed to be g⁴, yellow green ones simplex Gg³, light green ones duplex G²g² and dark green ones either triplex or quadruplex. One expectation from an allopolyploid with disomic behavior (autosyndetic pairing) would be a true breeding light green genotype, g₁g₁G₂G₂, (i. e. g₁²G₂²). None appeared in their studies. They determined the frequencies of the various phenotypes in several crosses but the critical test for association of the four homologues as a multivalent accompanied by interstitial crossing over is the behavior of Gg³ genotypes, i. e. the frequency of GG gametes from which a dark green plant, G³g could arise. The data are in Table 108.

Table 108. Observed segregation for light and dark green seedlings in the self progeny of Gg³ plants (Brix and Quadt 1953, from Table 4, p. 418, Zeits. f. Pflanzenzuchtung 32, Paul Parey, Berlin and Hamburg).

Plant No.	Observed	
	Light	Green (G ³ g)
2	100	1
5	133	2
7	40	6
10	39	2
15	432	1
27	<u>172</u>	<u>3</u>
Total	916	15

The green seedlings are expected if the four homologues associate as a multivalent and if crossing over occurs between the locus and the centromere. The numbers, a ratio of 61 light green: 1 dark green, indicate a high frequency of multivalent association. This agrees with the cytological observation that quadri-valents were found in a relatively high percent. For this one locus, this species behaves essentially like an autopolyploid.

That the genomes of certain of the diploid *Dactylis* species are not greatly differentiated is indicated by the observation by Myers (cited by Stebbins, 1950) that a *D. glomerata*-like plant arose from crossing diploid *D. aschersoniana* with some diploid species from Iran. The diploid hybrids were completely fertile.

Phleum

In a study of hexaploid timothy (Nordenskiöld, 1953), the segregation for white seedlings was shown by the use of very large numbers of offspring to agree with the expectations for hexasomic segregation in which practically only bivalents were formed but at random between the members of each hexasome. Of the 21 plants originally selfed the three which did not segregate for white seedlings in the first generation segregated in the second generation test. Hence all 21 had been heterozygous. Ratios not explainable on the basis of a single albino factor were explainable on the basis of additional albino factors located in other hexasomes. The theoretical expectations (for bivalent pairing only) for a few of the possible genotypes that she has listed are shown in Table 109. The doses of dominant and recessive alleles for a given locus are indicated by the superscripts; different loci are indicated by the different letters; the number of homologues, i. e. di-, tetra- or hexasomic is indicated by the total number of alleles for a given locus.

It will be noted that the expected F₂ ratios are in several cases the same for different genotypes but show very different types of behavior in F₃. In certain cases, they are distinguishable on the basis of the results in F₂ tests.

Nordenskiöld's studies show conclusively that segregation for white seedlings was hexasomic. In some cases the numbers fitted tetra-disomic segregation also but in no case did they fail to fit hexasomic segregation. None of the results for a given family could be fitted to disomic segregation. The material also segregated yellow-green seedlings but there was some indication that classification was not always reliable.

Table 109. Expected segregations from a number of genotypes with bivalent pairing but different assumed numbers of homologues, in F_2 and in F_3 (Nordenskiöld, 1953, from Tables 2, 3 and 4, p. 473-475, *Hereditas* Vol. 39).

Behavior	Genotypes	F_2 seg.	Behavior in F_3			Mono-hybrid
			non-seg.	tri-	di-	
disomic	Aa Bb cc	15:1	46.6	-	26.7	26.7
tetrasomic, disomic	Aa ³ Bb	15:1	26.7	13.3	33.3	26.7
tetrasomic	A ² a ² bb	35:1	25.7	-	51.4	22.9
hexasomic	A ² a ⁴	24:1	4.2	25.0	45.8	25.0
"	A ² a ⁴ X ² x ²	24:1	3.0	25.0	47.0	25.0
"	A ² a ⁴ X ² x ⁴	11.8:1	0.2	8.3	47.7	43.8
"	A ³ a ³	399:1	29.6	41.1	24.8	4.5
"	A ³ a ³ X ⁴ x ²	399:1	21.3	46.6	27.6	4.5

Cytological observations showed only an occasional cell with a multivalent, never more than one per cell. Nordenskiöld (1949) obtained a tetraploid from the diploid *Phleum nodosum*, and by further treatment of these produced two hexaploid plants which were comparable with some types of the natural hexaploid *P. pratense* ($2n = 42$). One had two, the other three extra chromosomes which behaved as univalents at meiosis. About 15% of the cells had a single quadrivalent. The later stages including the pollen quartets were mostly regular.

The synthetic hexaploid was crossed on a self-sterile plant simplex for albino seedlings; one from the study discussed above. Segregation in the progeny of the F_1 's again was of the hexasomic type in which the *pratense* parent probably had been simplex in one set, duplex in another and the synthetic hexaploid hexaplex.

The study from all aspects is conclusive in showing that *P. pratense* behaves essentially like an autopolyploid. It also demonstrated that such a species can be carrying many lethals and yet be fully viable. Ordinary procedures of inbreeding might be expected to be very ineffective in deriving homozygous superior lines. Plant breeders have found it very difficult to obtain selfed lines that breed true for stem rust resistance in timothy.

Aquilegia

A few examples of synthetic allopolyploids or interspecific crosses which show additional interesting features will be given here. Skalinska (1935) compared flower color inheritance before and after chromosome doubling in a species hybrid, *Aquilegia chrysantha* x *A. flabellata nana*, which had seven pairs of chromosomes in F_1 . There was about 25% of abortive pollen in F_1 but normal seed production. The data on segregation for flower color in F_2 from this F_1 and in F_2 after doubling the chromosome number of the F_1 are in Table 110.

