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THE ANEUPLOIDS OF COMMON WHEAT

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THE ANEUPLOIDS OF COMMON WHEAT

E. R. SEARS*

INTRODUCTION

In the organisms with which most genetic work has been done, the only aneuploid type generally obtainable has been the trisomic. In the hexaploid common wheat (*Triticum aestivum* L. *emend* Thell. ssp. *vulgare*), however, not only trisomics but also monosomics, tetrasomics, and even nullisomics are viable. Seventeen of the 21 possible nullisomics and one tetrasomic have been described briefly (Sears, 1944). All four series, monosomic, nullisomic, trisomic, and tetrasomic, have been completed. This means that a 0-4 dosage series is now available for each of the 21 chromosomes of wheat.

The chromosomes are numbered from I to XXI, with those of the *D* genome (the 7 chromosomes derived from *Aegilops squarrosa*) being designated XV to XXI. No distinction is made between chromosomes of the genome *A* (derived from a diploid species of *Triticum*) and the genome *B* (derivation unknown), these chromosomes being lumped together as numbers I to XIV. Larson (1952) suggests that chromosomes II, III, IV, V, VI, VII, and XIV may constitute the *A* genome, but it is clear that for at least one chromosome this grouping will not hold. From the observations of Pathak (1940) and Camara (1943), it may safely be concluded that one of the two nucleolar chromosomes of tetraploid wheat, which has genomes *A* and *B,* is in the *A* genome. Morrison (1953) shows that the two chromosomes concerned are I and X, neither of which is listed by Larson as belonging to the *A.* As Pathak points out, it is presumably the shorter, satellited nucleolar chromosome which was derived from diploid wheat, and this would be chromosome X. The long, secondarily constricted chromosome belongs, then, to genome *B;* and this is clearly chromosome I.

Largely through tests of the ability of particular tetrasomes to compensate for particular nullisomes, it has been possible to place the 21 chromosomes of wheat into seven homoeologous groups of three (Sears, 1952c). Within each group, the tetrasome of each chromosome compensates, at least in part, for the nullisome of each of the other two chromosomes (all but 3 of the 42 nullisomic-tetrasomic combinations possible

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within groups have been synthesized). None of the 29 between-groups combinations tested has shown compensation.*

In the descriptions to follow of the different aneuploid types, groupings according to homoeology will be used. The seven groups are:

1. I, XIV, XVII
2. II, XIII, XX
3. III, XII, XVI
4. IV, VIII, XV
5. V, IX, XVIII
6. VI, X, XIX
7. VII, XI, XXI

ORIGIN OF THE ABERRATIONS

The primary aberrations were monosomics, from which the nullisomics were subsequently derived, and trisomics, which gave rise to the tetrasomics. Thirty-five trisomes and more than 200 monosomes were identified in the process of obtaining the complete series. All of the aberrations occurred in a single variety, Chinese Spring Wheat (presumably identical with Crop Introduction No. 6223 of the U. S. Department of Agriculture).

The chief sources of monosomes and trisomes, as previously indicated (Sears 1939, 1944), were haploids and nullisomic III. Partially asynaptic nullisomic III, being a normal segregation product of monosomic III, was a particularly dependable source of aberrations, although each daughter of a nulli-III plant was of course deficient for chromosome III. Haploids were an excellent source of aberrations but were of sporadic occurrence. Only two euhaploids became available during the course of the work. Three others of aberrant constitution also occurred, one of which, with a supernumerary isochromosome, produced a number of aberrations.

Monosomes

Table 1 gives the frequencies with which the 21 different monosomes were obtained from the various sources. Under "miscellaneous" are grouped the 13 obtained from trisomics, 12 from monosomics, 5 from O'Mara's hairy neck material (O'Mara, 1951), 1 from a plant with a translocation (but the monosome not involving either of the chromosomes concerned in the translocation), and 3 from x-rayed pollen.

The data in Table 1 show some striking differences in the frequency of occurrence of the various chromosomes. Some of these differences are of very doubtful significance, however, because not all of the monosomes available were identified. Of the 94 monosomes tested from haploids, only 66 were identified. Identification was made by growing a population of about 40 seedlings and selecting any of them that were aberrant to grow to maturity. If there was any doubt as to the identity of the nullisomics obtained, crosses were made with testers for known chromosomes. Certain mono-

*Subsequent to the preparation of this bulletin, data have been obtained which suggest that tetra-XII can partially compensate for nulli-IV. Chromosomes IV and XII have also been found to have some pairing affinity.

TABLE 1--NUMBERS OF MONOSOMES IDENTIFIED FROM VARIOUS SOURCES.

Monosome	Source			Totals
	Haploids	Nulli-III	Miscellaneous	
I	4	3	2	9
II	5	6	0	11
III	6	0	4	10
IV	9	33	4	46
V	3	4	1	7
VI	5	5	0	10
VII	1	7	3	11
VIII	1	1	1	3
IX	3	11	1	15
X	3	1	3	7
XI	3	1	2	6
XII	2	0	0	2
XIII	3	0	1	4
XIV	1	0	2	3
XV	2	17	2	21
XVI	4	1	0	5
XVII	3	7	1	11
XVIII	0	4	2	6
XIX	4	8	5	17
XX	4	4	0	8
XXI	0	1	0	1
Totals	66	114	34	212

somics, such as III, IV, and XV, segregate nullisomics in high frequency (5-10%), which are easily separable as seedlings, and which have adult characteristics permitting positive identication. All such monosomics in a population would tend to be identified early. Monosomics that yield low frequencies of nullisomics, as do V, XVIII, and XXI, would tend to be in the portion of the population remaining unidentified at the end of the experiment, particularly if the nullisomics were difficult to distinguish from normal, like XXI, or were poorly viable, like XVIII.

Of the monosomes obtained from nulli-III, all but 4 of the 118 tested were identified. Therefore, the extreme differences in frequency of occurrence of certain of the monosomes in this material cannot be attributed to sampling error. As in the preliminary report (Sears, 1944) dealing with 58 of these monosomes, mono-IV and -XV again appear in unduly high frequency. Monosomes XII, XIII, and XIV did not occur at all, and VIII, X, XI, XVI, and XXI occurred but once each. These low frequencies are of doubtful significance, however, considering (1) the reduction in effective size of the population by the increased occurrence of IV and XV, (2) the existence of the four unidentified monosomes, and (3) the possibility of incorrect classification of mono-XIII as -II or -XX and mono-XIV as -I or XVII.

No abnormalities of distribution are obvious among the monosomes of miscellaneous origin. In this group, only three were not identified out of 37 tested.

Trisomes

The trisomes mostly came from the same sources as the monosomes, that is, from haploids and from nullisomic-III (Table 2). Several, however, arose as trisomes compensating for particular nullisomes, and others were obtained from a triploid. The triploid yielded many trisomes, but only a few of these had been tested when the trisomic series was completed. The triploid was not euploid but was mono-XI. It originated from a nulli-XI haploid pollinated by normal.

TABLE 2--NUMBERS OF TRISOMES IDENTIFIED FROM VARIOUS SOURCES.

Trisome	Haploids	Nulli-III	Compen-sating	Triploid	Iso-chromosome	Totals
I	0	2	0	0	0	3
II	1	1-3*	0	0	0	2-4
III	0	0	0	0	1	1
IV	0	2	0	0	0	2
V	0	1	0	0	0	1
VI	0	1	0	0	0	1
VII	1	1	1	0	0	3
VIII	1	1	0	0	0	2
IX	1	0	0	0	0	1
X	0	2	1	0	0	2
XI	1	0	0	0	0	1
XII	1	0	1	0	0	2
XIII	1	0-2*	0	0	0	1-3
XIV	0	0	1	0	0	1
XV	0	0	0	1	0	1
XVI	0	0	1	0	0	1
XVII	1	0	0	0	0	1
XVIII	0	2	0	1	0	3
XIX	1	0	0	0	0	1
XX	0	1	0	0	0	1
XXI	0	0	0	1	0	1
Totals	9	16	5	3	1	34

* Two trisomes were identified as either II or XIII.

The one other trisome originated from a plant with an isochromosome substituted for one normal chromosome. Plants of this constitution occasionally produce gametes with both the isochromosome and its normal homologue. Fertilization by a normal gamete gives a 43-chromosome plant, with the extra chromosome an isochromosome. From this secondary trisomic, the primary trisomic is easily obtained.

For identification of trisomes, the system used was different than for monosomes. Most chromosomes were tested as trisomes, rather than as the derivative extreme type, the tetrasome. Trisomics II, XIII, and XX could be distinguished as a group by the increased length of their awns, while tri-IX, with an extra dose of the squarehead gene, was compactoid. Other trisomics were classified only roughly as to chromosome length and then crossed with the appropriate testers. Toward the end of the search, when

but a few trisomes remained to be identified, crosses were made with only those testers necessary to identify the missing trisomes.

DESCRIPTION OF THE ANEUPLOIDS

General

Most of the nullisomics can be distinguished from normal by seedling characteristics, but in nearly every case positive identification of the nullisomic concerned can be made only on the basis of spike characters of mature plants. Certain homoeologous nullisomics are very difficult to distinguish from each other, requiring the making of crosses for final identification.

Monosomics, when grown under very favorable conditions, are difficult or impossible to distinguish from normal, except for mono-IX, which is speltoid, non-squarehead, and late-maturing, and mono-XVIII, which is late-maturing. Under less favorable circumstances, most of the others deviate from normal in the direction of the respective nullisomics.

Most trisomics also are normal in appearance, except for tri-IX, which is compactoid, and those in homoeologous group 2, which are narrow-leaved and small-stemmed, and have increased awns. In general the trisomics tend to resemble the respective tetrasomics, but usually not sufficiently that an individual trisomic plant can be distinguished from a normal with certainty.

Tetrasomics tend to differ from normal in the opposite direction from the corresponding nullisomics, but the deviation is almost always somewhat less. Vigor and fertility are below the normal to a varying extent, but not as much so as in the nullisomics. Every tetrasomic is both female and male fertile, whereas about half the nullisomics are sterile either on the female or male side.

Homoeologous Group 1

The three nullisomics of this group are reduced in plant height in varying degrees (Fig. 1) and have spikes that are a little less dense than normal, with slightly stiffer glumes (Fig. 2). All three nullisomics are both female and male fertile. On the basis of vigor and fertility of the nullisomics, chromosome I is the least essential of the three, with XIV slightly less essential than XVII. The tetrasomics are all slightly less fertile than normal, tetra-XIV being the least fertile. The monosomics and trisomics are essentially normal under favorable conditions.

Chromosome I

This chromosome has less effect on vigor and fertility than have most of the other chromosomes of wheat. Height is reduced around 20 per cent in the nullisomic, tillering is about 30 per cent less than normal, and fer-

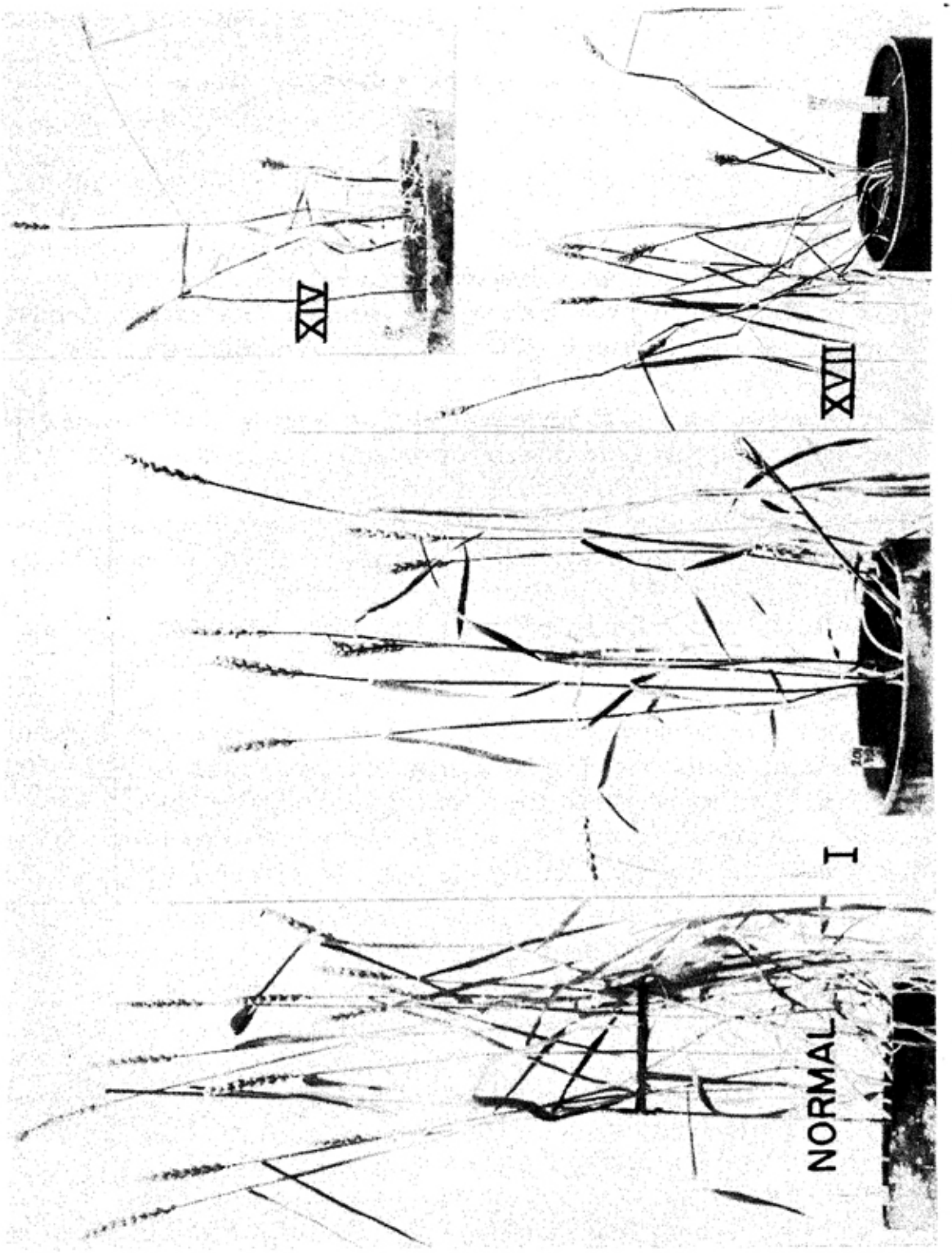

Figure 1. Nullisomic plants of homoeologous group 1 compared with normal Chinese. (0.12 natural size.)

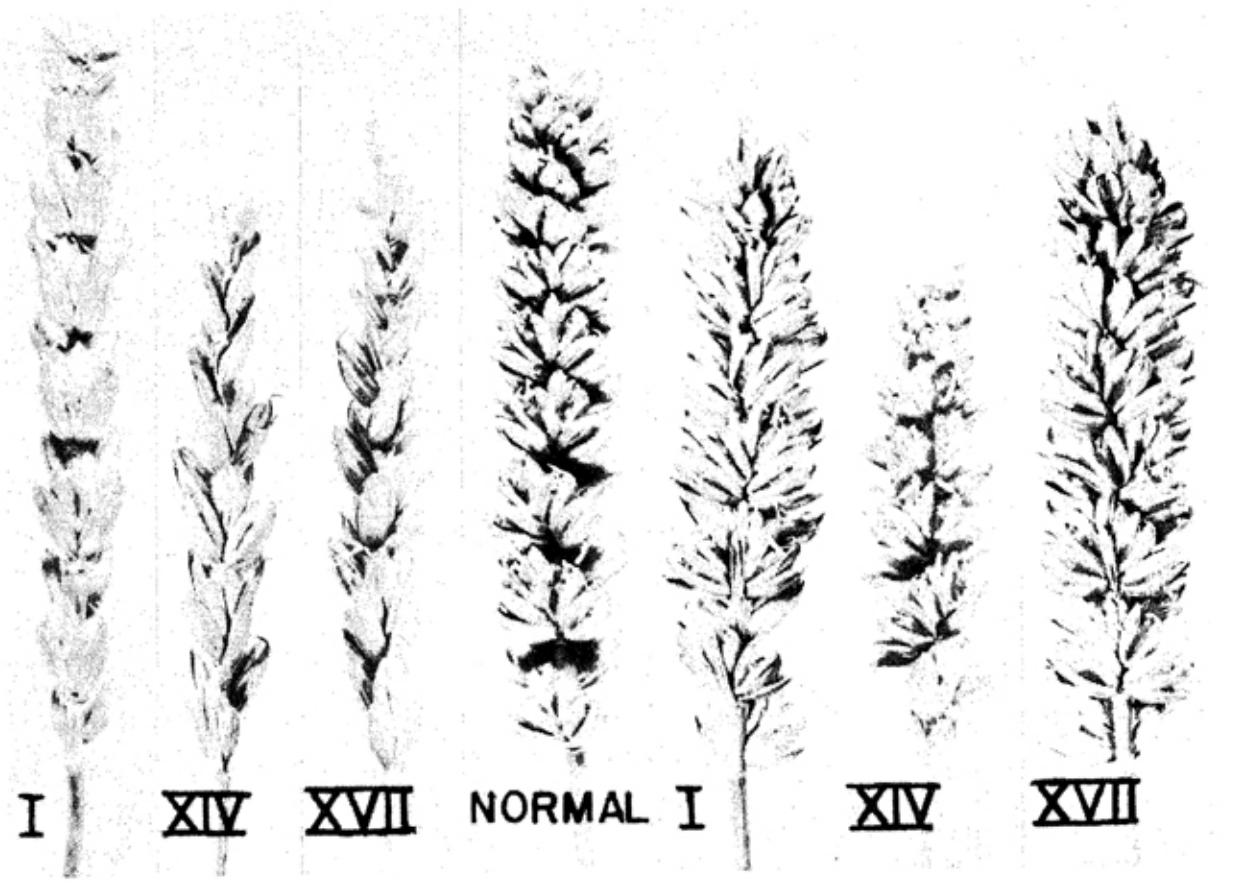

Figure 2. Spikes of nullisomics (left) and tetrasomics (right) of homoeologous group 1, compared with normal (center). (0.90 natural size.)

tility is down perhaps 75 per cent. The glumes are darker than normal. Unrau (1950) found that the gene for brown glumes carried by some varieties was located on chromosome I.

Chromosome XIV

Nulli-XIV is more dwarfed than nulli-I, being only about half normal height. It has leaves only one-half to two-thirds as wide as those of nulli-I, which are approximately normal, and its culms are only about two-thirds normal in diameter. Its spikes are shorter than those of nulli-I, and its fertility is substantially lower. Chromosome XIV carries the gene for pubescent glumes found in the variety Indian.

Chromosome XVII

Nullisomics for this chromosome are difficult to distinguish from nulli-XIV. They tend to be a little less vigorous than XIV, however, with tillering reduced to less than half of normal and fertility slightly less than XIV.

Homoeologous Group 2

This is a very distinctive group. All three nullisomics are very dwarfish, with greatly reduced tillering (Fig. 3). All are male fertile but female sterile.

