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CYTOLOGICAL STUDIES OF BARLEY

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Li-Hung Chu

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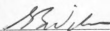
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CYTOLOGICAL STUDIES OF BARLEY

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CYTOLOGICAL STUDIES OF BARLEY

By

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I. Introduction

So far cytological studies in barley are meager when compared with those made on other cereals such as *Triticum*, *Secale* and *Avena*. Many problems remain to be studied. For instance, the cytological relationship between barley and other cereals is still obscure, and even relationship within the genus *Hordeum* is not clear. Many of the cultivated barleys and most wild barleys have a strong tendency towards diploidy though other cereals tend towards establishing polyploid varieties. Cultivated wheats and oats, for instance, are high polyploids. Why this should be constitutes a challenging problem. According to Chin(1941), the wild barley, *Hordeum bulbosum*, is an autotetraploid. Meiotic division at microsporogenesis was found to be rather irregular. The question of whether or not an allotetraploid barley, similar to wheat for example, would be produced by incorporation of a non-barley genome would seem to deserve more consideration.

Structural changes of chromosomes may arise spontaneously. Therefore varieties of barley derived from different sources may be found to be different in their chromosomal behaviours. Comparative cytological studies may well throw light on the nature of the genomic constitution in barley and on the relationship between them.

Preliminary studies have been carried out with a view to making certain of the chromosome numbers of different varieties of barley, both pure and hybrid, and to comparing the chromosomal morphologies. The meiotic division, in particular, was studied in detail. Further studies are obviously necessary.

Acknowledgement

The writer wishes to express his sincere indebtedness to Dr. G.B.Wilson for his valuable suggestions and inspiration in carrying out these studies. Also he wishes to thank Dr. K. J. Frey for his kindness in giving him the seeds and pedigrees for this study.

II. Review of previous work

In the cultivated barley, only diploid forms, $2n=14$, have been found, but in wild barley both diploid and polyploid forms have been reported by various authors. The $2n$ chromosome numbers of barley, both cultivated and wild, are listed in the Table I.

Table I. The somatic chromosomes of cultivated
and wild barley

Species	Cultivated or wild	Chromosome numbers($2n$)	Authors
<u>Hordeum</u>			
<u>chilense</u>	wild	14	Andres 1941
H. <u>marinum</u>	"	14	Wulff 1937a
H. <u>pusillum</u>	"	14	Kihara 1924
H. <u>spontaneum</u>	"	14	Aase & P. 1926
H. <u>vulgare</u>	cultivated	14	Kihara 1924
<u>distichon</u>	"	14	Kagawa 1929
<u>hexastichum</u>	"	14 (28)	Ghimpu 1929a Karpechenko 1938
H. <u>jubatum</u>	wild	14	Tanzi 1925
.		28	Aase & P. 1926
H. <u>murinum</u>	"	14	Stolze 1925
		28	Aase & P. 1926
H. <u>bulbosum</u>	"	28	Stahlin 1929
H. <u>hystrix</u> (<u>gussoneanum</u>)	"	14,28	Chin 1941
H. <u>nodosum</u>	"	14,28	Chin 1941
		42	Griffie 1927
H. <u>compressum</u>	"	14	Perak 1941
H. <u>stenostachys</u>	"	14	Perak 1941
H. <u>leporinum</u>	"	28	Perak 1941

Artificially induced modification of chromosome numbers have been reported by several authors. Peto(1936) obtained tetraploid pollen mother cells by means of heat treatment. With similar treatment, Muntzing(1937) obtained a tetraploid barley with the chromosome numbers ranging from 27 to 30. Luther Smith(1941) reported two tetraploid plants, one of which was in the progenies of the varietal cross of common barley, Trebi X Club Mariout, and another of which was produced by colchicine treatment. Auto-tetraploid barley was also obtained by Chen et al(1945) with colchicine. The fertility of $4n$ plants was found to be 43.67 per cent as compared with the 85.29 per cent in the diploid plants.

According to Muntzing(1938), out of 93 twin barley plants, one triploid and two haploids were observed. A mutant barley, known as Contabescent Anther, described by Luther Smith(1942), which arose by mutation, formed multiploid pollen mother cells at meiosis. At first metaphase, chromosomes formed a plate consisting of 7, 14, 21, 28, 35, and 42 pairs of chromosomes. In an extreme case 112 pairs of chromosomes in a single plate was found. This was considered to be due to a single recessive gene, which causes the pollen mother cells to form plasmodium-like masses of various sizes in which chromosomes lie in groups.