The F_2 data from the F_1 before doubling were interpreted as the result of interactions as follows: C-c, a factor pair for anthocyanin color vs. its absence, Rr and Ff, two pairs complementary for lavender blue color in the presence of C; Y linked with C,

y with c. The genotypes belonging to the four phenotypes in F_2 and the expected ratio are in Table 110.

Table 110. Segregation for flower color in F_2 of *Aquilegia chrysantha* x *A. flabellata nana*, from the 7 II F_1 , and from the 4n F_1 (Skalinska 1935).

Type of F_1		Anthocyanin			
		present		absent	
		Lavender blue	Pink	Yellow	White
7 II F_1	obs. in F_2	17	6	8	8
7 II F_1	calc. in F_2^*	16.5	5.5	7.3	9.8
7 II F_1	F_2 genotypes	27 CYRF	9 CYRf	9 CYrF 3 CYrf	9 cy RF 3 cy Rf 3 cy rF 1 cy rf
4n F_1	obs. in F_2	127	0	0	43

* based on theoretical 27:9:12:16 ratio.

The explanation offered for the presence of only two classes in the F_2 from the 4n F_1 was that in the allotetraploid the pairing was always between identical mates, auto-syndetic;

$$\frac{R}{R} \quad \frac{r}{r} \quad \frac{F}{F} \quad \frac{f}{f}, \text{ so that all gametes received both } R \text{ and } F.$$

The observed ratio of the two classes was 3:1. If the four chromosomes carrying the Cc and Yy loci pair as quadrivalents or at random as bivalents, a ratio of 25C:lc would be expected. If C always paired with c, the expected ratio is 15:1. Non-random segregation which brought the two CY chromosomes to one pole and the two cy chromosomes to the other, would explain the results. An F_3 test to determine genotypic frequencies might furnish an explanation.

Other examples

A probable example of an allopolyploid that is relatively true breeding because of autosyndesis is *Spartina townsendii* ($2n = 126$). Huskins (1930) concluded from its characters that it arose in nature by hybridization of *S. alternifolia* with *S. stricta* whose $2n$ numbers are 70 and 56 respectively. *S. townsendii* forms bivalents at meiosis, is very vigorous and fertile. Another example is an allotetraploid *Rubus* from *R. rusticanus* and *R. thyriger* in which the *R. rusticanus* type of prickles bred true while the type of prickles from the other parent could not be recovered (Crane and Darlington, 1927). When complete autosyndesis does occur and the genes from one species are in one genome and their alleles in a different genome, heterozygosity in a sense will be maintained in a true-breeding condition. Such allopolyploids may in certain cases be very vigorous. Certain characters may be suppressed, others accentuated. To take advantage of any heterozygosity in the original parents, it will be necessary to produce many F_1 's to sample the possible gametic combinations from both parents. As a further step in a plant improvement program, these might be intercrossed.

"Shift"

Somewhat different from the behavior described above are the interspecific crosses which fail to give segregation of the parental types in F_2 or later generations. No chromosome doubling has occurred. The explanation offered by Darlington (1928) is based on allosyndetic pairing. For example, Biffen (1916) reported no segregation for chaff color in the progeny of Rivet, a variety of Triticum turgidum with grey chaff crossed with T. polonicum having white chaff. Almost 100,000 plants were grown up to F_6 from 20 F_1 plants of that cross.

An explanation based on Darlington's suggestion is the following: in T. polonicum W_1 and W_2 , suppressors of the grey-chaff characters, are assumed to be carried on different chromosomes that pair allosyndetically in the F_1 i.e. $\frac{W_1}{W_2} \frac{w_1}{w_2}$. All the re-

sulting gametes have Ww and no segregation of grey-chaff color would be expected. To explain the unexpected pairing, it is possible that these two chromosomes of T. polonicum are more nearly homologous than either is with the corresponding chromosomes in T. turgidum.

As another example, the cross of Triticum polonicum ($n = 14$) with T. durum ($n = 14$), a cross which Aase reported formed 14 II or as few as 12 II, plus 4 I, segregated in F_2 in a ratio of one long glume: two intermediate: ~~two~~ short but the long-glumed ^{one} types were shorter than those in the T. polonicum parent (Engledow 1920, 1923). This segregation may be explained in a similar manner, except that in addition to a major factor pair for ~~awn~~ ^{glume} length there are dominant short modifiers contributed by the T. durum ^{glume} parent. The following genotypic and pairing scheme is a modification of that proposed by Darlington (1928).

<u>T. polonicum</u>	x	<u>T. durum</u>
L (long glume)		1 (short glume)
d_1 alleles of D		D_1 (short glume in one genome)
d_2		D_2 (short glume in second genome)
$\frac{L}{1}$		$\frac{D_1}{D_2} \quad \frac{d_1}{d_2}$

Here, glume length will segregate in a 1:2:1 ratio, but every gamete gets one of the dominant D modifiers, as a result of the pairing of chromosomes from different genomes. Hence, none of the plants would have glumes as long as those of T. polonicum. Only if pairing occurred between D and d would the $LL d_1 d_1 d_2 d_2$ genotype be produced.

Aneuploidy in allopolyploids

Progeny with chromosome numbers above and below the normal somatic number have been reported in a number of allopolyploid species. In general, the trisomics do not differ as much morphologically as do the trisomics from diploid species. In contrast with diploids, monosomic ($2n - 1$) plants usually can be established in polyploids, and in some instances nullisomics (lacking one pair) may be viable.

Types having an isochromosome or a telocentric chromosome have been found also, i.e. monosomic plus iso or monosomic plus telo; and nullisomic plus iso or nullisomic