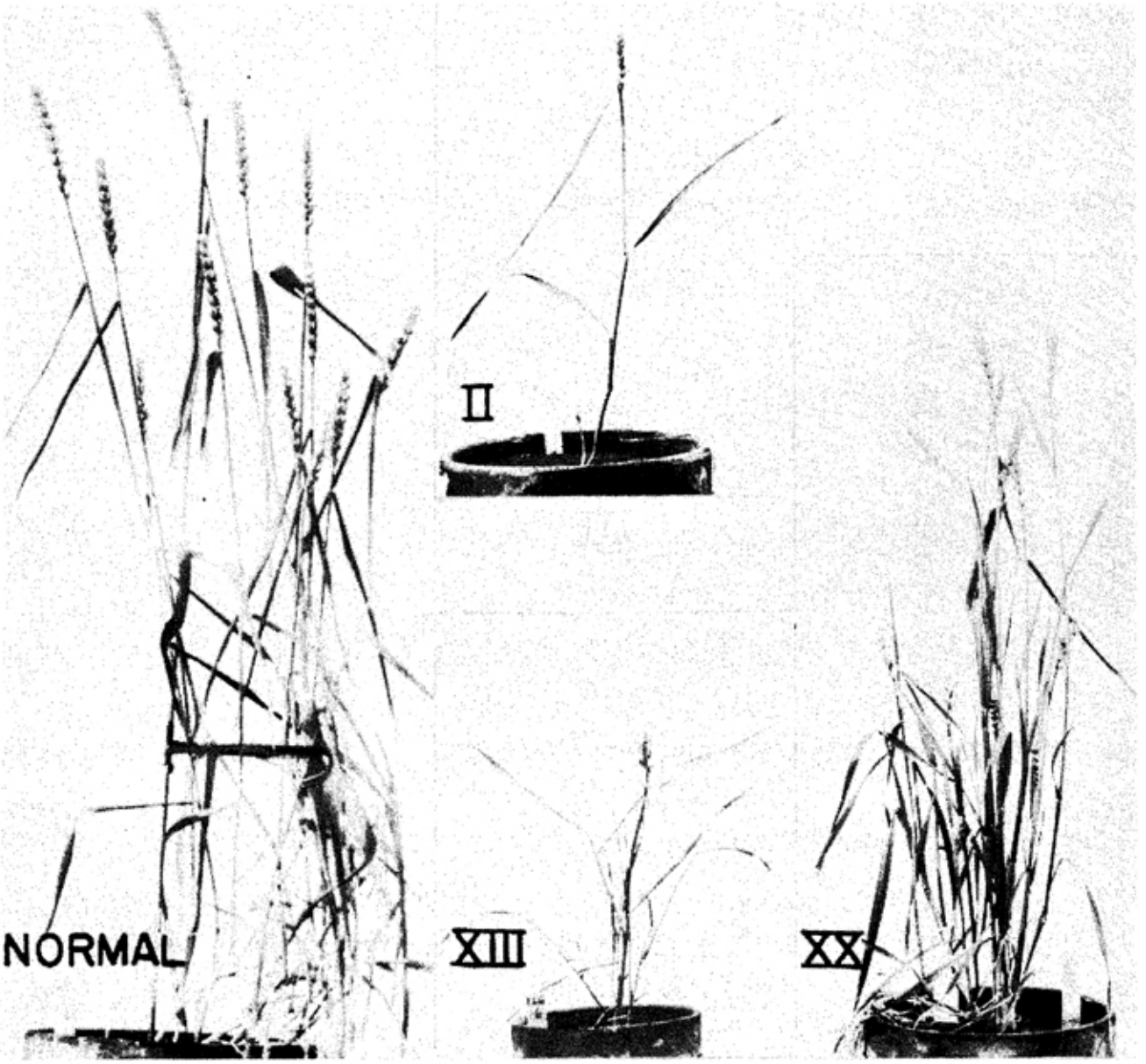

Figure 3. Nullisomic plants of homoeologous group 2 compared with normal Chinese. XX shows more tillering than is usual for this nullisomic. (0.13 natural size.)

The spikes (Fig. 4) have thin, papery glumes and are completely awnless. The three tetrasomics are virtually indistinguishable from each other. All have small culms and narrow leaves, with increased awn length, and with glumes somewhat stiffer than normal. The trisomics are distinguishable from normal by their rather narrower leaves and longer awns. The monosomics tend to be coarser than normal, with slightly shortened awns and reduced fertility except under very favorable conditions. In this series, deficiency for chromosome II seems to cause the greatest abnormality and XX the least.

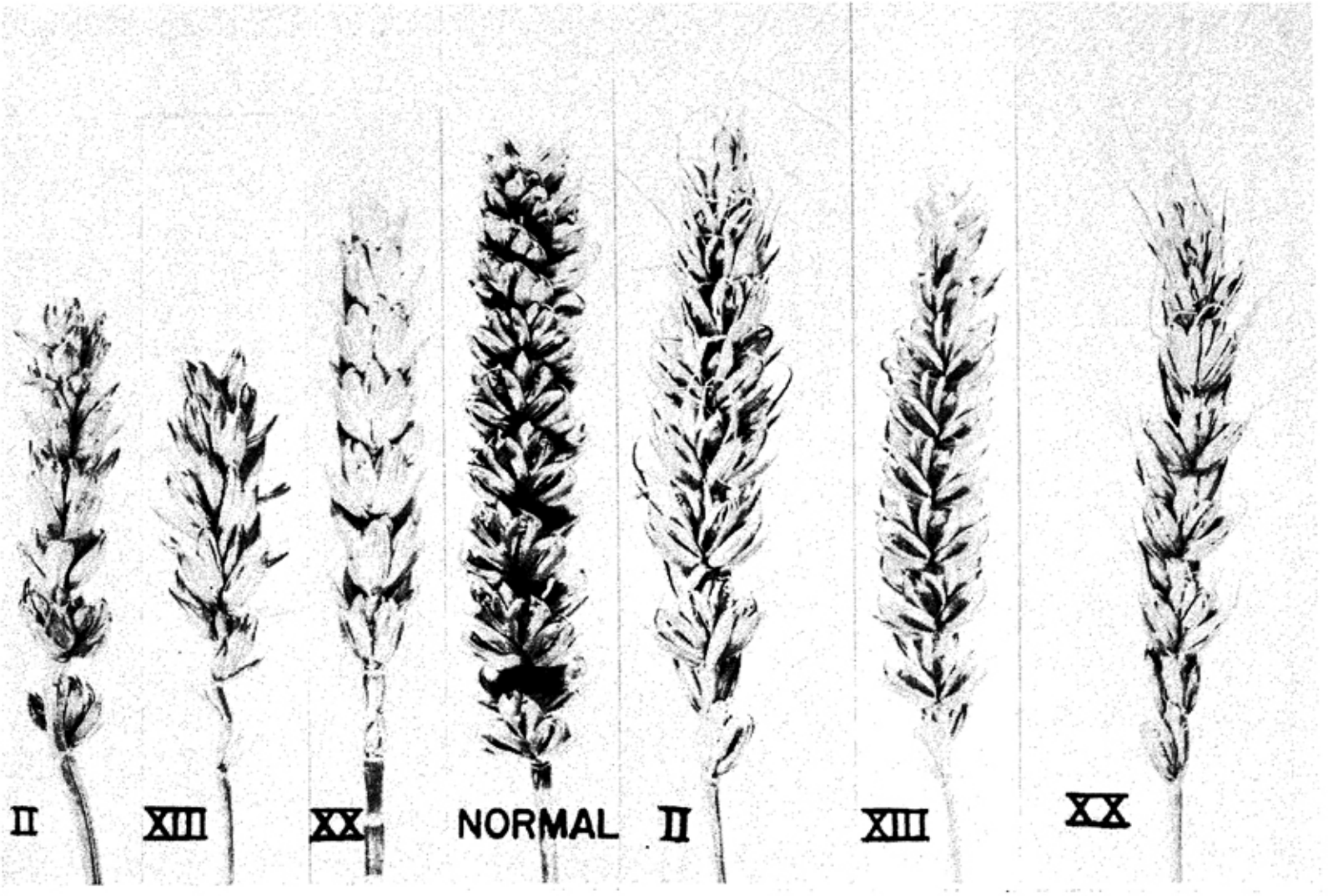

Figure 4. Spikes of nullisomics (left) and tetrasomics (right) of homoeologous group 2, compared with normal (center). The specimen of tetrasomic-XIII is atypical in awn development, in that tetra-XIII is normally similar to tetra-II and tetra-XX in this respect. (Natural size.)

Chromosome II

Nullisomics are dwarfed to half or less of normal height, and tillering is also reduced to half or less. Leaves are shorter and broader than normal, and culms are abnormally large. Maturity is delayed. Spikes usually have one or more nodes with an extra spikelet borne below the normal one. Structures ranging from a narrow bract to a complete set of flowering parts frequently occur between the outer glume and the lemma. Anthers are distinctly larger than normal. There is considerable asynapsis at meiosis. The coarseness of stem and broadness of leaf found in the nullisomic occurs also in the monosomic. Culms of both are about one-third greater in diameter than normal, but those of the nullisomic are relatively coarser because of their shortness. As Larson (1952) points out, culms of both nulli- and monosomic II are somewhat hollower than normal. The leaves of the monosomic are, like those of the nullisomic, about 50 per cent wider than normal, but those of the monosomic are of normal length and those of the nullisomic are short. Trisomics and tetrasomics are perhaps a little shorter than normal, and fertility of the tetrasomic is somewhat reduced.

Chromosome XIII

Nulli-XIII has short leaves, but in contrast to -II, these are narrower than normal—reduced about 50 per cent. Culms are smaller than with nulli-II, being about normal in diameter. Plants reach about the same height as those of -II, and maturity is also delayed. Spikes are characterized by the presence of several abortive or poorly developed spikelets at the base. The monosomic is more similar to mono-II than is the nullisomic to nulli-II. Leaves of the mono are somewhat broader than normal, though not so broad as mono-II. Culms are a little thicker than normal. Larson (1952) notes a gene on chromosome XIII of Chinese which inhibits solidness of culm.

Chromosome XX

Nullisomics are taller than either nulli-II or -XIII and tillering is somewhat nearer normal. Leaves are perhaps slightly narrower than normal, but their shortness makes them appear broad. Reduplication of spikelets occurs, as in nulli-II. Monosomics have slightly thicker culms than normal, but leaves may be a little narrower than normal. Seeds of the tetrasomic are small. Unrau (1950) has located the gene for compactum (club) head type on this chromosome. Larson (1952) finds a gene on chromosome XX for inhibition of solidness of culm. The variety Red Egyptian carries a gene on XX for seedling resistance to black stem rust, *Puccinia graminis tritici* (Sears and Rodenhiser, unpublished). The work of Peterson and his colleagues (Peterson and Masson, 1939; Goulden, 1950) had shown that the same gene, giving resistance to a large number of races, was present in

McMurachy and certain Kenya varieties; and recent findings of Peterson and A. B. Campbell (private communication) confirm the presence of this gene on chromosome XX.

Homoeologous Group 3

Nullisomics of group 3 are recognizable as seedlings by their narrow, short, stiff leaves. Mature nullisomic plants (Fig. 5) are dwarf and narrow-leaved, with short spikes (Fig. 6). Both female and male fertility are exhibited, but both are very low in nulli-XVI. Monosomics, trisomics, and tetrasomics tend to be nearly normal, but with considerable reduction in fertility of the tetrasomics, particularly in the upper half of the spike. The tetrasomics are rather late in maturing. Chromosome XVI appears to be most essential to the plant and chromosome XII least essential.

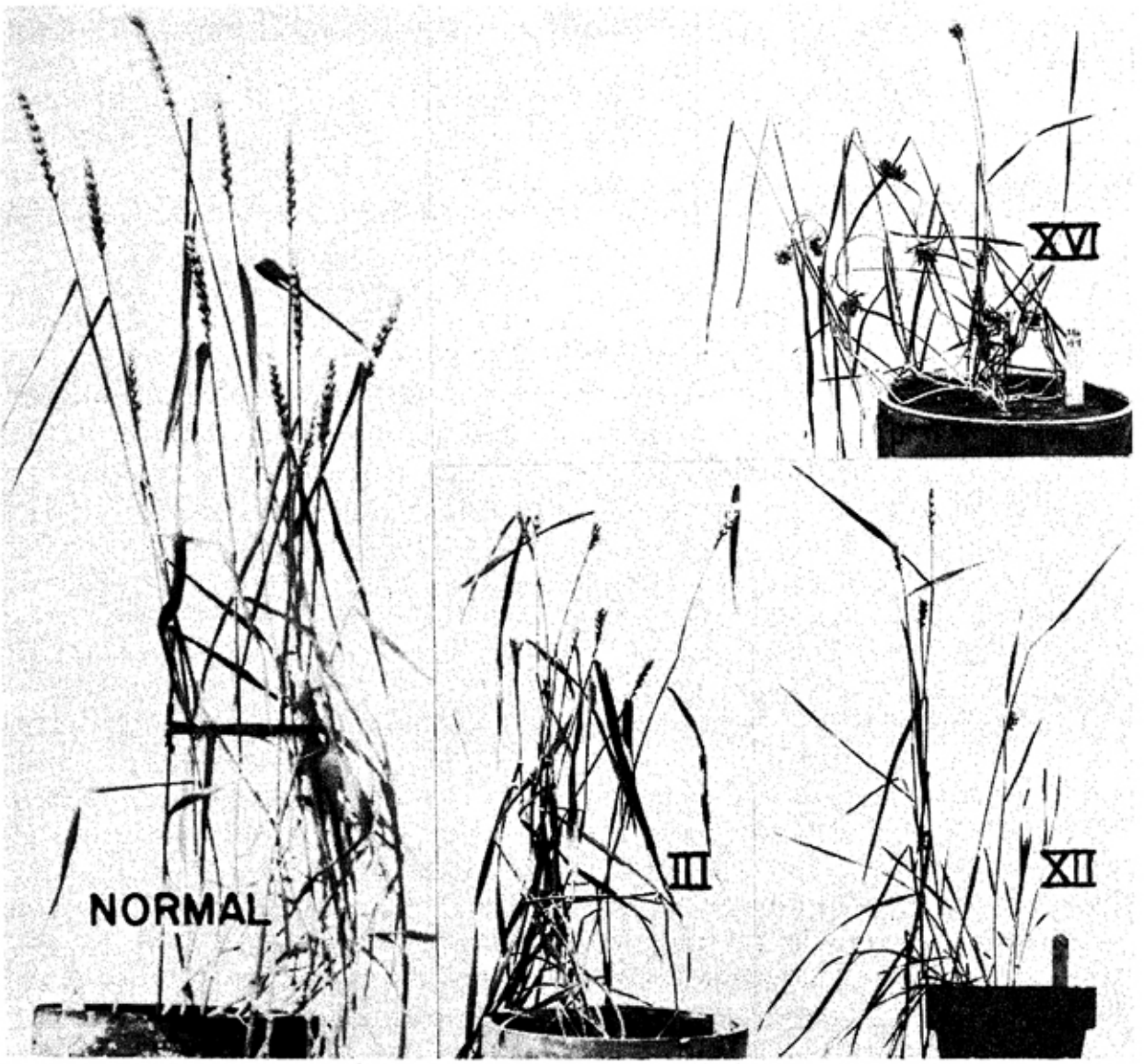

Figure 5. Nullisomic plants of homoeologous group 3 compared with normal Chinese. (0.12 natural size.)

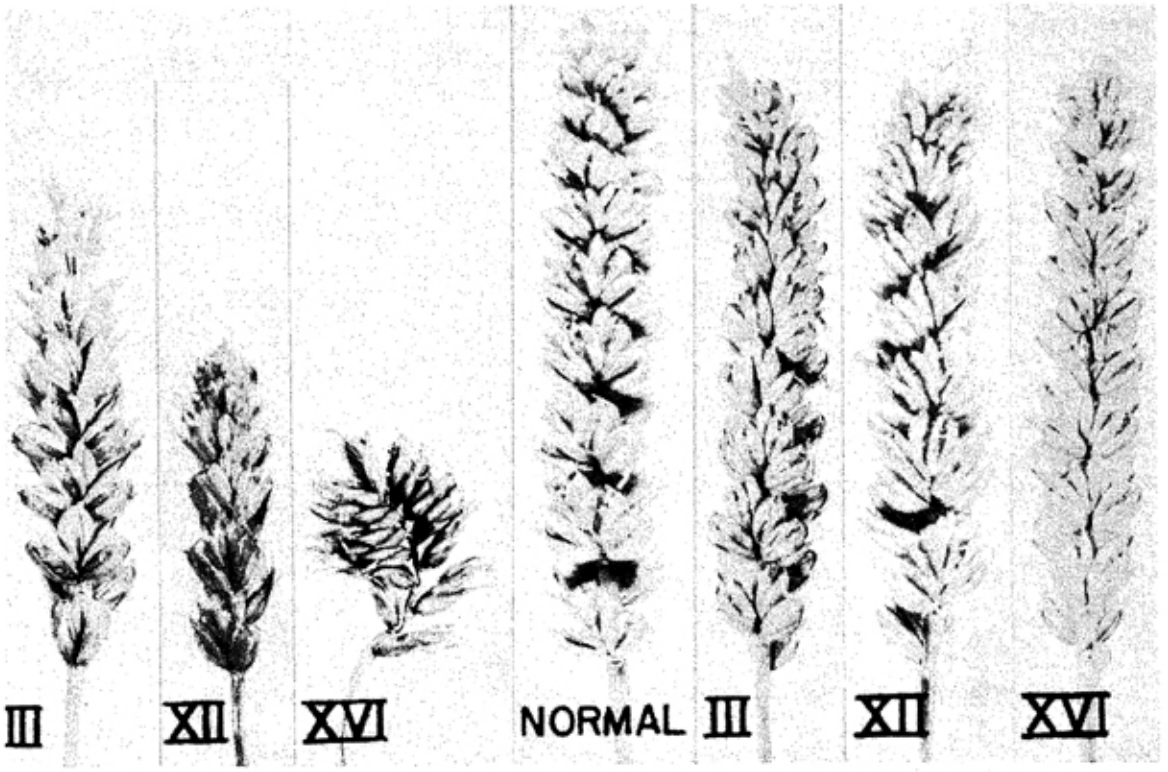

Figure 6. Spikes of nullisomics (left) and tetrasomics (right) of homoeologous group 3, compared with normal (center). (0.85 natural size.)

Chromosome III

Nulli-III plants are usually about half normal height. Tillering is about normal. Leaves are about one-half normal width. Culms are only slightly, if any, smaller than normal. Partial asynapsis occurs at meiosis. Neatby's (1933) virescent gene is located on this chromosome, as is a gene for necrotic leaves obtained by the late Dr. Luther Smith of Washington State College from atomic-bombed material (Smith, private communication, and Sears, unpublished).

Chromosome XII

The nullisomics are taller than nulli-III, sometimes attaining about three-fourths normal height. They are little, if any, more fertile than nulli-III. Leaves are about as narrow as those of nulli-III, but are somewhat longer.