As to the morphology of barley chromosomes, so far no descriptions have been given in detail. The presence of SAT-chromosomes in barley has been recognized by several authors. According to Heitz(quoted by Gosta 1939), Hordeum vulgare has two pairs of SAT-chromosomes. The same two types were reported by Lewitsky (quoted by the same author 1939) in H. distichum. Chromosome I

by his numeration is almost equal-armed, and has a long satellite, while type II has a short satellite on an arm which is much shorter than the other. Lewitsky also reported the occurrence of four satellites in Hordeum vulgare. Gosta(1939) found in haploid barley two satellites, in addition to plates with one or no satellite. The appendage of chromosome I does not lie on a straight line with the arm of the chromosome, but generally makes a characteristic sharp turn at the achromatic region. In diploid plants he found four satellites. However Ruttle and Nebel(quoted by Gosta 1939) reported that only one pair of SAT-chromosomes was observed in barley at metaphase of mitosis. According to Chin(1941), in cultivated barley, all without exception possess two pairs of chromosomes with satellites, but in the wild barley the situation is quite different. He found in diploid wild barley only one pair of chromosomes with satellites but two pairs of SAT-chromosomes in tetraploid wild barley. On the basis of these observations he concluded that the relationship between cultivated and wild barley may not be close.

Some cytological studies of barley, both cultivated and wild, have been made by several authors. Studying haploid barley, Gosta (1939) found known irregularities at meiosis which are characteristic of haploid plants. Swenson(1940) observed only micronucleus formation and the presence of open type bivalents in varietal hybrids between Brachytic and normal barley. According to Chin(1941) the wild barley, Hordeum bulbosum, behaved as an autotetraploid giving a maximum association of seven quadrivalents. He also observed bridges both at first and second anaphases. Luther Smith (1942) in studying a mutant gene in Contabescent Anther barley,

found that the separation of chromosomes in both divisions was rather normal. The same author(1941) reported the occurrence of an inversion, a reciprocal translocation and trisomics in cultivated barley. An inversion was observed in two plants of a "Sterile Flowers" stock selected from Hordeum deficiens nudideficiens(C.I. 2229). Although the MI was normal with seven pairs of chromosomes, he found 24 per cent of cells had either bridges or both bridges and fragments in one plant. In other plant, the value was 14 per cent. Furthermore, 20 per cent of quartets were found to have bridges with or without fragment. In another mutant he found a reciprocal translocation and trisomic, the chromosomes of a trisome in the trisomic plant tended to misdivide. As a result of this misdivision half chromosomes were formed with terminal centromeres.

Intrageneric and intergeneric hybridization studies have been made with different results(Malloch 1921; Kuckuck 1934; Quincke 1940; Smith 1942; Brink, Cooper and Ausherman 1944; Cooper and Brink 1944; Thompson and Johnston 1945). In general, no chromosomal homology was observed between barley genome and that of other cereals. The results in crosses within the genus *Hordeum* reported by different authors were, however, not consistent, which may be due to the different material and methods in dealing with hybridization by different workers. Unfortunately little or no cytological observation was made during most of the hybridization studies.

Many genetical investigations have been made in common barley (Robertson 1939; Robertson, Wiebe and Shands 1947). Seven linkage groups have been established and new genes are being discovered.

New characters may be induced by artificial methods. Some of these characters prove to be of potential economic value. Gustafsson(1940, 1941), by means of X-ray irradiation, obtained a number of mutations most of which rendered the chlorophyll development abnormal, but some of which may be of potential value. A so-called erectoid mutation caused the ear to be more compact and erect and the straw shorter and stiffer, thus rendering the plants more wind-resistant. Another one also resulted from irradiation, which caused the outer glumes to look like lemmas each of them having an awn of the same length as that of lemmas, and this mutant has large seeds and is completely fertile.

III. Materials and methods

Nineteen varieties of common 6-rowed and 2-rowed barley, Hordeum vulgare and H. distichum were obtained from the Department of Farm Crops, Michigan State College. Some of these are heterozygotes resulting from varietal crosses between varieties cultivated under widely different environments.

The varieties used for this study and their pedigrees are given in Table II.

Table II. Pedigrees of 19 varieties of common barley
(Hordeum vulgare and H. distichum)

Planting number	Names of Varieties	Type of spike	Meiotic behaviour	Origin
1'	Peatland (C.I.5269)	6-rowed		A selection from seeds from Switzerland
2'	Lion (C.I.923)	6-rowed		Imported from Russia
3'	Spartan (C.I.5027)	2-rowed	chromatid bridges; 2.25% of microspores with micronuclei	From cross Mich. Two-rowed X Black Barbless, Black Barbless from Lion, Mich.
4'	Chevron (C.I.1111)	6-rowed	Fragments in AI cells, 1.15% of microspores with micronuclei	A selection from seeds from Switzerland
5'	Plains (C.I.7564)	6-rowed	0.78% of microspores with micronuclei	From cross Peatland X Dryland
6	W4 Oderbrucker (C.I.7563)	6-rowed		From cross Murasaki Mochi X Oderbrucker, Oderbrucker imported from Germany

7	W4 Oderbrucker (C.I.7564)	6-rowed		Same as W4 Oderbrucker(C.I.7563)
8'	Manchuria (C.I.2947)	6-rowed	Fragments in AI cells; and 2.73% of introduction from microspores with micro-nuclei	Selection from an Manchuria
9'	Mars (C.I.7015)	6-rowed		From cross Minn462 X Peatland. Minn462 from cross(Lion X Manchuria) X Manchuria
10'	Jeebar	6-rowed		
11	Vantage (C.I.7324)	6-rowed		From cross Newal X Peatland X Plush ²
12	Minn-II-41-2			From cross Barbless X Peatland X Minsturdi
13	619808	6-rowed		Selection from Alpha X Wis 38. Wis38 from cross Oderbrucker X Lion
14	619924	6-rowed		Same as 619808
15	Kindred	6-rowed		Selection from a field of Wis37. Wis37 from same source as Wis 38
16'	Alpha	2-rowed	Fragments in AI cells; 3.78% of microspores with micro-nuclei	From cross Manchuria X Champion. Champion came from Vermont
17	Trebi (C.I.936)	6-rowed		Selection from a bulk lot of seeds from the South Shore of the Black Sea in Turkey
18'	Moore	6-rowed	Bridge in AI cells	From cross Wis38 X Chevron X Olli ²

19'	Bay (C.I.7113)	6-rowed	Bridges in AI & AII cells; trans- location; fragmentation; desynapsis; 4.11% of mi- crosprores with micronuclei	Selected from a cross Minn 450 X Spartan; Minn 450 from cross Manchu- ria X Lion X Sandrel
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' Representing varieties in which heads were fixed for meiotic studies.

" Exponents indicating the times of entering the crosses.

The technique employed in this study was as follow: Part of the seeds of each of the varieties mentioned above was germinated in Petri dishes. Root tips were fixed in three parts absolute alcohol to one part of glacial acetic acid for 24 hours, and then transferred to 70 per cent alcohol for storage. Preparations were made by the Feulgen squash method. All slides for mitotic observations were made permanent by soaking off the cover slips in 95 per cent alcohol and mounting in diaphane. Another part of the seeds of each variety was planted in the green house in pots. Whole spikes were fixed in the fixative for 24 hours as used for root tips with subsequent storage in 70 per cent alcohol. Smears were made in aceto-carmin, pressed, and sealed with paraffin. No permanent slides were made.

All observations were carried out with Bauch and Lomb compensating 15X oculars and 97X or 120X 1.5 mm apochromatic objectives. Camera lucida drawings were made at magnifications of 1975X, 2000X, 2200X, 3040X, 3100X, 3300X, and 4000X. All these magnifications have been reduced to one half in reproduction.

IV. Observations and discussion

A. General

All seeds of the above-mentioned varieties were planted in early October, 1948, in the green house. Unfortunately all varieties did not grow normally, although the germination was excellent. Instead of growing upward with stiff stems they were bushy and weak at the soil level. Early January, 1949, electric light was employed but no improvement in growth was found. At the end of that month, some varieties began heading and their heads were immediately fixed in 3:1 alcohol-acetic acid solution. Some varieties did not flower at all. Those in which spikes had been fixed for meiotic studies are indicated in Table II. No attempt was made to analyze the factor or factors involved in this abnormal growth, which may be due to insufficient nutrient supplies, too high a temperature, too low light intensity, or other factors. Also no attempt to correlate the meiotic abnormalities with the abnormal environments was undertaken.