Chromosome XVI

This nullisomic is conspicuously weaker than either III or XII. Tillering is only about one-half normal. Root development is so poor that plants frequently break loose from their root system. Leaves are less than half the normal width. The culm is twisted in the internode just below the spike, and the spike itself is bent and twisted. Awns are somewhat increased in length. Maturity is delayed, and fertility is almost entirely lacking. Chromo-

some XVI carries a gene for red seeds in the variety Chinese (Sears, 1944). The gene responsible for the characteristics of *T. sphaerococcum* is also located on this chromosome (Sears, 1947). Unrau (1950) found a modifier on Chinese XVI affecting the resistance of Federation 41 to bunt.

Homoeologous Group 4

This is the most heterogeneous of the seven groups. Chromosomes IV and XV have very similar effects, but VIII differs considerably. Nullisomics of all three have narrow leaves and slender culms. Mature plants (Fig. 7) are dwarfed and male sterile. Chromosome VIII is clearly the most essential of the three, with XV probably slightly more essential than IV.

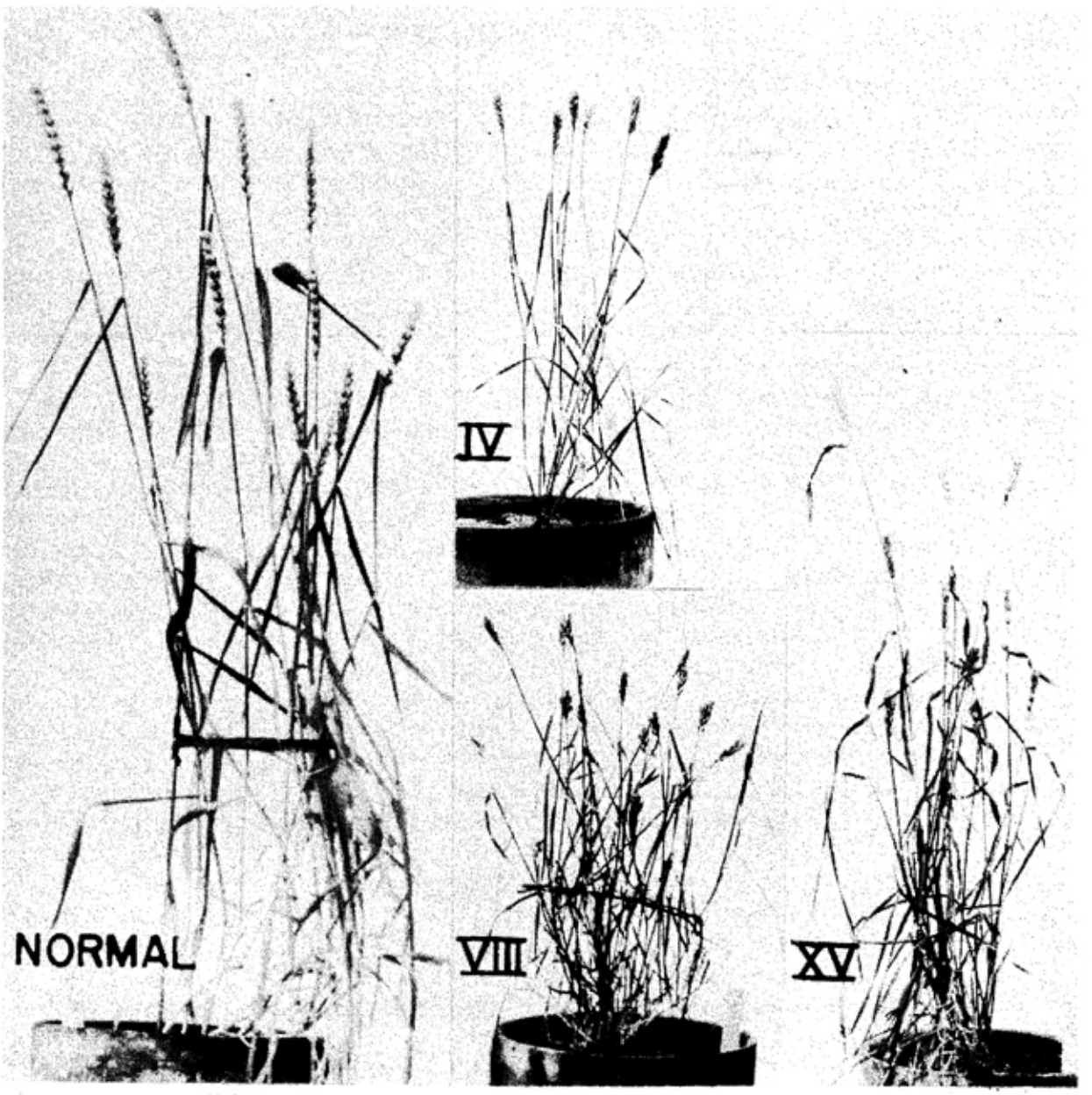

Figure 7. Nullisomic plants of homoeologous group 4 compared with normal Chinese. The nulli-IV plant was grown in a less favorable season than nulli-XV, which it normally resembles in size and vigor. (0.13 natural size.)

Chromosome IV

Nullisomic IV plants have leaves about one-half normal width, but of approximately normal length. Culms are about one-half as thick as normal. The mature plant is one-half to two-thirds normal in height. Anthers do not ordinarily dehisce. Seeds of the nullisomic tend to be longer and shallower than normal, while those of the tetrasomic are short. Monosomic and trisomic plants and spikes are very similar to normal, and the tetrasomic differs only in a slight reduction in fertility.

Chromosome VIII

Nulli-VIII differs from nulli-IV in being narrower leaved (about one-third normal), shorter in height (one-half normal or less), profuse in tillering (about twice as many tillers as normal), and later in maturity. The spike (Fig. 8) is only about half as long as that of nulli-IV. The tetrasomic has most of the expected plant characters, including a tendency toward thick culms, but each of its leaves has one or more necrotic areas. The leaves tend to wither and die prematurely, and the plants grow slowly and mature late. Spikes (Fig. 8) are poorly fertile and often deformed. Chromo-

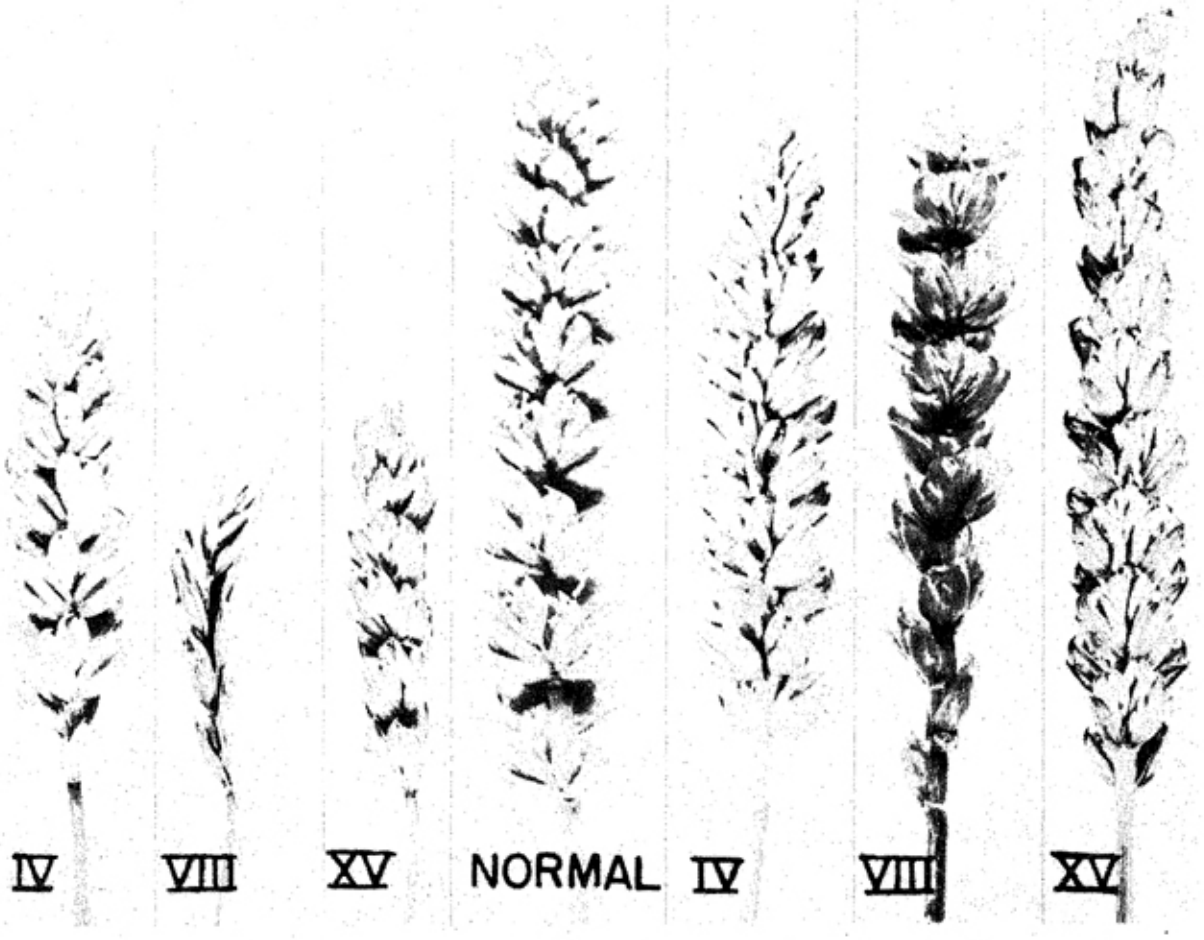

Figure 8. Spikes of nullisomics (left) and tetrasomics (right) of homoeologous group 4, compared with normal (center). (Natural size.)

some VIII carries the dominant hooded gene, which causes the awn to be short and bent. The nullisomic therefore differs from normal and the other aneuploids in having longer, straighter awns. Larson (1952) found a gene on Chinese VIII which promotes solidness of culm, and Sears and Rodenhiser (unpublished) located seedling resistance to stem rust on Hope VIII.

Chromosome XV

This chromosome is difficult to distinguish from IV by its effects. Nulli-XV, however, bears a shorter spike, which protrudes less above the uppermost leaf. Also, its anthers normally dehisce. The pollen produced is normal in appearance, but is unable to induce seed development.

Homoeologous Group 5

The chromosomes of this group have in common a tendency to increase the diameter of culms and the breadth of leaves. Nullisomics (Fig. 9) consequently all have narrow leaves and slender culms. The effect on culms carries over into the tetrasomics, which have thicker culms than normal. The nullisomics are all late in maturity. Their spikes (Fig. 10) are reduced in size and have small glumes and seeds. They are female fertile and male sterile. Chromosome XVIII is the most essential, with V perhaps slightly more essential than IX.

Chromosome V

Leaves of the nullisomic are about one-half normal width, and culms are slightly more than one-half normal thickness. The plants reach about two-thirds to three-fourths normal height. Maturity is delayed a few days. Monosomics tend to have narrow culms and small spikes. Tetrasomics are shorter than normal, with culms about 25 per cent thicker than normal. Tetrasomic spikes tend to be shorter and broader than normal, with coarse glumes and somewhat larger seeds.

Chromosome IX

This is the speltoid chromosome, which, in the variety Chinese, carries a recessive gene *Q* for suppression of the speltoid effect and for squarehead spike,* and a dominant gene for pubescent nodes. The nullisomic is consequently speltoid, non-squarehead, and non-pubescent. Leaves and culms are about one-half normal width. Glumes are small and stiff. The monosomic has a culm of about two-thirds normal diameter and a spike which

*Speltoid suppression and squarehead were formerly attributed to two different genes, *k* and *q*, located about 65 crossover units apart. Mac Key (1954), however, shows that both effects are due to one and the same gene. He considers this gene to be dominant, "since it results in a distinct departure from type when heterozygous," and accordingly designates it *Q*. In the variety Chinese the gene is only partially dominant; in fact it is fully recessive as far as the squarehead effect is concerned. Mac Key shows, however, that in certain other varieties of wheat the heterozygote is closer to vulgare than to speltoid if all the pleiotropic effects of *Q* are considered.

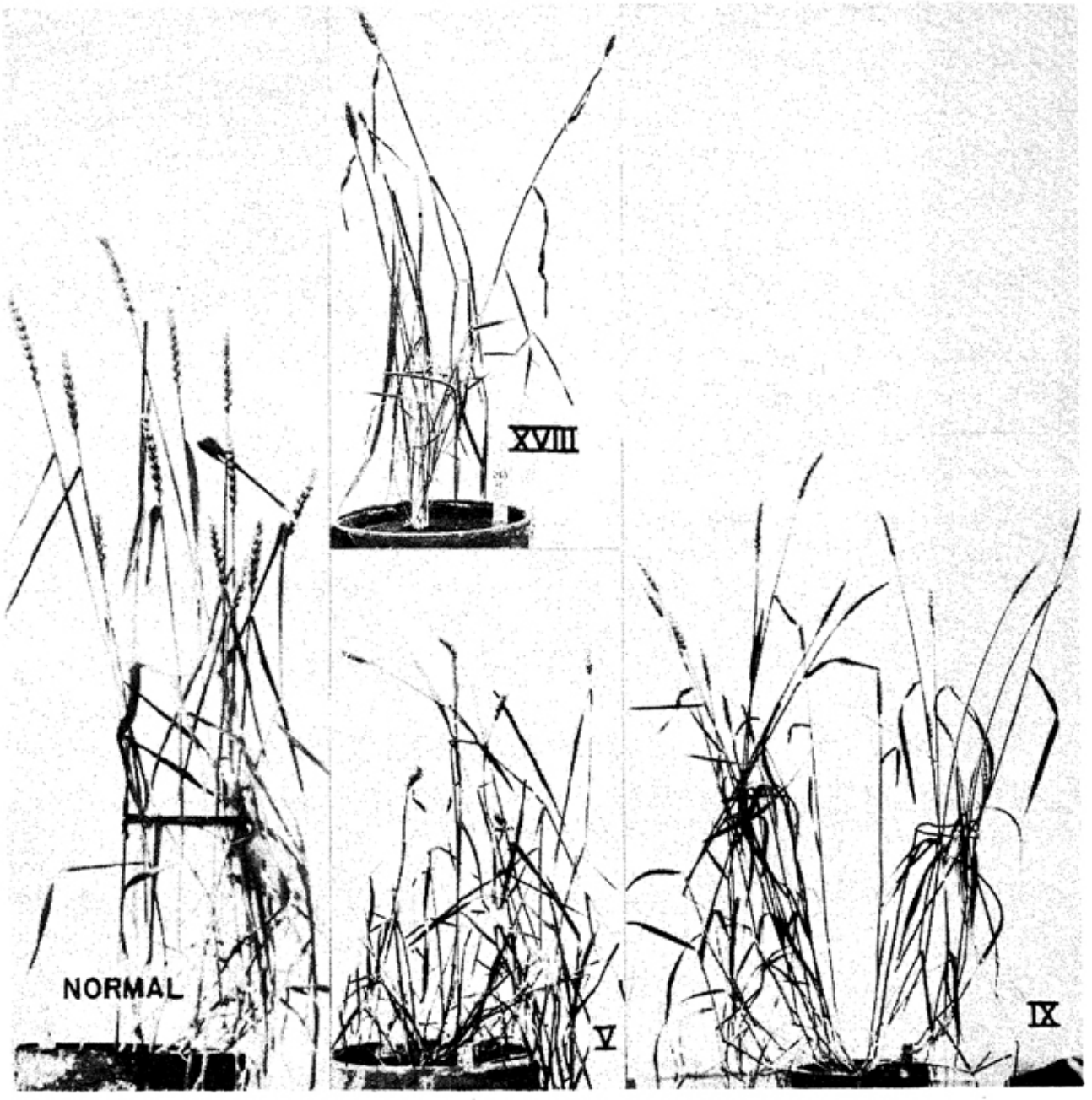

Figure 9. Nullisomic plants of homoeologous group 5 compared with normal Chinese. The nulli-IX plant, grown under especially favorable conditions, shows unusual vigor for this nullisomic. (0.115 natural size.)

is easily identifiable by the stiffness of its glumes (speltoid effect) and laxity (non-squarehead effect). The monosomic spike, with a non-compact tip, is longer than normal. The gene *Q* in three doses (trisomic) gives a compactoid spike, and the tetrasomic is similar to *T. compactum.* There is also an effect on plant height, presumably due to *Q.* Under the most favorable conditions, the nullisomic is tallest, followed by the monosomic, the disomic, the trisomic, and the tetrasomic, respectively. In diameter of culm a graduated effect is also present, each additional dose of chromosome IX making for greater thickness, until the tetrasomic is about one-third thicker than

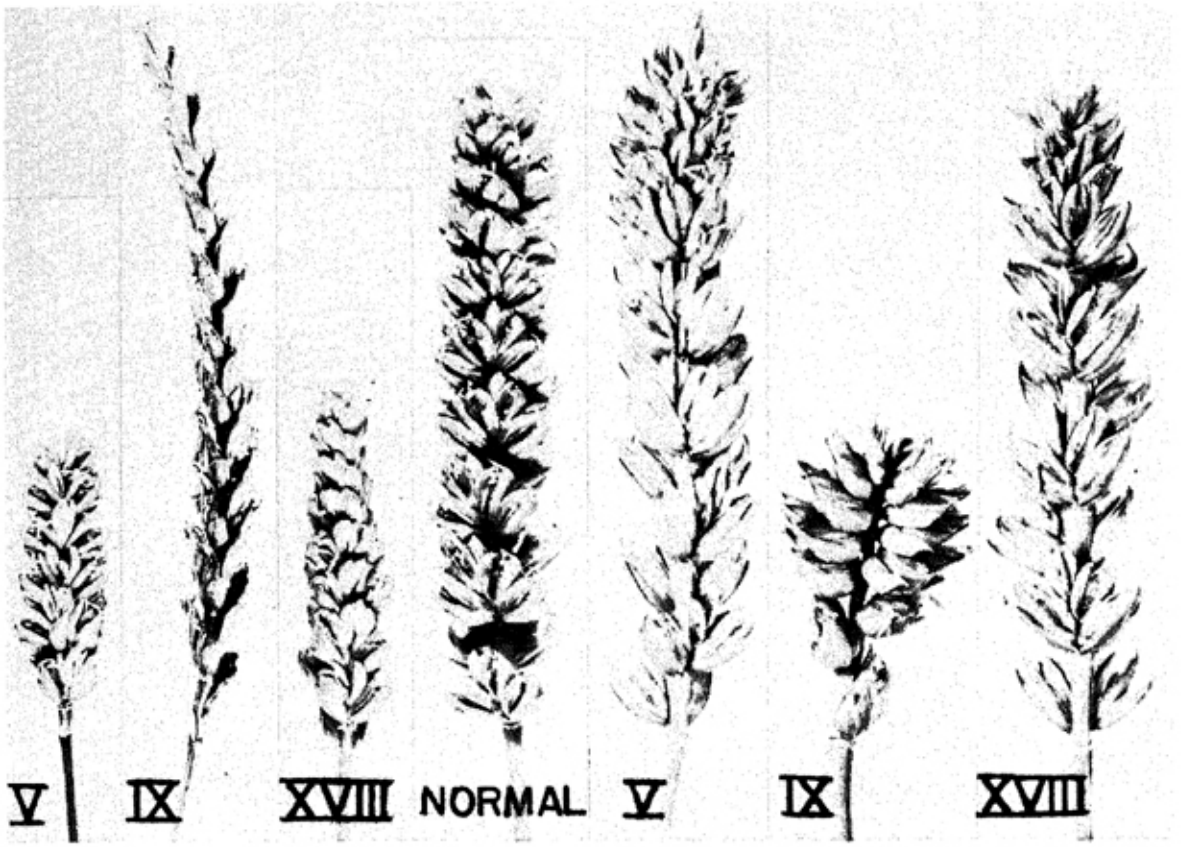

Figure 10. Spikes of nullisomics (left) and tetrasomics (right) of homoeologous group 5, compared with normal (center). (0.85 natural size.)

normal. The gene *Q* in single dose is relatively ineffective in suppressing the speltoid condition, but in extra dose (trisomic and tetrasomic) it results in larger, more fragile glumes. Pubescence of node shows an increasing effect with dosages up to and including four. Chromosome IX in Chinese carries a gene or genes promoting early maturity, but to a lesser extent than does chromosome IX of the variety Hope. Unrau (1950) found IX to have one of the two genes for spring habit in Chinese. The b_1 gene for non-inhibition of awn development is located on this chromosome, but little effect of dosage is apparent, except that nullisomics may have slightly increased awns (Sears, 1944).