All degrees of meiotic irregularities have been observed in material thus collected. Perfectly normal division was not found. Failure of pairing of certain chromosomes, elimination of chromatic material, micronucleus formation and chromatid bridge were frequently observed (Fig. 5, 8-9), and translocation accompanied by bridges, disorganization of nucleus, unequal distribution of chromosomes and desynapsis (Fig. 4, 10-19) were rarely found. How much of this abnormality was more or less direct result of the conditions of the experiment is difficult to determine, but at least the more extreme deviations from normal were found in known hybrids. So far it would appear that few cytological studies in pure lines of barley

have been made. It is possible that supposedly pure strains of barley may have some degree of abnormalities at microsporogenesis. It is not impossible that material not described as hybrid may be, to some extent, heterozygous itself.

Except in case of asynapsis, the early stages of meiosis were not studied. The chromosomes of barley are entangled together in early stages, thus rendering it difficult for analysis. All other stages were comparatively easy to observe. In the majority of cases, seven bivalents may be seen in diakinesis and first metaphase (Fig.2,6).

B. Morphology of barley chromosomes

Except for SAT-chromosomes, no description of barley chromosomes was found(Heitz 1931; Lewitsky 1931; Ruttle and Nebel 1937; quoted by Gosta 1939). In this study two pairs of SAT-chromosomes were found in all the material and the somatic chromosome number was found to be 14 without exception. In agreement with Lewitsky(1931) it was found that one pair of SAT-chromosomes is nearly equal-armed, while the other pair has arms of different length with the satellite on the short arm(Fig.1,3). However contrary to Lewitsky the satellites in these two pairs of SAT-chromosomes were found to lie on the straight line with the arms of the chromosomes, instead of making a characteristic sharp turn at the achromatic region. Furthermore it was found that the satellites on the unequal-armed chromosomes are usually difficult to identify, being intimately connected with the arms on which they are situated, in comparison with those on the equal-armed chromosomes. In all cases, the chromatin thread connecting the satellite with the chromosome arm was not observed, which of course did not mean the absence of such chromatin thread, because the satellite appeared almost always in the same position. It might be due to the fact that such portion was not properly stained, or that such threads are too delicate. No measurement was made on the size of such satellites, but it is obvious that the satellites on the unequal-armed chromosomes are somewhat smaller than those on the equal-armed chromosomes (Fig.3).

In barley no chromosome except two SAT-chromosomes with secondary constriction has been reported. All except the SAT-chromosomes look much alike. However, from the observations on somatic chromo-

somes (Fig.1) and metaphase chromosomes at meiosis of microsporogenesis(Fig.2), four types of chromosomes may be seen. These are two pairs of SAT-chromosomes, one pair of chromosomes with median centromeres, one pair of chromosomes with subterminal centromeres, and the other three pairs with submedian centromeres. The unequal-armed pair of SAT-chromosomes has a subterminal centromere. At meiotic metaphase the satellites could not be seen. The subterminal chromosomes are particularly distinct at meiotic metaphase when the chiasma on the short arm was usually resolved, thus rendering the bivalent rod-shaped, while other bivalents were still of ring types. It appears that the opening out of chiasmata on the short arms of subterminal chromosomes at meiotic metaphase may account for their early separation. Often such bivalents were found to be separated in advance of others. The different rate of separation might be explained on the basis that after opening out of the chiasmata on the one end the chiasmata on the other end would be more unlikely to resist repulsion between homologous centromeres than others still held together by chiasmata on both ends.

C. Meiotic irregularities at microsporogenesis

a. Bridge formation

Bridges were observed in some varieties such as Moore, Spartan, and Bay, either at first or second or both meiotic divisions. Fragments were not usually found when bridges occurred. Rarely, double bridges were also observed. In the variety Bay, bridges were encountered in 9 per cent of first anaphase cells, while in Moore only 1.9 per cent was observed. In one case no clearcut distribution of chromatic material was found in a late telophase cell, in which chromatic material was seen stretching between the poles of the cell, as if many bridges were found, and to some extent, fused together (Fig.9). A similar case was reported by Muntzing(1941) in rye, which was attributed to abnormal premeiotic division. In this case, it might be possible that either a number of chromatid inversions were involved, resulting AI bridges having later fused together, or they may be the result of some phenomenon such as "sticky chromosomes".