Chromosome XVIII

Plants nullisomic for chromosome XVIII are more difficult to grow than any other nullisomic. They grow very slowly in the seedling stage and often do not survive this early period. Presumably this slow early growth is the result of the absence of a gene or genes for early maturity carried by this chromosome. At any rate, nulli-XVIII is the latest maturing of all the nullisomics. Tillering is reduced to less than half of normal, and leaves and culms are only about half the normal diameter. The spike is

similar to that of nulli-V. Monosomics are identifiable by their lateness. Tetra-XVIII is very similar to tetra-V. It is the earliest maturing of all 21 tetrasomics.

Homoeologous Group 6

The nullisomics of this group (Fig. 11) are characterized by narrow leaves, slender culms, and narrow, spreading outer glumes which give the spikes (Fig. 12) a straggly appearance. All three nullisomics are female fertile, although the fertility of nulli-X may be very low due to pistillody. Nulli-VI and particuarly nulli-XIX are somewhat fertile as males. Monosomics, trisomics, and tetrasomics differ little from normal. Chromosome XIX is clearly the least essential of this group, and chromosome X probably the most essential.

Chromosome VI

Nullisomic plants are dwarf—only about one-half normal height. Tillering tends to be reduced. Leaves are one-half to two-thirds normal

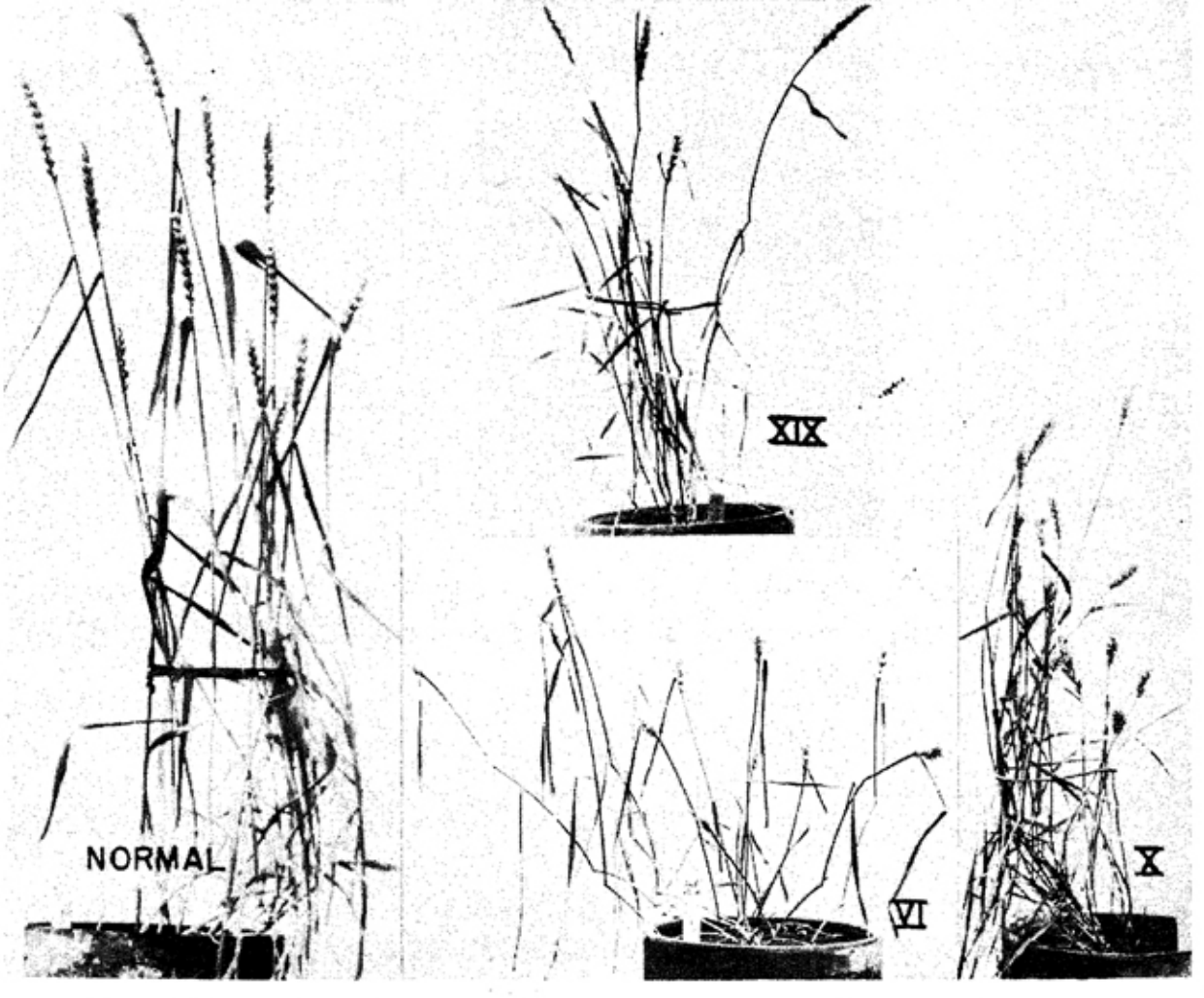

Figure 11. Nullisomic plants of homoeologous group 6 compared with normal Chinese. (0.115 natural size.)

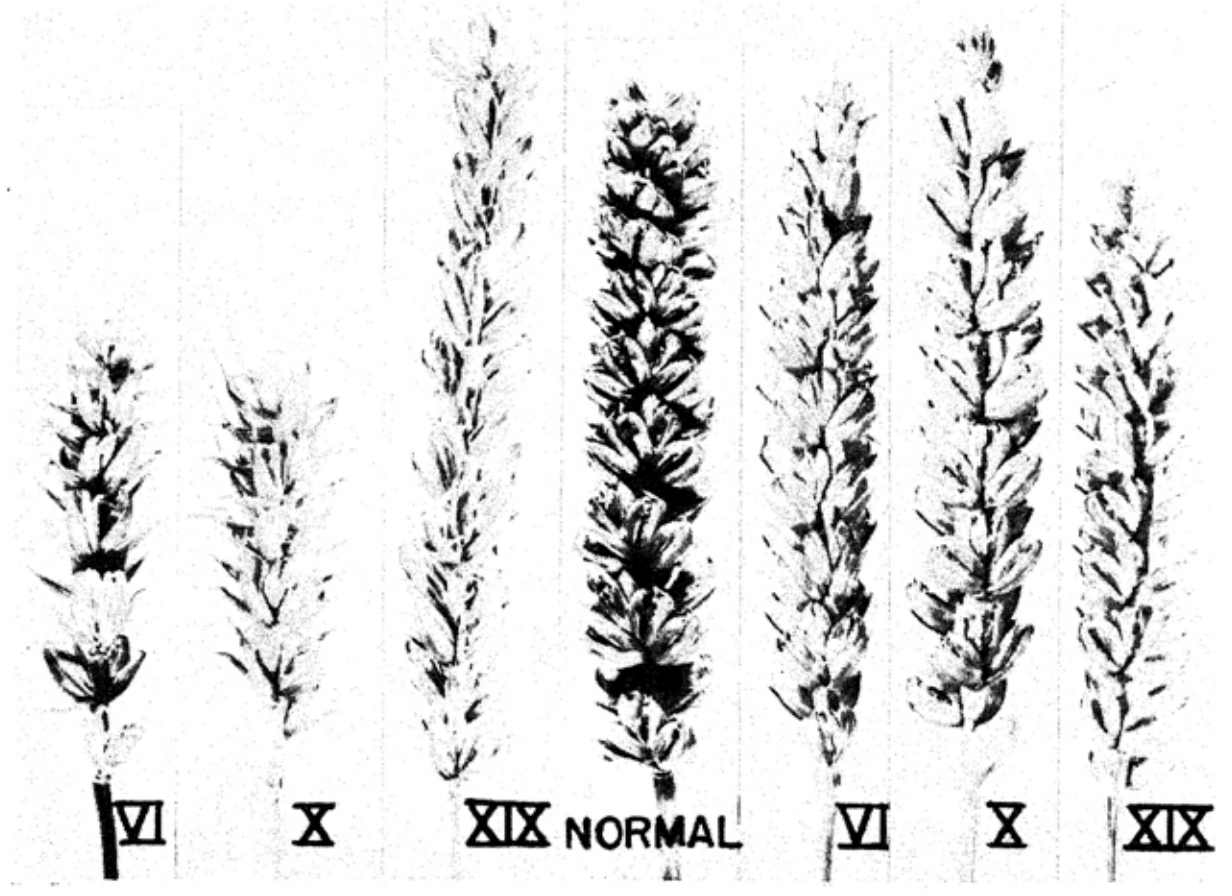

Figure 12. Spikes of nullisomics (left) and tetrasomics (right) of homoeologous group 6, compared with normal (center). (0.90 natural size.)

width, and culms about three-fourths normal diameter. Spikes are about one-half normal length. Chromosome VI of the variety Red Egyptian carries a gene for seedling resistance to stem rust (Sears and Rodenhiser, unpublished).

Chromosome X

Nulli-X is similar in plant characteristics to nulli-VI, although the amount of tillering tends to be nearer normal in -X, and in some seasons nulli-X has necrotic patches similar to tetra-VIII. In the variety Chinese, the spikes (Fig. 11) are strikingly different in that nulli-X has increased awn development. This is because chromosome X carries a dominant gene for inhibition of awns. Pistillody of nulli-X results in some florets having all three stamens replaced by pistils; and many florets with fewer than three pistilloid stamens are also infertile. In addition to the awn inhibitor, chromosome X carries two complementary dominant genes for stem-rust resistance (in the variety Timstein; Sears and Rodenhiser, 1948), one of two complementary genes for seedling leaf-rust resistance (in the variety Pawnee; Livers, 1949), and a gene for mature-plant resistance to leaf-rust (in Chinese; Unrau, private communication). The awn inhibitor has little, if any, increased effect in the trisomic and tetrasomic.

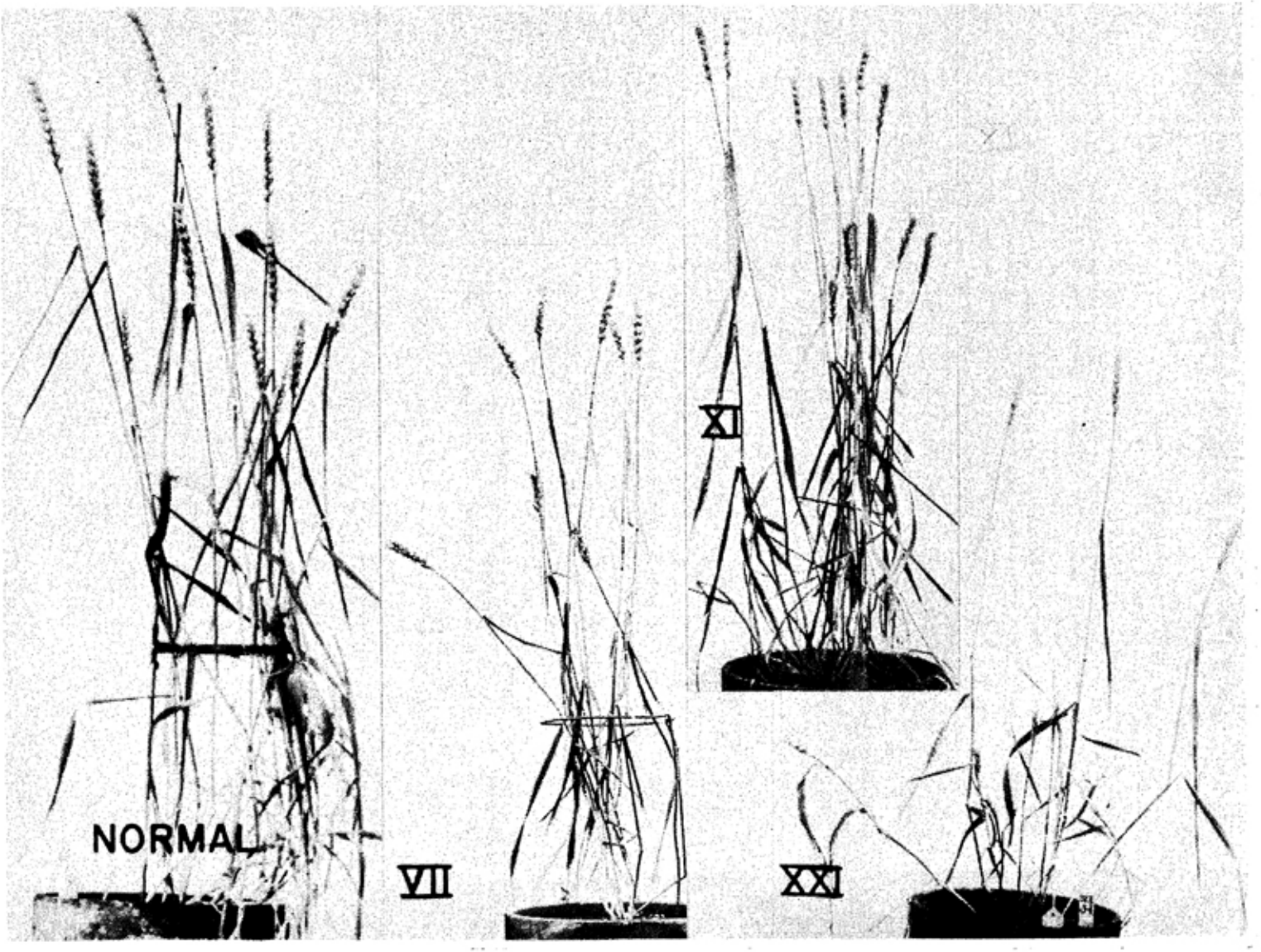

Figure 13. Nullisomic plants of homoeologous group 7 compared with normal Chinese. (0.12 natural size.)

Chromosome XIX

Nulli-XIX can be described easiest as a taller and slightly more vigorous nulli-VI, with longer, more fertile spikes. Plants are about three-fourths normal height and spikes about as long as normal. The best spikes on highly vigorous plants set a few seeds from selfing. This chromosome in the variety Thatcher carries a gene for seedling resistance to stem rust (Sears and Rodenhiser, unpublished). On Chinese XIX there is a gene which inhibits solidness of culm (Larson, 1952).

Homoeologous Group 7

These three chromosomes are less essential to the plant than any others, apparently in the order VII, XXI, XI, with VII only slightly less essential than XXI. Nullisomics differ very little from normal in the seedling stages, and adult plants (Fig. 13) are distinguishable only by a slight reduction in vigor and height and by certain spike characters (Fig. 14). The fertility of nullisomics VII and XXI is nearly normal, but is greatly reduced in XI by pistillody. Monosomics and trisomics are essentially normal, but all three tetrasomics are reduced in vigor and fertility. In fact, the tetrasomics of this group are among the least vigorous of the entire series.

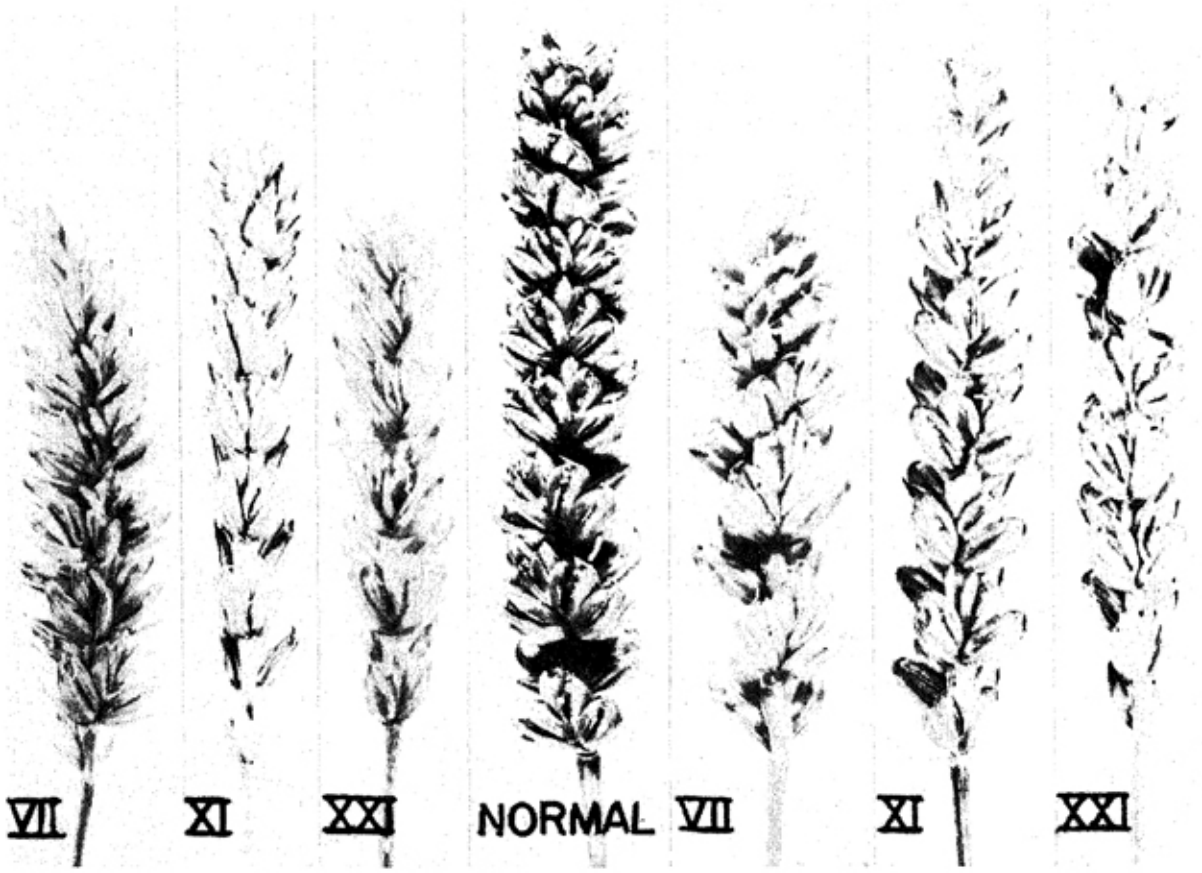

Figure 14. Spikes of nullisomics (left) and tetrasomics (right) of homoeologous group 7, compared with normal (center). (0.95 natural size.)