Inversions were observed in a "Sterile Flowers" of Hordeum deficiens by Luther Smith(1941). Bridges and fragments at AI and AII or TII in pollen mother cells were found, and the percentage of cells with either bridges or both bridges and fragments was 14-24 per cent. Twenty per cent of the quartets also had bridges with or without fragment. In this study no bridge has been found in quartets, and the frequency of bridge formation in general was low. In all except the variety Bay the fragments, if any, were found to be very small, a fact which might explain the apparent absence of fragments in the majority of cases, since their small size would make them difficult to see. Further, it would be reasonable to suggest

that the inversion segment would not be long. In Bay large fragments were observed, and bridges at AI and AII and double bridges at AII were relatively frequent, thus the inversion segment in this variety would be relatively long(Fig.4). According to Darlington(1937),the double bridges found in such varieties as Spartan and Bay might have arisen as a loop chromatid formed at AI which in turn resulted from crossing-over in the inversion with a chiasma proximal and disparate to it, or two loop chromatids were formed which resulted from the occurrence of two complementary chiasmata in the inversion with a chiasma proximal and disparate to it. In the latter case two fragments could be formed. In the case of Bay, two fragments were sometimes found to be associated with the double bridges.

b. Reciprocal translocation and fragmentation

A group of four chromosomes was found in a first anaphase cell of Bay, in which one satellite chromosome was seen to be involved (Fig.4). This group had the arrangement of an open ring. At some points in the ring chiasmata were not terminalized. Aside from this ring, fragmentation, and bridge and fragments were also observed in the same cell(Fig.4). The exact nature of fragmentation is still unknown.

Fragments were observed in the three varieties indicated in Table III.

Table III. Frequency of first anaphase cells with fragments

Variety	No. of cells with fragments	No. of cells observed	% of cells with fragments
Manchuria	4	164	2.44
Chevron	3	124	2.42
Alpha	2	58	3.45

Fragments which had already rounded up to form micronuclei were not included in Table III. In other varieties, no pollen mother cells in suitable stages for fragment analysis were available, only the frequency of micronuclei in the microspores were calculated (Table IV). In Bay, fragments were observed to occur in various stages of both first and second meiotic divisions. Because of the large number of aberrations in this variety, it has been treated separately.

It was found that the occurrence of fragments could not be simply explained as being secondary products of crossing-over in the inversion region. Because in the three varieties in Table III, no bridge or other irregularity was found except occurrence of fragments. Similarly in Bay the occurrence of all fragments could not be explained in this way. Since the frequency of fragments is higher than could be accounted for by bridge formation. It is possible that the occurrence of fragments must be relatively frequent even in a "pure" individual under normal conditions. According to Chen et al (1945) the pollen fertility in 2n barley was 85.29 per cent as compared with that of 4n plant which was 43.67 per cent. Thus even under normal conditions the nonhybrid individual would not necessarily show absolutely normal cell divisions.

The ring formation observed here, thus, must have originated from reciprocal interchange between nonhomologous chromosomes in which one pair of SAT-chromosomes was involved. Furthermore, the chiasmata in the ring were not completely terminalized, the separation would be, at least mainly, non-disjunctional, this fact may, in addition to other irregularities, lead to highly

abnormal behaviours observed in later stages. Unfortunately, due to shortage of material further studies of this translocation were rendered impossible for the present. Fragments need not originate from crossing-over in an inversion. According to Darlington(1937), illegitimate crossing over between nonhomologous chromosomes would lead, in some case, to formation of dicentric chromosomes and acentric fragments following breaks and reunion. Thus it is evident that before translocation and interchange can take place, breaks must happen somewhere under specific internal and external conditions. So far no satisfactory explanation for the exact nature of breakage is known.

c. Micronucleus

Micronuclei were frequently observed both during the progress of meiotic divisions(Fig.5) and in the microspores. Even in the microspores, some eliminated fragments were not rounded up to form micronuclei, but remained distinct. Unfortunately no mature pollen grains were available to study the correlation between the chromosomal behaviour and fertility.