Chromosome VII

Nulli-VII has slightly narrower leaves than normal, is a little shorter than normal, and has spikes of about three-fourths normal length which tend to be sterile toward the tip. Tetrasomic plants are a little shorter than normal and have spikes shortened about one-third in length and tending toward poor fertility.

Chromosome XI

The effects of chromosome XI are fairly distinct from those of VII and XXI in the nullisomic. Nulli-XI spikes usually show considerable pistillody and are relatively infertile. Plants are little different, showing some reduction from normal in tillering and being of essentially normal height and appearance. The tetrasomic has narrow leaves and slender culms. Chromosome XI in the variety Hope carries a gene for red color of coleoptile, and in the variety Axminster (Sears and Rodenhiser, unpublished) carries a gene for resistance to mildew *(Erysiphe graminis tritici).*

Chromosome XXI

Nulli-XXI is very similar to nulli-VII, although tillering is perhaps a little less. Tetra-XXI is dwarfed somewhat more than tetra-VII. According to Larson (1952) this chromosome strongly inhibits solidness of culm in the varieties S-615 and Chinese.

MORPHOLOGY OF CHROMOSOMES

Efforts to identify the chromosomes of wheat by their morphological characteristics (Camara, 1943, 1944; Levitsky, *et al.,* 1939) have been only partly successful, because some chromosomes are almost identical with others. The measurements have been made on root-tip chromosomes.

With monosomics it is possible to study chromosome morphology at meiosis, because a monosome does not pair at the reduction division like the rest of the chromosomes, but instead remains alone off the plate until the paired chromosomes have separated and started to the poles. Then it usually comes onto the plate and divides. At the second division the behavior of its daughter halves is again exceptional, in that they do not divide but lag on the plate and either go at random to one pole or the other or else misdivide (Sanchez-Monge and Mac Key, 1948; Sears, 1952a; Morrison, 1953). Measurement at meiosis has the advantage that the identity of the chromosomes being measured is known independently of the measurement.

Morrison (1953) made second telophase (T II) measurements of all the chromosomes except XIV, presenting his results in the form of idiograms. He noted a secondary constriction in chromosome I and a similar constriction, not always present, in X. These constrictions are assumed to represent nucleolus-organizing regions.

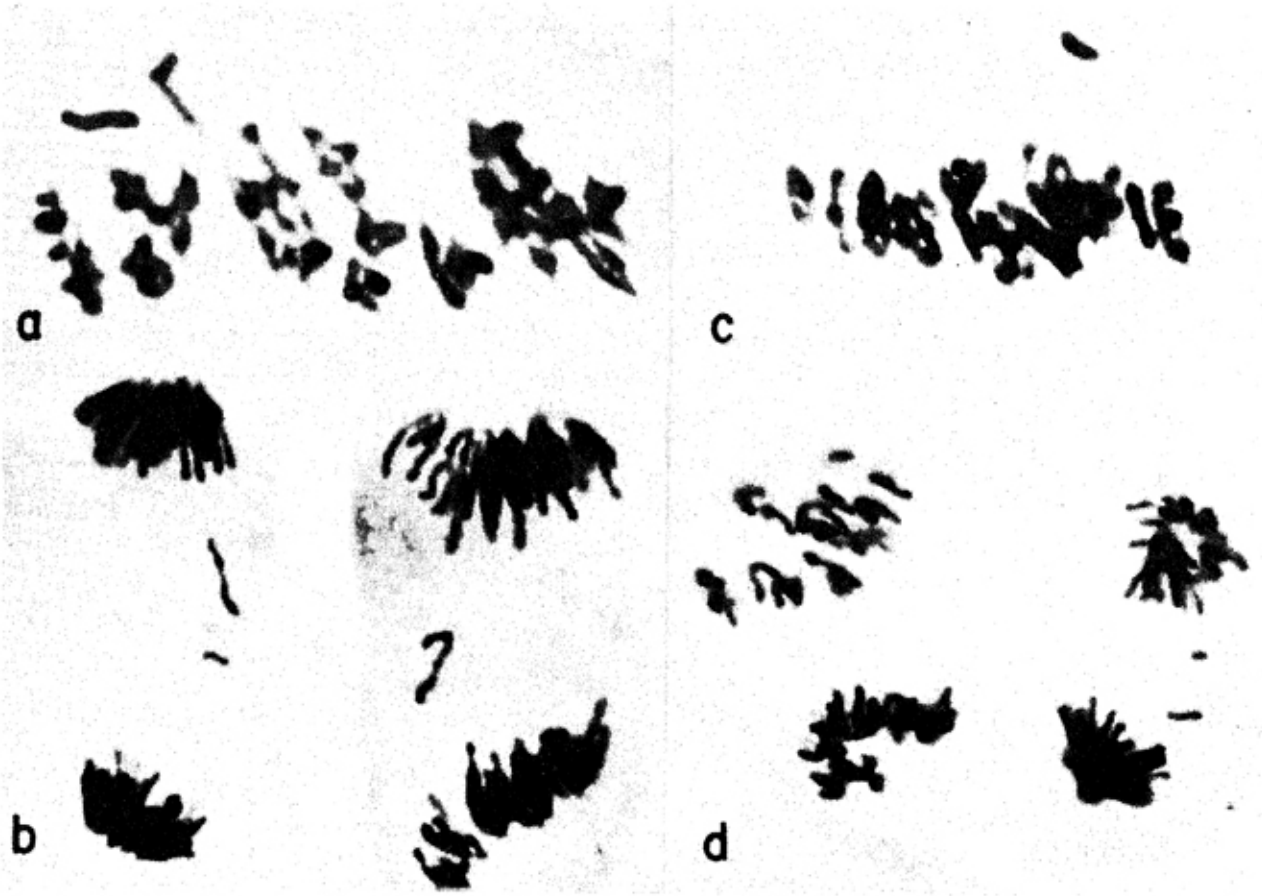

Figure 15. Monosome V (a) at metaphase I and (b) at telophase II, and monosome XVII at (c) MI and (d) TII, to illustrate a long and a short monosome at these two stages. The disparity in length between the two chromosomes is greater at TII than at MI.

In Table 3 are presented measurements from camera lucida drawings of the monosomes at first metaphase (M I) and T II. As indicated, the number of measurements made was greater than six in only one case, and sometimes was only two; consequently, no significance can be attached to the smaller differences. The greatest variation at M I was shown by chromosome VIII, which ranged from 5.28 to 6.62 in four measurements, and at T·II by chromosome XV, which varied from 5.28 to 8.38 in three measurements. Some of the T II variation may have been due to occasional use of univalents which had failed to be included in either daughter nucleus at T I, although these were excluded from the computations wherever they could be identified with certainty. Such chromosomes are often much longer than normal T II univalents.

It is clear that differences in length are more pronounced at T II (Fig. 15b, d) then at M I (Fig. 15a, c). The four shortest chromosomes at T II averaged only 24 per cent longer than at M I, while the four longest were 67 per cent longer at T II than at M I. This augmentation of length differences, coupled with the fact that the two arms can be measured separate-

ly at T II but usually not at M I, makes T II the preferable stage for study. In general, the total length at T II appears to be closely correlated with that at M I.

The measurements obtained at T II are in reasonable agreement with Morrison's idiograms. The greatest discrepancies are for chromosome III, which Morrison shows to be shorter and less nearly equal-armed; V, shorter and more nearly equal armed; VI, longer; VIII, longer; XII, longer and less nearly equal-armed; XIII, more nearly equal-armed; XVII, longer; XVIII, longer. Smaller differences may be noted for II, which Morrison shows longer and more nearly equal-armed; VII, less nearly equal-armed; IX, shorter; and XVI and XX, less nearly equal-armed. Presumably most of these differences are attributable to variations between plants or even between individual cells, with the true mean values lying somewhere between those given in Table 3 and those given by Morrison. As far as total

TABLE 3--TOTAL LENGTH AT FIRST MEIOTIC METAPHASE AND SECOND TELOPHASE, AND ARM RATIO AT SECOND TELOPHASE, OF THE MONOSOMES OF TRITICUM AESTIVUM VAR. CHINESE SPRING

Chromosome	Number of observations		Total length in microns		Arm ratio
	MI	TII	MI	TII	at TII
III	3	2	6.87	12.32	1.29:1
V	5	2	6.71	11.34	2.65:1
XIII	6	5	6.87	10.92	1.25:1
I	6	3	6.47	10.42	1.38:1
IX	5	4	6.43	9.81	1.79:1
X	6	3	6.61	9.10	1.05:1
XI	3	4	6.27	9.10	1.21:1
XXI	6	4	6.16	9.06	1.17:1
IV	6	3	5.54	9.04	1.13:1
VII	12	3	5.93	8.76	1.24:1
XII	6	5	6.21	8.50	1.15:1
XX	6	3	5.58	8.18	1.23:1
II	6	3	5.52	8.11	1.26:1
VIII	4	2	5.85	7.91	1.55:1
XVI	3	3	5.86	7.45	1.37:1
XIV	6	5	4.67	7.34	1.91:1
XV	6	3	4.90	6.85	1.80:1
VI	6	5	4.71	6.26	1.12:1
XIX	5	3	4.22	5.90	1.11:1
XVIII	6	4	4.83	5.77	1.82:1
XVII	4	3	5.02	5.55	1.82:1

lengths are concerned, the M I measurements may be used as a check on T II. For chromosomes III and XII, the M I data agree with Morrison's idiograms in indicating that the T II values in Table 3 are too large for III and too small for XII.

As indicated by Morrison, chromosome I has a secondary constriction in the short arm. This constriction divides the arm into a proximal 65 per cent and a distal 35 per cent. None of the chromosome X's observed at T II

had a secondary constriction, but Morrison did not find the constriction in all cells either.

It is evidently not possible to distinguish all the chromosomes on the basis of T II measurements. XV, XVII, and XVIII, for example, are not much different in total length, and have nearly the same arm ratio. VI and XIX are similar, which is of special interest because these two chromosomes are genetically homoeologous. Likewise, II and XX, both in homoeologous group 2, measure about the same. IV and XXI, though belonging to different groups, measured very nearly the same.

The most unequal-armed chromosome is V, which also has the longest single arm. The nearest to having equal arms apparently is X; although several others, including the short chromosomes VI and XIX, are perhaps not significantly less nearly equal-armed.

Efforts to use the meiotic measurements to identify the chromosomes measured by Camara (1943, 1944) meet with little success. In part this must be the result of inaccuracies due to small numbers of measurements in the present study (and presumably in Morrison's), and in part it may be attributed to differences of varieties, many of which possess reciprocal translocations with respect to each other. Possibly length relationships may be different at T II than in root tips. Whether due to these or other causes, there are some striking differences in the results. About the only thing which seems certain is that Camara's chromosome 4 is chromosome I. In his list the only long, strongly heterobrachial chromosome is his number 1, belonging to the *D* genome, whereas in the present study the most heterobrachial chromosome, V, is in the *A* or *B* genome and is second longest of the entire 21. Two long, strongly heterobrachial chromosomes are listed by Camara in the *D* genome, whereas none was noted in the present study nor in Morrison's. On the other hand, Camara found no short, strongly heterobrachial *D*-genome chromosomes, while the present study showed three of these, and Morrison noted four with an arm ratio of at least 1.5 to 1. Camara lists only three short *D*-genome chromosomes instead of four as found here. Camara's measurements are roughly comparable to the present M I measurements, although the longest chromosomes measure slightly longer in the root tips.

BREEDING BEHAVIOR

Monosomics and Nullisomics

In a previous report (Sears, 1944) data were given on the frequency with which nullisomics had been obtained from the respective monosomics. It was pointed out that these frequencies apparently depended on the amount of male transmission, female transmission being about 25 per cent (=75 per cent transmission of the deficiency) regardless of the chromosome concerned. Subsequent work has not altered this conclusion; in fact, analysis of 785 female gametes of mono-IX showed 23.4 per cent transmission of the

monosome or derivative isochromosomes and telocentrics (Sears, 1952a). Additional data have been obtained on the frequency of nullisomic offspring from all but one of the 17 monosomes included in the 1944 report, and four monosomes subsequently identified. The data for all 21 are given in Table 4.

Some of the frequencies given in the table are more reliable than others. As indicated previously, most families were classified as seedlings and all plants discarded except the suspected nullisomics and a few others. These were then grown to maturity (except in some families involving chromosomes III and IV), and part or all were examined cytologically. One obvious source of error in this procedure is that some nullisomics are difficult to distinguish from normal, and thus some of the nullisomics in certain families may have been discarded as seedlings. This would apply particularly to nullisomics I, VII, XI, and XXI. In the case of XXI, however, the only families considered in making the calculation in Table 4 were those in which

TABLE 4--FREQUENCIES OF NULLISOMICS IN PROGENIES FROM SELF-POLLINATED MONOSOMICS

Monosome involved	Number plants	Number nullisomic	Percent nullisomic	No. nullisomics confirmed cytologically
I	671	16	2.4	10
II	962	48	5.0	26
III	2682	205	7.6	84
IV	2159	138	6.4	52
V	1431	14	1.0	5
VI	598	15	2.5	5
VII	885	12	1.4	10
VIII	192	7	3.6	3
IX	832	28	3.4	1
X	1457	13	0.9	6
XI	331	11	3.3	8
XII	125	3	2.4	3
XIII	255	6	2.4	0
XIV	381	8	2.1	6
XV	1924	113	5.9	38
XVI	712	35	5.8	17
XVII	1109	27	2.4	17
XVIII	575	5	0.9	2
XIX	1084	30	2.8	11
XX	572	25	4.4	9
XXI	177	2	1.1	2

all the plants, or a random sample, had been grown to maturity and analyzed cytologically.

A second source of error in the procedure above is that some nullisomics could not be distinguished with certainty from plants with a monotelo- or mono-isosome except through cytological study. Since these derivative monosomes occur with fairly high frequency in the variety Chinese

(Sears, 1952a), an appreciable fraction of the indicated nullisomics may actually have been monosomic. The nullisomics difficult to distinguish from plants with a monotelo- or mono-isosome are III, IV, V, VI, VII, IX, XI, XII, XV, XVIII, and XXI. Probably the only chromosomes where this source of error was actually of importance, however, were III, IV, and VI. Nulli-III is readily distinguishable from monotelo-III at maturity, but many plants classified as nulli-III were discarded as seedlings, at which time the distinction is not easily made. Plants with an isochromosome for the long arm of V, IX, or XVIII are essentially normal; hence, it is likely that monosomics for just the short arm of any of these chromosomes would be very similar to the particular nullisomic. Such nullisomic-like monosomics have not been found, however, and the data for these three chromosomes are too few to indicate much concerning the possible frequency of these monotelosomics. An appreciable frequency would mean that male gametes carrying this telocentric have a great advantage over the totally deficient gametes, and this seems unlikely. Although nullisomics for VII, XI, XII, and XXI are not easily distinguished from the monotelosomics, most or all of the presumed nullisomics for these chromosomes were confirmed cytologically. Mono-XV gives rise only rarely to monotelo- and mono-isosomes.

Although the frequency of nullisomics obtained from mono-XXI is given in Table 4 as 1.1 per cent, this nullisomic has actually never been obtained in pure Chinese material. The two nullisomic plants accounting for the 1.1 per cent were obtained following hybridization with other varieties. One came from an F_2 involving the variety Pilot and one after the second backcross to mono-XXI following hybridization with Thatcher. Nullisomics were also obtained in the second and fourth backcrosses to mono-XXI Chinese following hybridization with Hope. There is reason to suspect that this and other nullisomics may appear with increased frequency in segregating generations. On the other hand, although the value of 1.1 per cent may be too high for the occurrence of nulli-XXI from mono-XXI in pure Chinese wheat, there is little reason to believe that the real frequency is zero. Before it was realized that nulli-XXI was indistinguishable from normal in the seedling stage, over 1500 seedlings were grown, but fewer than 10 per cent of these were grown to maturity and examined cytologically. Only 78 were analyzed which constituted entire families or which were reasonably random samples from larger families.

In summary, the frequency of nullisomics given is probably too small in the case of chromosomes I, VII, and XI, and somewhat too large for III, IV, and VI.

Data are available concerning the constancy of a few nullisomic lines—those which set selfed seed. These data are presented in Table 5. Not included is nulli-III, which sets selfed seed but is partially asynaptic and hence

TABLE 5--CHROMOSOME CONSTITUTION OF SELFED OFFSPRING OF NULLISOMIC PLANTS

Chromosome concerned	No. offspring grown	No. with 20″	No. with 19″ 1′	No. with 19″ 1‴
I	68	65	1	2
VII	66	61*	3	2
XI	15	10	3	2
XII	9	9	0	0
XIV	12	11	0	1
XVII	4	4	0	0
XIX	2	2	0	0
XXI	15	13	1	1

* Includes one plant with an isochromosome replacing one member of one of the 20 pairs.

not suitable to maintenance as a nullisomic line. The eight nullisomics listed are reasonably stable, only 17 offspring of aberrant constitution having been noted among a total of 191. In at least four of the eight offspring with a trisome, the trisome was one that compensated to some extent for the nullisome. These were the two from nulli-I, the one from nulli-XI, and the one from nulli-XIV. This is in line with the results of Kihara and Wakakuwa (1935) and Matsumura (1947) with nullisomics of the *D*-genome (chromosomes XV to XXI) of wheat. Compensating trisomes appeared in several of their nullisomic lines. Male gametes possessing an extra chromosome are favored when the extra chromosome tends to compensate for the missing one.

Trisomics and Tetrasomics

In a previous paper (Sears, 1944) preliminary observations were reported on the breeding behavior of trisomics. Data have subsequently been collected for all but tri-IX and are presented in Table 6. Tri-IX is excluded because tetra-IX was obtained in the progeny of a plant which was monosomic for an unidentified chromosome as well as trisomic for IX.

The percentages given for frequency of tetrasomics are minimum values in almost all cases, since usually less than half of each population was examined cytologically. However, practically all populations were grown to maturity, at which time all of the tetrasomics were distinguishable. There remains the possibility that a few tetrasomics may have been overlooked in some of the earliest-grown families, when the characteristics of the tetrasomics being sought were not yet known.