Table IV. Frequency of microspores with micronucleus

Variety	Micronuclei				No. of microspores observed	% of microspores with micronuclei
	1	2	3	4		
Spartan	1	-	1	1	133	2.25
Bay	8	2	2	-	292	4.11
Alpha	4	-	1	-	148	3.78
Plains	1	-	-	-	115	0.78
Chevron	3	-	-	-	259	1.15
Moore	-	-	-	-	300	0.00
Manchuria	4	1	1	-	220	2.73

In Table IV results obtained from several varieties are given. In some varieties the percentage is very low or even zero. This may suggest that disorganization of cells with eliminated chromatic material may be going on in parallel with the progress of meiotic divisions. In some varieties in which no micronuclei were found, irregularities were observed before the completion of meiotic divisions.

The relationship between the irregular behaviour at meiosis and the frequency of micronuclei was variable. For instance, in the variety Bay, numerous irregularities were observed and the variety had the highest frequency of micronuclei in microspores, whereas in Alpha, where little abnormality was found during meiosis, there was also a high frequency of micronuclei.

d. Desynapsis

One case was found in one plant of the variety Bay, in which chromosomes in diakinesis were found to scatter all over the cell (Fig.14) without pairing, and the individual chromosomes were highly contracted. No later stage of first division was found. In second division various abnormalities as described below were found.

Due to the fact that the barley chromosomes are small and always crowded and entangled together in the early prophase, it is very difficult to study structural changes and to trace each individual chromosome at this stage. In diplotene (Fig.10) all chromosomes were seen to be crowded in the center of the nucleus with their ends stretching out. But in a few figures some whole chromosomes could be examined directly, from which it is clear that chiasmata have already become terminalized. The points of cross-

sing between loops(Fig.10) are twists not chiasmata.It is, of course, not certain whether or not chiasmata were only formed at the two ends. If the hypothesis that the pairing of homologous chromosomes starts from the region of centromeres is correct, then chiasmata would be expected to occur along the whole chromosome.Thus the fact that at diplotene they are present only at ends would indicate terminalization.

At early diakinesis chromosomes were seen still paired, highly contracted and attenuated, centered around a single nucleolus, the individual bivalents could not be distinctly identified. In later stage(Fig.11) most chromosomes fall apart, only two bivalents could be seen to be paired end-to-end. Two nucleoli may be seen around which many univalent chromosomes centered. The chromosomes were attenuated as observed in early diakinesis. At late diakinesis all chromosomes were found to scatter all over the cell(Fig.13-14), only in one case two halves of the bivalent were seen to be connected by a fine thread.The chromosomes in this stage were extremely contracted. Thus the desynapsis must begin at early diakinesis, and even in late diakinesis some chromosomes may still be connected by a fine thread. The relative position taken by univalent chromosomes was usually such as indicate the previous relationship of homologues.

Another preparation made from the same spike of the variety Bay as that in which the desynapsis just described was found showed many irregularities in second meiotic division. In all cells thus far observed no complete set of chromosomes was seen in second division cells(Fig.12,15-19), and the distribution of chromosomes in second anaphase also was abnormal. In one case the

cells of a quartet were very abnormal(Fig.18). Eliminated chromatic material could be seen. One cell with no chromatic material at all was found, and in one cell disorganization of the nucleus leaving chromatic material scattered through the cell appeared to have taken place. Such cells would be undoubtedly abortive. Bridges were frequently observed(Fig.12,16-17), and a cell with one chromatic fragment was found(Fig.18). Some of these irregularities resulted from the abnormal behaviour at the first division, but it seems unlikely that desynapsis alone could account for all of them.

Asynapsis and desynapsis have been reported and studied in detail in such plants as rye(Prakken 1943), wheat(Li et al 1945), *Godatia*(Hakansson 1943), *Pisum*(Koller 1938), *Datura*(Bergner et al 1934), *Oenothera*(Catchside 1939), *Crepis*(Richardson 1935), *Zea mays*(Beadle 1930,1933), *Allium*(Levan 1940), oats and wheats(Huskins et al 1933), and *Musa*(Wilson 1946). In all these studies asynapsis and desynapsis were found to be due either to a single mendelian recessive gene(Prakken; Li et al; Bergner; Beadle; Catchside), or to gene-controlled factors(Hakansson; Koller; Richardson; Levan; Huskins). In some cases environmental factors were found to be effective in influencing the frequency of asynapsis and desynapsis. According to Hakansson(1943), increase of humidity of the soil and the air may increase the frequency of asynapsis in *Godatia*. Li et al(1945) also found that the expression of desynapsis was found to be more pronounced at low temperature under which the desynaptic wheat grew. Therefore it seems reasonable to assume that the expression of certain characters controlled by a gene or genes should show fluctuations under different envi-