Numbers are obviously so small for XIII and XIX that no significance can be attached to the high values obtained for tetrasomic frequency. Actually, with no population having more than five tetrasomics, the error is large for every tetrasomic frequency. As indicated in the previous publication, the range in frequency of tetrasomics is comparable to that for nullisomics from monosomics—from around 1 per cent to about 10 per cent.

It was suggested in the 1944 paper that female transmission of the extra chromosome was about 40 per cent, with somewhat higher pollen trans-

TABLE 6--FREQUENCIES OF TETRASOMICS IN PROGENIES OF SELF-POLLINATED TRISOMICS

Chromosome concerned	No. offspring grown	No. analyzed cytologically	No. tetrasomic	Percent tetrasomic
I	69	11	2	2.9
II	41	5	4	9.8
III	96	39	1	1.0
IV	78	73	3	3.8
V	30	4	1	3.3
VI	39	39	1	2.6
VII	29	6	1	3.4
VIII	130	115	2	1.5
IX	0	0	0	---
X	52	13	3	5.8
XI	34	13	1	2.9
XII	109	37	3	2.8
XIII	8	4	1	12.5
XIV	24	6	1	4.2
XV	20	2	2	10.0
XVI	183	49	1	0.5
XVII	69	15	1	1.4
XVIII	109	26	2	1.8
XIX	8	7	1	12.5
XX	50	2	2	4.0
XXI	58	9	5	8.6
Total	1236	475	38	3.3

mission of the extra chromosome than of the deficiency for the same chromosome from monosomics. This is borne out by data from families that were completely analyzed cytologically (Table 7). The five different tri-

TABLE 7--CHROMOSOME CONSTITUTION OF OFFSPRING OF TRISOMIC PLANTS IN COMPLETELY ANALYZED FAMILIES

Chromosome concerned	No. plants	No. tetrasomic	No. trisomic	No. disomic	Percent trisomic
III	23	0	12	11	52
IV	55	1	19	35	35
VI	39	1	22	16	56
VIII	115	1	50	64	43
XVI	47	0	22	25	47
Totals	279	3	125	151	45

somes show frequencies of from 35 to 56 per cent trisomic offspring, with an average of 45 per cent. To obtain the observed frequency of tetrasomes in this group of populations would require that only 2-3 per cent of the male gametes carry the extra chromosome. The five trisomes concerned here, however, happen to be ones which gave low frequencies of tetrasomes. On the average, considering all 20 trisomes in Table 7, about 7 per cent of male transmission is indicated. This is about twice the frequency of functioning chromosome-deficient male gametes from monosomics. However, this is only an average, and it would appear that deficiencies for certain chromosomes, as III and XVI, may be more readily transmissible through the pollen than are duplications for the same chromosomes.

Most of the tetrasomic lines have been fairly constant, producing 80 per cent or more of tetrasomic offspring (Table 8). Some, however, notably III, IV, XII, and XVI, have yielded only about 50 per cent tetrasomic offspring. Most of the non-tetrasomics produced have been trisomics, and a few have been normal disomic offspring.

TABLE 8--CHROMOSOME CONSTITUTION OF OFFSPRING OF TETRASOMIC PLANTS

Chromosome concerned	No. plants grown	No. analyzed	No. tetra.	Percent tetra.	No. trisomic	No. disomic	No. other
I	30	11	9	82	1	0	1 iso-chr.
II	72	30	24	80	6	0	0
III	34	22	11	50	9	1	1 haploid
IV	48	30	16	53	12	2	0
V	34	18	15	83	3	0	0
VI	40	15	12	80	2	1	0
VII	62	29	24	83	5	0	0
VIII	62	60	47	78	13	0	0
IX	35	15	14	93	1	0	0
X	32	18	16	89	2	0	0
XI	29	14	14	100	0	0	0
XII	67	39	20	51	18	1	0
XIII	34	20	16	80	3	1	0
XIV	14	7	6	86	1	0	0
XV	16	14	14	100	0	0	0
XVI	31	20	9	45	11	0	0
XVII	54	28	21	75	7	0	0
XVIII	59	30	20	67	9	1	0
XIX	32	20	13	65	4	2	1 telo
XX	34	16	14	87	2	0	0
XXI	14	6	6	100	0	0	0

TELOCENTRICS AND ISOCHROMOSOMES

Origin

Either a telocentric or an isochromosome or both have been obtained for each of the 21 chromosomes. Extensive data for chromosome IX (Sears, 1952a) showed that on the female side about 18 per cent of transmitted monosomes were telocentric and 12 per cent iso for one or the other arm. These values translate into 4.2 per cent and 2.8 per cent of female gametes carrying a telo and iso, respectively, since 76.4 per cent carried no chromosome IX or derivative. On the male side, there is probably very little transmission of either telo- or iso-IX except telo-IX involving the long arm. Pollen carrying this chromosome should compete fairly successfully with normal, whereas that with the short-arm telo, short-arm iso, or long-arm iso would be so seriously unbalanced as to have little chance of functioning in competition with normal.

The only data available for the other 20 chromosomes are from selfed monosomics. These data are presented in Table 9. The figures are mainly of value for indicating that the telos and isos appear rather frequently. In most cases the percentage of isos and telos, calculated from the number of plants examined cytologically, is probably too high, for the plants exam-

TABLE 9--FREQUENCIES OF TELOCENTRICS AND ISOCHROMOSOMES AMONG THE OFFSPRING OF MONOSOMIC PLANTS

Chromosome concerned	No. plants grown	No. examined cytologically	No. nulli-somic	No. with telo-centric	No. with iso	Percent exam. with telo or iso
I	671	75	16	4	0	5.3
II	962	110	48	5	2	6.4
III	2682	174	205	12	5	9.8
IV	2159	178	138	11	4	8.4
V	1431	80	14	2	2	5.0
VI	598	83	15	7	7	16.9
VII	885	55	12	2	7	16.4
VIII	192	25	7	2	0	8.0
IX	832	23	28	0	3	13.0
X	1457	74	13	5	1	8.1
XI	331	88	11	2	0	2.3
XII	125	28	3	3	0	10.7
XIII	255	31	6	3	2	16.1
XIV	381	36	8	1	2	12.0
XV	1924	108	113	1	0	0.9
XVI	657	75	35	1	2	4.0
XVII	1109	90	27	2	0	2.2
XVIII	575	48	5	0	5	10.4
XIX	1084	64	30	1	3	6.2
XX	572	78	25	1	6	11.1
XXI	1002	197	2	6	0	3.0

ined in most families were not a random sample but were largely those which were suspected of being nullisomic. Any telocentric or isochromosome which was transmitted in appreciable frequency through the pollen would tend to be concentrated in the sample examined, provided that plants carrying the telo or iso were less vigorous than those with the intact monosome. For example, telocentrics and isochromosomes for one arm of chromosome VI are evidently transmitted readily through the pollen, and about 75 per cent of the male gametes carrying them combine with deficient female gametes to produce plants with a monotelo- or mono-isosome. These are difficult to distinguish from nulli-VI plants, with the result that about half the seedlings that appear to be nullisomic turn out to carry a monotelo- or mono-isosome. Indeed, since only 5 of the 15 plants listed in the table as nullisomic were confirmed cytologically, it is possible that several of the other 10 actually possessed a monotelo- or mono-isosome, in which case more than half of the suspected nullisomics were monotelo- or mono-isosomic. A similar situation probably accounts for the high frequencies of telos and isos reported from mono-III, mono-VII, and mono-

XIII. Even though the frequencies were high in the samples examined, it is likely that in the complete populations most of the telos and isos were overlooked. This is because most of those produced on the female side must have been covered up by the predominantly normal male gametes, with the production of normal-appearing plants, few of which were analyzed cytologically.

For some chromosomes, it may be assumed that relatively few telos and isos came through the pollen, and therefore that the sample, loaded with nullisomics, had fewer than a random number of telos and isos. With chromosome XV, for example, the 108 plants examined cytologically included 37 nullisomics.

For a few chromosomes, data are available on the chromosome constitution of entire families, or of reasonably random samples therefrom. These data, presented in Table 10, are not extensive enough to show whether or

TABLE 10--FREQUENCIES OF TELOCENTRICS AND ISOCHROMOSOMES IN COMPLETELY ANALYZED FAMILIES FROM MONOSOMIC PLANTS

Chromosome concerned	No. plants	No. with monotelo	No. with bivalent involving		Percent with	
			Telo	Iso	Telo	Iso
II	20	0	1	2	5.0	10.0
III	13	0	0	0	0.0	0.0
IV	21	1	1	0	9.5	0.0
VI	29	1	0	0	3.4	0.0
XI	34	0	0	0	0.0	0.0
XVI	12	0	0	0	0.0	0.0
XX	49	1	0	2	2.0	4.1
XXI	155	0	5	0	3.2	0.0
Totals	335	3	7	4	3.0	1.2

not there are differences between chromosomes in the frequency of producing telocentrics and isochromosomes. The totals for the eight chromosomes concerned, though somewhat below those for IX (3.0 per cent *vs.* 4.2 per cent for telos and 1.2 per cent *vs.* 2.8 percent for isos), do not differ significantly from the values for mono-IX given by Sears (1952a). It may be significant that in this sample no offspring occurred with a mono-isosome. Since most isochromosomes do not pass readily through the pollen in competition with normal, the mono-iso plants would be largely those resulting from union of a nullisomic male gamete with an iso-carrying egg, and these would be rare. Their frequency would usually be increased by selection of plants resembling nullisomics for examination, and many monoisosomics were observed in the larger, non-random sample of Table 9, including some for each of the chromosomes of Table 10 except XI and XXI.

Breeding Behavior of Monotelo- and Mono-isosomics

For most of the monotelo- and mono-isosomes there is no reason to think that their transmission on the female side differs appreciably from that

of normal monosomes. For telo- and iso-IX (Sears, 1952b) no significant difference from normal was found either in transmission frequency or in rate of misdivision.

On the male side the amount of transmission of a monotelo- or mono-isosome is determined by the degree of advantage enjoyed by pollen carrying the telo or iso in comparison with nullisomic pollen. With some telos, such as the long arm of IX, the advantage is about the same as that of normal *vs.* nullisomic pollen (Sears, 1952b). In most cases, however, gametes carrying a telocentric instead of a normal chromosome have less advantage over deficient gametes, with the result that more nullisomic pollen functions. The difference is even more pronounced with mono-isosomes, where the gametes carrying them are not only deficient for one arm but duplicated for the other. For the long arm of chromosome IX, Sears (1952b) reported that 26.4 per cent of functioning male gametes from mono-isosomic plants were nulli, 30.0 per cent had a derived monotelosome and only 43.6 per cent were mono-iso. For a chromosome XIII mono-iso the figures, based on only 30 male gametes analyzed, were 33.3 per cent nulli, 62.4 per cent mono-iso, and 4.4 per cent monotelo. In both cases the frequency of functioning nullisomic pollen was much higher than from ordinary monosomics. The frequency of derived telocentrics transmitted was much higher with IX than with XIII, which suggests that the poor transmission of iso-XIII is largely due to deficiency for one chromosome arm, rather than to duplication for the other arm; and the telocentric therefore has little advantage over the isochromosome.

More extensive data are available on transmission of mono-iso- and monotelosomes following selfing (Table 11). The indicated frequencies of nullisomics, determined on the basis of the total number of plants, are subject to some of the same reservations as the frequencies of nullisomics reported for ordinary monosomics (Table 4). In particular, some nullisomics tend to be missed, because they do not differ conspicuously from the monotelosomics.

The frequencies of nullisomics obtained from mono-iso- and monotelosomics are in general distinctly higher than from normal monosomics. This is particularly true for the mono-isosomics and is attributable to the relatively high fraction of nullisomic pollen which functions. Eight of the 14 telos tested (excluding XVIII, which had but 6 offspring) gave rise to few, if any, more nullisomics than did the corresponding normal monosomics. These were telo-I, -IV, -VI, -IX, -XV (telo-L), -XVII, -XIX, and -XXI Presumably, pollen carrying these telocentrics enjoyed about the same competitive advantage over nullisomic pollen as does normal pollen, and hence little nullisomic pollen functioned. As expected, in almost every case where data were available for both a mono-iso and a monotelo for a particular

TABLE 11--CHROMOSOME CONSTITUTION OF SELFED OFFSPRING OF PLANTS WITH A MONO-ISO- OR MONOTELOSOME. WHERE DIFFERENT ARMS OF THE SAME CHROMOSOME ARE INVOLVED, THESE ARE IDENTIFIED AS R (RIGHT) AND L (LEFT)

Chromosome concerned	No. plants	No. analyzed	No. nulli	Percent nulli	No. with mono-telo	No. with mono-iso	No. with di-telo	No with di-iso	No. with telo+iso
I telo	60	24	0	0.0	21	0	3	0	0
II iso-R	18	13	5	27.8	0	7	0	1	0
III telo-R	157	78	20	12.7	40	0	18	0	0
IV iso	92	47	29	31.6	3	14	0	0	1
telo	24	14	2	8.3	9	0	3	0	0
V iso	271	51	11	4.1	6	26	0	8	0
VI iso	51	15	7	13.7	1	7	0	0	0
telo	127	46	5	3.9	32	0	9	0	0
VII iso	12	9	2	16.7	0	5	0	2	0
IX iso	276	161	38	13.8	25	68	0	21	9
telo	450	376	14	3.1	354	--	--	0	8
X iso-R	155	72	6	3.9	0	40	0	25	1
telo-R	21	12	2	9.5	5	1	4	0	0
XI iso	38	33	7	18.4	15	8	0	0	3
XII telo	54	26	7	13.0	19	0	10	0	0
XIII iso-R	2	2	0	0.0	0	2	0	0	0
telo-R	6	3	1	16.7	1	0	1	0	0
XIV iso	65	29	4	6.2	0	18	0	3	2
XV telo-R	40	18	7	17.5	11	0	0	0	0
telo-L	155	72	5	3.2	51	0	16	0	0
XVI iso-L	67	22	8	11.9	0	14	0	0	0
telo-R	149	56	17	11.4	26	0	13	0	0
XVII iso	45	12	6	13.3	0	5	0	1	0
telo	168	65	2	1.2	45	2	16	0	0
XVIII iso	369	102	23	6.2	0	58	0	20	1
telo	6	4	0	0.0	2	0	2	0	0
XIX iso	37	5	3	8.1	0	2	0	0	0
telo	85	43	3	3.5	31	0	9	0	0
XXI telo	662	79	0	0.0	58	0	21	0	0

chromosome arm, as many or more nullisomics were obtained from the iso as from the telo. Chromosome XIII cannot be considered an exception, because so few data are available. With chromosome X, also, the data have no statistical significance, although here, as will be pointed out later, the isochromosome is subject to certain unusual behavior.

The two telocentrics for chromosome XV involved different arms of the chromosome. One resulted in a considerably higher frequency of nullisomics than the other.

Where an iso and telo are included for the same chromosome, these involve the same arm in all cases except XVI.

In general the data in Table 11 on the numbers of mono-iso- and monotelosomes and iso and telo pairs agree very well with the assumption that female transmission of monotelo- and mono-isosomes is essentially the same as for normal monosomes. On this basis, where the frequency of function-

ing nullisomic pollen is negligible, monosomic offspring are expected to be about three times as numerous as the disomics. With increasing frequencies of nullisomic pollen, the ratio of monosomic to disomic increases slightly, but does not reach 4:1 until there is 50 per cent nullisomic pollen, a frequency beyond any encountered here. Combining the data for all the chromosomes listed (except telo-IX, offspring of which were classified genetically and could not therefore be scored as to whether ditelo or mono-iso), there were 678 monosomic and 223 disomic plants. Considering the individual isos and telos, there are only three which deviated greatly from expectation, IV iso, X iso, and XVI iso, and none of these deviated significantly at the 1 per cent level. With IV and XVI, furthermore, where there was a deficiency of disomic offspring, it is possible that the di-iso types were particularly weak and tended to fall in the portion of the population not analyzed. Iso-X, on the other hand, produced more disomic offspring than expected, and there was no obvious difference between di-iso and mono-iso which would have led to inclusion of more of the former in the analyzed portion of the population. Furthermore, Dr. H. H. Li (personal communication) noted in China a tendency for this isochromosome to be transmitted in unduly high frequency. Evidently iso-X is not lost during meiosis with as high frequency as other monosomes. Since Li's material was the same as that studied here, the conclusion applies only to this particular iso-X. Whether iso-X's of independent origin and telo-X derived from the peculiar iso-X would show similar behavior remains to be determined.

Monotelosomics and particularly mono-isosomics are useful for the production of nullisomics in relatively high frequency. Also as a source of nullisomic gametes for certain crosses, they are greatly preferable to ordinary monosomics, because the monosome when transmitted is cytologically distinguishable from a normal chromosome.

Description of Monotelo- and Mono-isosomics

Monotelo- and mono-isosomics also assist in the mapping of chromosomes, since the presence or absence of a certain genic effect in one of these deficient types shows whether the gene concerned is located on the arm that is missing. On this account it is desirable that the monotelo- and mono-isosomics thus far observed be briefly described. To expedite comparisons of related chromosomes, the homoeologous groupings will be followed.

Homoeologous Group 1

Telo-I: The most conspicuous effect of telo-I is an increase in fertility over that of the nullisomic. This arm evidently carries the genes for inhibition of stiffness and coloration of glumes, but it does not inhibit the tendency toward lax spikes exhibited by the nullisomic.

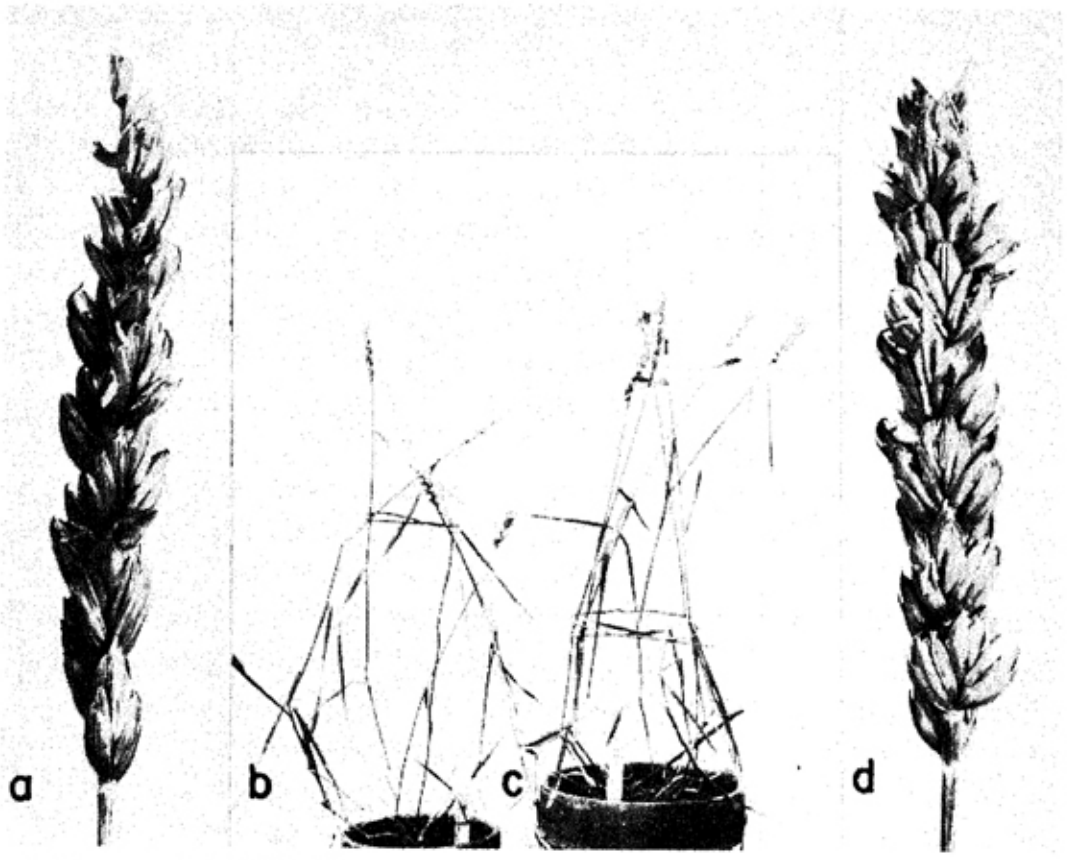

Figure 16. (a) Spike and (b) plant of nullisomic XVII, and (c) plant and (d) spike of mono-iso-XVII. (Plants 0.09 natural size; spikes natural size.)

Telo- and Iso-XIV: The one telo and two isos observed have involved the same arm. The mono-isosomic is a slightly more vigorous, wider-leaved, thicker-culmed plant than nulli-XIV, with spikes nearly normal in size and appearance, but of only about half normal fertility. The mono-telosomic is more or less intermediate between mono-iso-XIV and nulli-XIV.

Telo- and Iso-XVII: This arm of XVII has its main effect in increasing fertility, one dose (telo) being practically as effective as two (iso). Seed sets are increased to over 50 per cent in some spikes. Spike size in the mono-isosomic (Fig. 16 c, d) remains about the same as in the nullisomic (Fig. 16 a, b), and plant vigor is only slightly increased.

Homoeologous Group 2

Telo- and Iso-II: Mono-isosomes have been observed for both arms of chromosome II, and telocentrics for what may be called the right arm. The right arm carries genes for normal synapsis, for female fertility, for toughness of glumes, and for promotion of awn growth. Right-arm mono-isosomics are fairly fertile, but spikes (Fig. 17 c) have long internodes similar to the nullisomic (Fig. 17 a) and may have reduplicated spikelets. The mono-telosomic (Fig. 17 b) tends to be intermediate in appearance between the mono-iso and the nullisomic, and is almost completely female sterile. The left arm carries the gene or genes for normal internode length but appar-

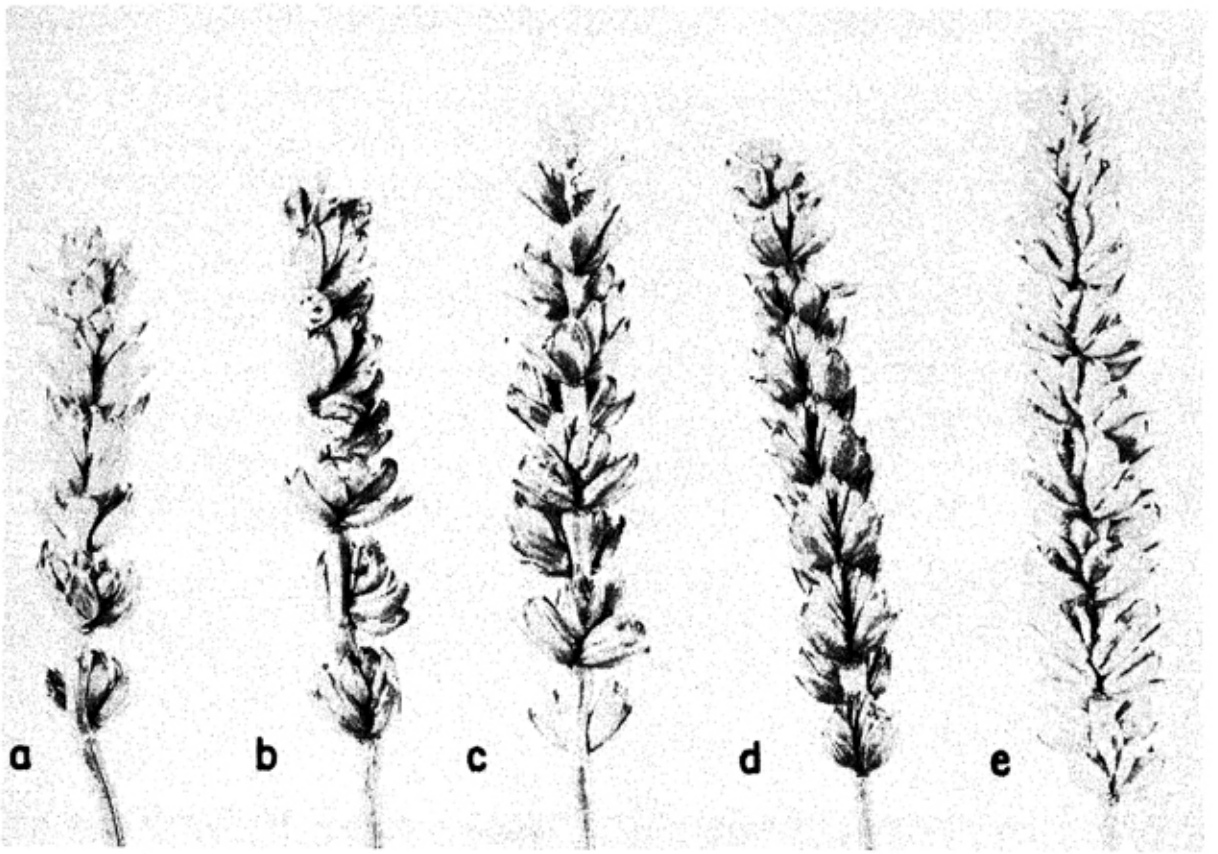

Figure 17. Spikes of (a) nullisomic II, (b) right-arm monotelosomic-II, (c) right-arm mono-isosomic-II. (d) left-arm mono-isosomic-II, and (e) monosomic-II. (0.95 natural size.)

ently has little effect on fertility, left-arm mono-isosomics (Fig. 17 d) being completely female sterile. Glumes are thin and papery in mono-iso-L.

Telo- and Iso-XIII: The right arm of XIII carries most of the genes necessary for female fertility, the gene (or genes) for promotion of awn growth, and the gene (or genes) for normal spike-internode length. Similar genes are present on the homoeologous chromosome II, but there the gene for normal internode length is on a different arm from the awn-promoting gene. Right-arm mono-isosomics (Fig. 18) are fairly normal in plant and spike characteristics, but are poorly fertile. A left-arm monotelosomic observed was much like nulli-XIII in appearance and was also completely female sterile.

Telo- and Iso-XX: Both telo and iso have been obtained for the left arm, and an isochromosome for the right arm. The monotelo- and mono-isosomic for the left arm are only slightly different from the nullisomic in plant characteristics. Spikes are similar to the nulli, except that internodes are of about normal length. Fertility is extremely low. Iso-R has only been observed in combination with a normal XX. It is clear, however, that the gene for awn promotion lies in this arm. Presumably the arm also carries most of the genes for female fertility as well. Apparently chromosome XX

Figure 18. Spikes of mono-iso-XIII. (Natural size.)

resembles II rather than XIII in having its gene for normal internode length on the opposite arm from the awn-promoting gene. The gene for suppression of spikelet reduplication is evidently on the same arm (right) as the awn-promoting gene, XX differing from II in this respect.

Homoeologous Group 3

Telo-and Iso-III: What may be called the right arm of III carries the normal allele of the gene for asynapsis, while the left arm carries most of the genes for plant vigor and normal spike characteristics. Hence right-arm monotelo- and mono-isosomics have normal synapsis but are almost as dwarfed and short-spiked as nullisomics. Left-arm monotelosomics are of nearly normal height and have a fairly normal-appearing spike (see Fig. 2 in Sears, 1952b), but are partially asynaptic. Neatby's (1933) virescent gene is located on the left arm.

Telo-XII: This monotelosome increases slightly the size and vigor of plants carrying it, but its chief effect is in increasing fertility.

Telo- and Iso-XVI: Mono-iso-L plants are vegetatively almost as dwarfed as nulli-XVI, and are difficult to distinguish from nullisomics in early

stages. Their spikes are nearly normal in length under very favorable conditions and may reach 50 per cent of full fertility. Awns are distinctly increased. Seeds are white. Monotelo-R plants are more vigorous and nearer normal, being distinguishable from nullisomics as seedlings. Spikes are short, but in ditelo plants under the most favorable conditions are nearly of normal length. Fertility is low in the monotelo, but may run over 50 per cent in the best spikes of ditelos. Awns and seed color are normal, showing that the right arm carries genes for awn inhibition and red seed color.

Homoeologous Group 4

Telo- and Iso-IV: The arm involved here has little effect on plant (Fig. 19) or spike, but restores male fertility. There is some improvement in vigor, particularly with the mono-iso (Fig. 19 c). Mono-isosomic plants have

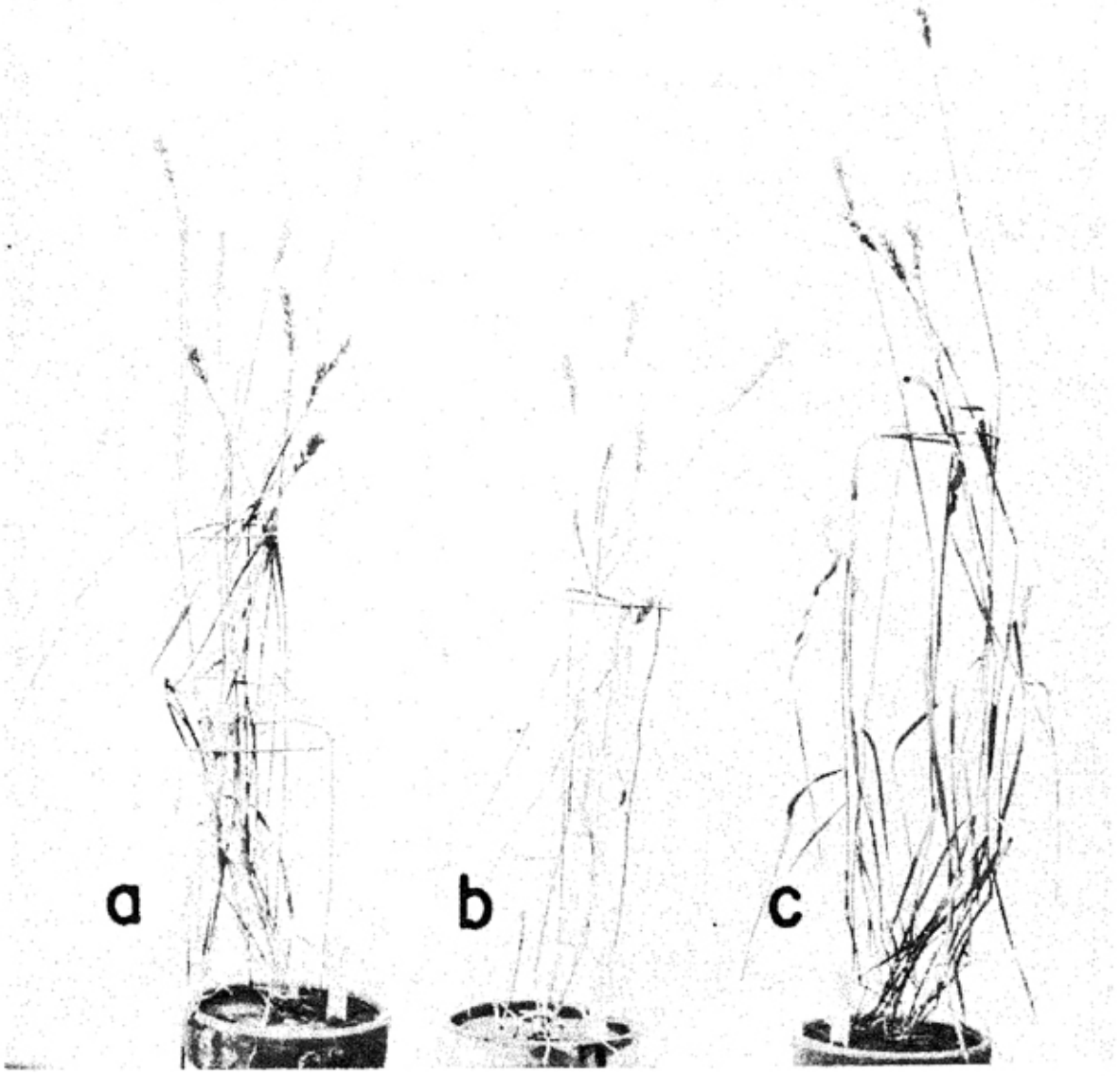

Figure 19. Plants of (a) nullisomic IV, (b) monotelo-IV, and (c) mono-iso-IV. (0.12 natural size.)

somewhat coarser culms and broader leaves than the nullisomic, but these are still below normal in width.

Telo- and Iso-VIII: The arm that has been obtained as telo and iso increases plant height and vigor somewhat (Fig. 20) and restores male fertility. Seed sets from selfing are low, however, with both mono-iso and monotelo. In the mono-isosomic (Fig. 20 c), particularly, tillering is more nearly normal than in the bushy nullisomic, and culm diameter and leaf width are increased toward normal. The gene for hooded awns is not located on this arm.

Telo-XV: Both monotelosomics are difficult to distinguish from nulli-XV in seedling stages, with telo-R (Fig. 21 b) more nearly normal at later stages. Telo-L has spikes very similar to nulli-XV but with sufficient male fertility to set an occasional seed. Telo-R spikes (Fig. 21 c) are somewhat longer and are more fertile.

Figure 20. Plants of (a) nullisomic VIII, (b) monotelo-VIII, and (c) mono-iso-VIII. (0.11 natural size.)

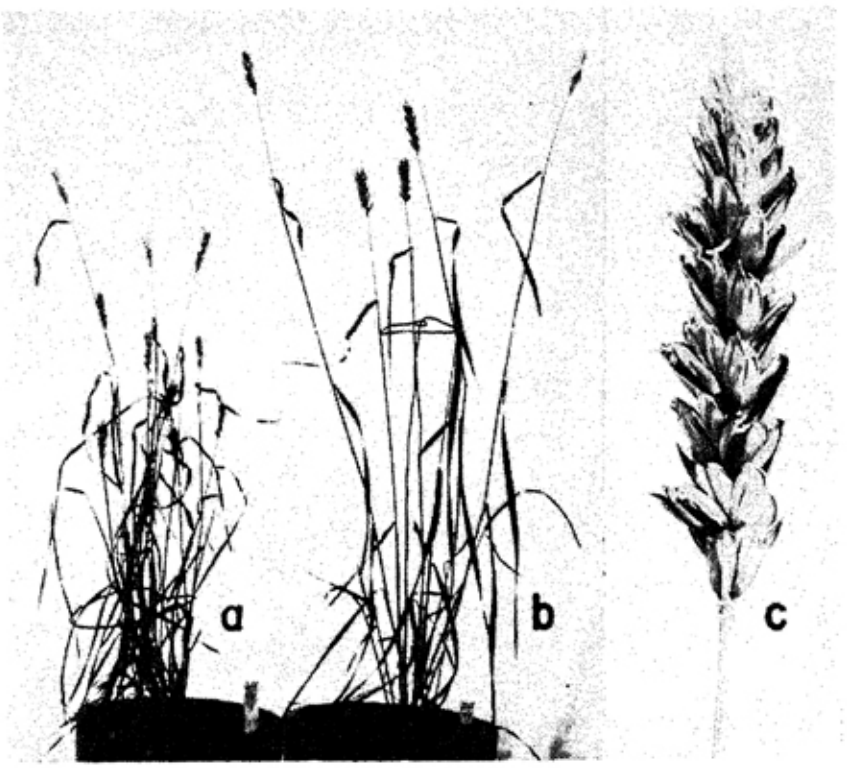

Figure 21. Plants of (a) nullisomic XV and (b) right-arm montelo-XV, and (c) spike of right-arm monotelo-XV. (0.09 natural size and natural size, respectively.)

Homoeologous Group 5

Telo- and Iso-V: The arm for which telos and isos have been obtained is the long arm and apparently contains the large majority of the genes affecting size, vigor, and fertility. Mono-isosomics resemble the normal rather closely in all plant and spike characters, but are slightly reduced in height (see Fig. 4 in Sears, 1952b).

Telo- and Iso-IX: The effects of this arm, which is the longer one, have been described before (Sears, 1952a). The genes for speltoid suppression, pubescent node, spring habit of growth, and awn suppression, as well as practically all of the genes for vigor and fertility, are located on it. Mono-isosomic plants and spikes (Fig. 22 a; see also Fig. 1 in Sears, 1952a) are essentially normal.

Telo- and Iso-XVIII: One arm of XVIII carries almost all of the effective genes of this chromosome. It is this arm for which the iso and telo have been obtained. The mono-isosomic (Fig. 22 b, c) is accordingly relatively normal in all its characteristics. The monotelo resembles the normal monosomic in being somewhat late, but otherwise differs little from normal.

Homoeologous Group 6

Telo- and Iso-VI: The isos and telos obtained for VI (Fig. 23 a, b) have little effect except in producing male fertility.