ronmental conditions, both internal and external. This is true of gene-controlled asynapsis and desynapsis in which a gene or genes react with specific conditions to govern the mode of pairing, formation of chiasmata, and other aspects of chromosome behaviour. In the case of barley, the cause or causes of failure of pairing at diakinesis are still unknown. Since the variety Bay in which desynapsis was observed was hybrid in nature and furthermore was grown under rather unfavorable conditions it may be that its very hybridity rendered it more susceptible to environmental effects. In the progenies of a hybrid between two wheat varieties Li et al (1945) found desynapsis which was considered to arise spontaneously. In their opinions desynapsis in that case was caused by a specific gene and some modifying factors the expression of which varied considerably under different environmental conditions.

The terms asynapsis and desynapsis are frequently erroneously used. Asynapsis means literally lack of synaptic pairing, yet in many cases where the term is used both synapsis and chiasma have been reported. Desynapsis would seem to be the more suitable word for describing the result of these conditions. When half bivalents become separated prior to metaphase, the results are to some extent similar to those of asynapsis so far as chromosome distribution is concerned. Prakken(1943) found in asynaptic rye none or one or two chiasmata after diplotene, most of which were terminalized. Catcheside(1939) reported 0.68 average chiasma per pollen mother cell at MI of asynaptic *Oenothera*. Richardson(1935) observed that the change of chiasma frequency for the whole nuclear complement in asynaptic *Crepis* at mid-diakinesis was from

4.0 in the normal to 2.4 or 1.8. Again in desynaptic wheat Li et al(1945) found that variation of the frequency of bivalents was from 0 to 21, and that bivalents were found to possess terminal, rarely interstitial chiasmata. Thus it will be obvious that both the so-called asynaptic and desynaptic plants showed synapsis at early stage of meiosis and chiasmata were formed, which were partially or completely resolved prematurely whether as result of genic action or environmental effects or both.

Asynapsis in Hordeum vulgare was once reported by Ekstrand (quoted by Prakken 1943). According to Prakken asynapsis in plants was clasified into three categories, viz., weak, mean strong, and complete. Asynapsis in barley was put into the first category by him. Desynapsis similar to that found in the present has not previously been reported. If clasified according to the degree of intensity of premature resolution of chiasmata, then this case in barley is an example of complete desynapsis.

Desynapsis here described was observed during this study. Due to shortage of material detailed study of all phenomena mentioned above, desynapsis in particular, was rendered impossible.

V. Summary and conclusions

A breakdown in genic balance would be expected where hybridization has occurred in barley. An unstable condition would be produced when genomes even with slightly different structural or genic differences were brought together. It must be evident that varieties of barley, being self-fertilized plants, would possess, under long period of cultivation, their own genic and structural constitutions, perpetuated under normal conditions. No doubt, crosses between them would disturb the normal process of growth, until a new stable point of equilibrium is again reached.

Nineteen varieties of barley derived from different sources were used for this study. In all cases the somatic chromosome number was found to be fourteen without modification.

Four types of chromosomes have been observed, viz., one subterminal, one median, three submedian and two SAT-chromosomes. SAT-chromosomes could be distinguished again by the fact that one was found to be nearly equal-armed with a rather long satellite, while the other is subterminal, and with a comparatively short satellite. The satellite in the latter, sometimes, was found to be intimately associated with the chromosome, rendering it difficult to examine.

Bridges were usually found in these varieties: Moore, Spartan, and Bay. The last-named had double bridges and fragments, while in the other varieties, only single bridges without fragments were observed.

A case of reciprocal translocation was encountered in Bay. A ring of four chromosomes was found, in which one satellite chromosome was involved. Fragmentation was also observed in this

variety, which, in addition to the inversion, accounted for the frequency of fragments.

Micronuclei were frequently observed in even "pure" lines. No strict correlation between meiotic irregularities and frequency of micronuclei was found.

Desynapsis was observed in one preparation of the variety Bay at meiotic division of microsporogenesis. Chromosomes at late diakinesis scattered all over the cell with rare pairing. It was found that desynapsis started at early diakinesis and showed maximum effect at late diakinesis in which complete desynapsis was seen. The second division was found to be very abnormal. It is suggested that desynapsis in this case might be the result of unfavorable growth conditions, genic and structural differences combined together.

Explanations of figures

- Fig.1. Somatic chromosomes of cultivated barley, $2n=14$.
4000X.
- Fig.2. First metaphast of meiosis at microsporogenesis showing
7 bivalents. 1975X.
- Fig.3. Idiogram of two SAT-chromosomes. a) nearly equal-armed
with a long satellite; b) subterminal with a rather
short satellite.
- Fig.4. First anaphase showing a ring of four chromosomes, a
bridge accompanied by a large fragment, and fragmentation;
the points at which fragmentation would probably occur
are indicated by arrow heads. 2000X.
- Fig.5. First telophase showing a micronucleus. 2000X.
- Fig.6. Diakinesis showing 7 bivalents and probably 3 nucleoli
two of which are fusing. 3330X.
- Fig.7. First anaphase showing a single bridge. 2000X
- Fig.8. First metaphase showing 6 bivalents and two univalents.
1975X.
- Fig.9. First telophase showing incomplete separation of chro-
matic material. 2000X.
- Fig.10. Diplotene showing two pairs of chromosomes and chromosome
loops.
- Fig.11. Early diakinesis showing 10 univalents and two end-to-
end bivalents, most of the chromosomes centered around
the nucleoli. 3040X.
- Fig.12. Second anaphase from the desynaptic plant showing unba-
lanced set of chromosomes and bridges. 2200X.
- Fig.13. Late diakinesis showing 12 univalents and one end-to-end

bivalent. 2200X.

Fig.14. Late diakinesis showing 14 univalents, a case of complete desynapsis. 2200X.

Fig.15. Second telophase from desynaptic plant showing incomplete division and a fragment. 2200X.

Fig.16. Second division from the desynaptic plant. 2200X.

a) second anaphase showing unequal distribution of chromosomes.

b) second anaphase with unbalanced set of chromosomes and occurrence of bridges.

Fig.17. Second anaphase from the desynaptic plant showing a bridge and a fragment. 2200X.

Fig.18. A cell with only one chromatic fragment at the end of second division. 2200X.

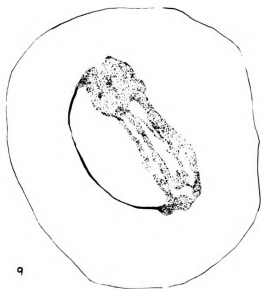
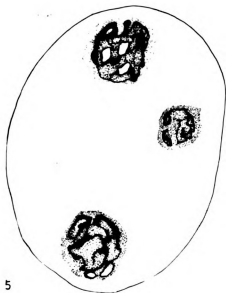
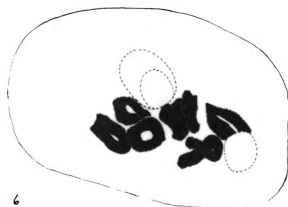
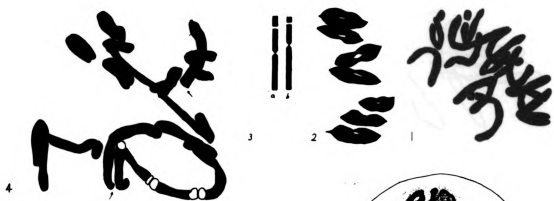
Fig.19. A quartet from the desynaptic plant. 3100X.

a) a cell with a micronucleus and fragments.

b) a cell without chromatic material at all.

c) a cell showing disorganization of nucleus.

d) a cell relatively normal with a micronucleus.

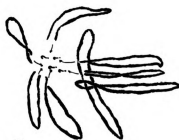




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11



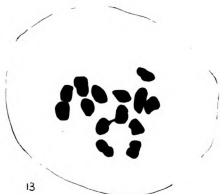
10



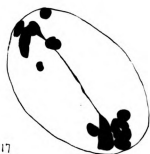
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14



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17



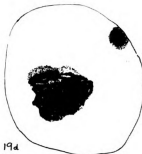
16



18



19b



19d



19a



19c

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