Telo- and Iso-X: The right-arm has little effect on the morphology of the plant, mono-iso-X (Fig. 23 d) being difficult to distinguish from nulli-

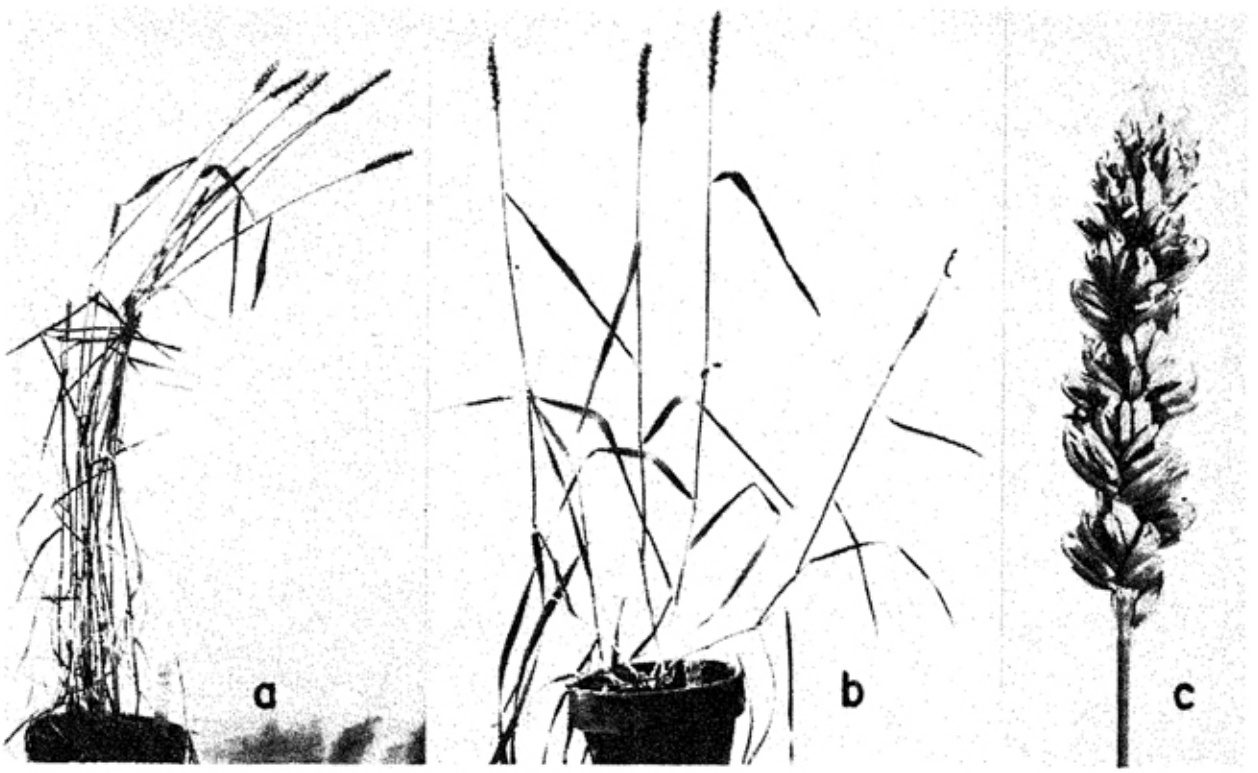

Figure 22. Plants of (a) mono-isosomic-IX, (b) mono-isosomic XVIII, with a nullisomic tiller (right), and spike of (c) mono-iso-XVIII. (0.09 natural size, 0.106 natural size and natural size, respectively.)

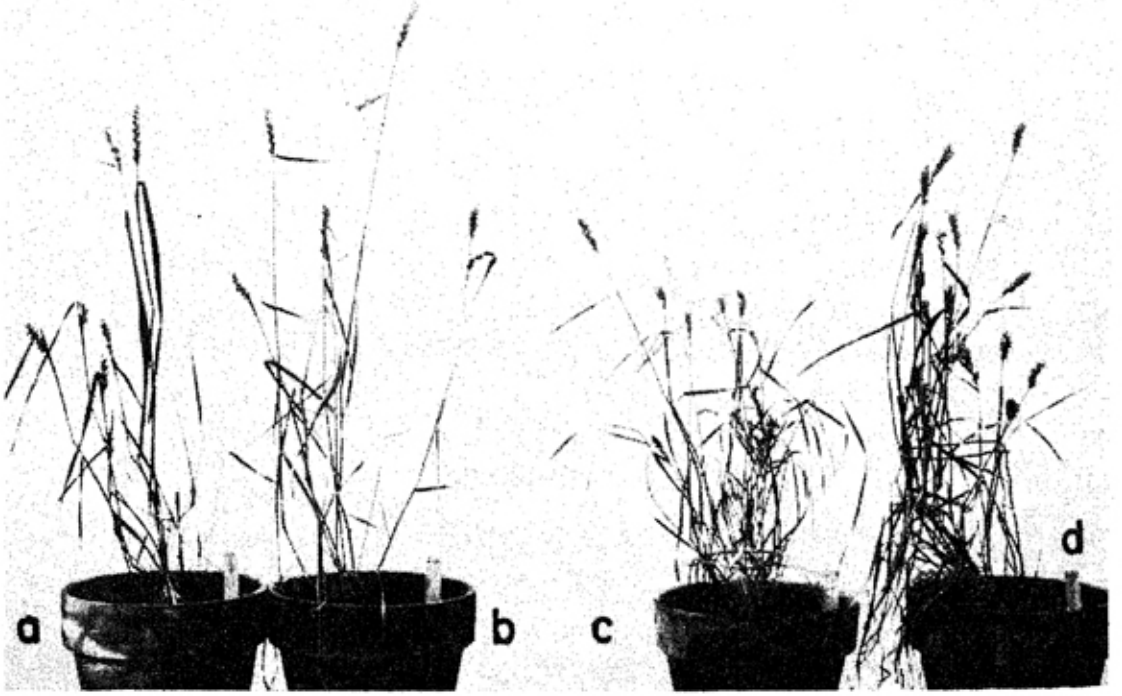

Figure 23. Plants of (a) nullisomic VI, (b) mono-isosomic VI, (c) nulli-X, and (d) mono-iso-X. (0.09 natural size.)

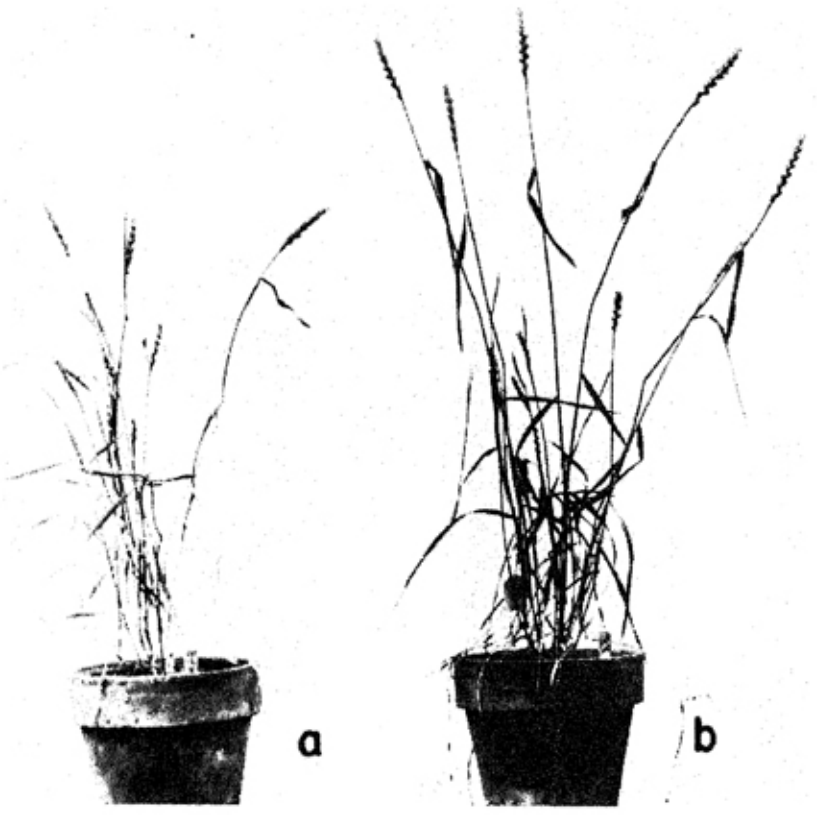

Figure 24. Plants of (a) nullisomic XIX and (b) telomono-XIX. (0.09 natural size.)

X (Fig. 23 c). However, the arm does suppress the tendencies toward leaf necrosis and pistillody which characterize the nullisomic, and it restores male fertility. It does not carry the suppressor of awns located on chromosome X. The effect of two doses of the isochromosome is little, if any, different from that of one dose. As noted previously, female transmission of the isochromosome appears to be abnormally high. The left arm contains the awn-suppressing gene, B_2, and also makes for normal glume characteristics and male fertility. Spikes of monotelo-X(L) are small but otherwise more or less normal in appearance, and show up to 50 per cent sets of seed.

Telo- and Iso-XIX: Here again the chief effect of the arm concerned is to raise fertility to around 50 per cent in some spikes. Plant and spike characters remain much the same as in the nullisomic (Fig. 24).

Homoeologous Group 7

Telo- and Iso-VII: This arm of VII apparently has little or no beneficial effect on plant or spike. In fact, there is some indication that the mono-isosome decreases fertility in comparison with the nullisomic. The di-iso, with four doses of the arm, is extremely dwarfish and almost sterile (Fig. 25 a), being greatly inferior to the tetrasomic.

Telo- and Iso-XI: The chief effect of the arm involved here is to increase fertility (Fig. 25 b). This is achieved, at least in part, by suppression of the tendency toward pistillody exhibited by nulli-XI.

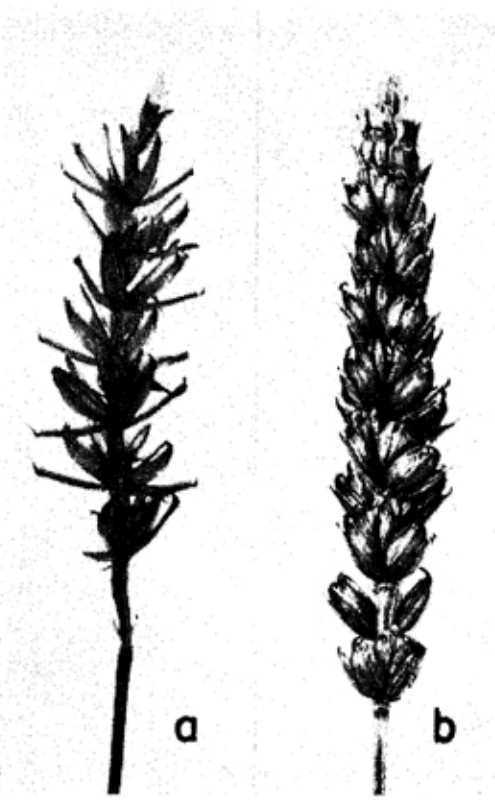

Figure 25. Spikes of (a) di-isosomic VII and (b) mono-iso-XI. (Natural size.)

Telo-XXI: As with chromosome VII, there is considerable doubt that the monotelosomic is improved over the nullisomic in vigor or fertility. Data are not available as to whether the arm is deleterious in higher doses. Clearly the arm has an advantage in pollen competition, as shown by the rarity of functioning nullisomic pollen from monotelo-XXI.

CHIMERAS

Numerous chimeras have been observed which were due to somatic loss of a telocentric or to its conversion into an isochromosome. Loss of one or both arms of an isochromosome also has been noted, as well as formation of an added telocentric from an isochromosome. These chimeras have been most thoroughly studied for iso- and telo-IX, but they occur also with other telocentrics and isochromosomes (Fig. 22 b). They have already been dealt with in considerable detail in another publication (Sears, 1952b).

A different type of chimera involves loss or duplication of entire chromosomes. These chimeras, which are evidently rather rare anyway, probably escape observation in most cases, in as much as they usually consist only of sectors with trisomes and monosomes. In a monosomic plant, somatic loss of the monosome would give rise to a nullisomic sector and this sector would often be detectable. No such sectors have been observed in monosomics.

Several chimeras have been found in nullisomic plants. Two of these are illustrated in Figure 26. Both of these plants in early stages were typi-

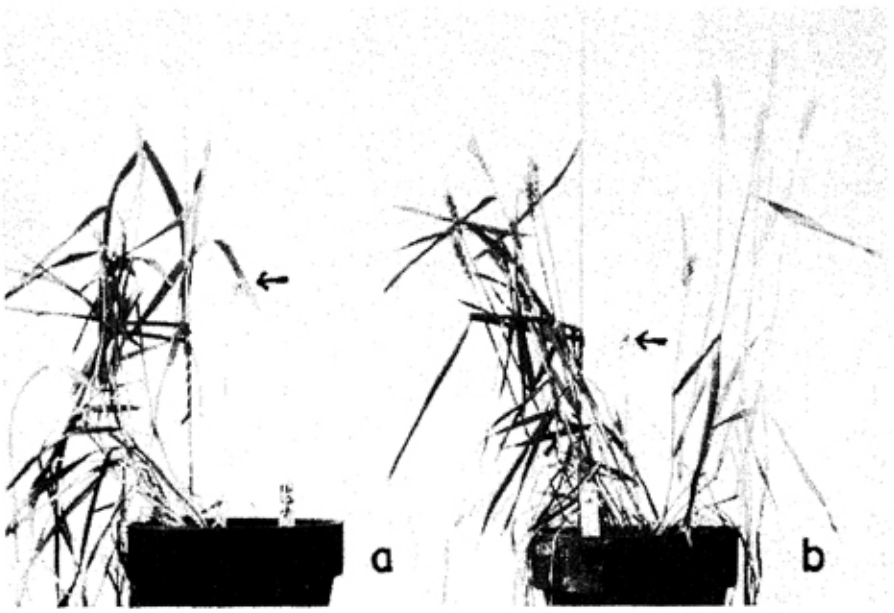

Figure 26. Chimeral plants from nulli-XVI. The first tiller (indicated by arrow) of each plant was typical nulli-XVI, but in (a) the later tillers had 16 disomes, 2 trisomes, and 2 monosomes; while in (b) they had 12 disomes and 8 trisomes. (0.10 natural size.)

cal nulli-XVI. As tillers developed, however, these were mostly non-nullisomic in appearance. Cytological examination of the non-nullisomic portions revealed that in one plant (Fig. 26 a) there were 2 trisomes and 2 monosomes plus 16 disomes, and in the other plant (Fig. 26 b) 8 trisomes plus 12 disomes. Clearly the non-nullisomic characteristics of these two plants may be attributed to the presence of one or two homoeologous trisomes able to compensate to some extent for the absence of chromosome XVI.

Another chimeral plant was nulli-III in all but one tiller. This one tiller had a large yellowish sector, involving more than half the first leaf. Later leaves, which developed when temperatures were higher and thus more favorable to chlorophyll development, did not show pronounced chlorophyll deficiency. This tiller attained only about one-half the normal length for nulli-III, and the spike produced was small, abnormal, and quite sterile. Chromosome III is known to carry a gene which presumably is involved in chlorophyll production, since it is the normal allele of Neatby's virescent. That complete loss of this gene does not lead to chlorophyll abnormality suggests that there is a duplicate locus on at least one other chromosome. In nulli-III then, loss of this duplicate locus, even of only one member of the gene pair, might lead to defective chlorophyll. Thus this chimera seems best explained as a sector from which at least one whole chromosome had been lost.

The one other chimera occurred in an F_1 hybrid between mono-XXI and Neatby's virescent. Presumably the plant was originally a simple mono-

somic. One of the several tillers was about half of virescent phenotype. Since virescent is recessive and ineffective when hemizygous, it was clear that this sector must have carried two doses of the virescent gene. No virescent offspring were obtained, either from the spike borne on the affected tiller or from other spikes. It would appear, then, that there was a somatic segregation such that the virescent sector received two doses of the virescent gene and the rest of the plant became deficient for virescent. The virescent sector involved only a small fraction of the plant, not including any germinal tissue. That the segregation depended upon aberrant distribution of whole chomosomes is indicated by the fact that the non-virescent sector proved to be mono-III (as well as mono-XXI and trisomic for an unidentified chromosome). Since chromosome III carries the virescent gene, *v* (Sears, 1953), and since this gene is presumably effective in two doses even in the presence of one or more doses of *V,* it seems clear that the chromosome carrying *v* must have undergone non-disjunction to produce one sector *vvV* (virescent) and another sector *V* (non-virescent).

The four chimeras described all suggest mitotic non-disjunction affecting two or more chromosomes at once. In one case both halves of all eight chromosomes concerned went to the same pole, while in the other two analyzed cases, some went to one pole and some to the other. With the nulli-XVI chimeras it may be assumed that the complementary sectors, each monosomic for at least one of the homoeologues of XVI, were unable to compete successfully in growth and hence were not discernible in the mature plants. In the mono-XXI chimeral plant, no portions were found with the parental constitution, suggesting that the segregation took place at a very early stage.

DISCUSSION

The Genic Basis of the Nullisomic Effect

It has been established that the 21 chromosomes of wheat fall into seven "homoeologous" groups of three. Within each of these groups, the tetrasome of any one chromosome will compensate, at least in large part, for the nullisome of either of the other two. Stated another way, a particular nullisomic shows the effect of the loss of certain genes, and either of the two homoeologous tetrasomes will compensate for these lost genes. A reasonable explanation of this behavior is that the homoeologous chromosomes carry duplicates of the lost genes, and that the normal gene dosage is therefore restored by increasing the number of either homoeologue to four. The genes concerned in the nullisomic effect are thus normally present in six doses, and the effect is due to reduction of the dosage to four.

In a non-polyploid organism, it is comon for genes to reach a saturation level at one dose, with little or no additional effect resulting from in-

creasing the dose to two or more. This is the basis for the phenomenon of dominance. Since wheat is a hexaploid, one might expect that some of its genes would fail to reach the saturation level in one dose, and this has proved true for several of the genes thus far studied. However, one would not expect a high proportion of the genes of a hexaploid to fail to reach the saturation point in four doses, three being the equivalent of one dose in a diploid. Thus it is *a priori* likely that few genes are involved in the production of the nullisomic effect, these being genes which show a pronounced effect of reduction in dosage from six to four.

There is experimental evidence that few genes are responsible for the characteristics of nullisomics. If many genes were involved, they ought to be distributed more or less at random throughout the chromosome. There are three chromosomes, V, IX, and XVIII, however, for which complete deficiency of one arm brings practically no part of the nullisomic effect. This strongly suggests that only a few of the genes on each chromosome are concerned in the nullisomic effect, and that in the three mentioned cases these genes happen to lie on only one arm, the longer one. Data for other chromosomes tend to confirm that few genes are involved in the nullisomic effect. Deficiency for one arm produces some of the characters of the nullisomic, while deficiency for the other arm gives rise to the other nullisomic characteristics. This is what would be expected with only a few effective genes on each chromosome, each gene largely or entirely controlling the expression of a particular character.

Genes Ineffective When Hemizygous

Although only about 20 wheat genes have been studied in such a way (dosage series) as to permit determination of their effectiveness when hemizygous, at least three have been found to be relatively ineffective—that is, they are nearly or completely recessive to their deficiency. These three are Neatby's virescent on chromosome III, the gene for speltoid suppression and squareheadedness on chromosome IX, and the sphaerococcum gene on chromosome XVI. It appears, therefore, that this type of gene may be fairly common in hexaploid wheat. The reason for the occurrence of such genes in wheat, although they are practically unknown in diploid organisms, presumably lies in the polyploid nature of wheat (Sears, 1953). A gene which in a diploid expresses itself in a single dose, is subject in a hexaploid to the action of modifiers from two additional related genomes. It is not surprising that under these circumstances one dose of the gene may not be sufficient to bring it to the threshold of expression.

Gene Evolution in Wheat

One of the hemizygous-ineffective genes, namely Neatby's virescent *(v)*, provides evidence concerning gene evolution in wheat. The virescent

gene interferes with chlorophyll production—only slightly or not at all in one dose, but with increasing effectiveness in two and three doses. Its normal allele, *V*, shows no significant effect on chlorophyll in dosages of 0 to 4, thereby identifying itself as a null allele. This null allele cannot be a deficiency, however, because the virescent gene arose from it by mutation, and genes presumably do not arise *de novo*.

There are two known types of gene to which the *V* allele might belong. One of these is the gene which has been inactivated or masked, as discovered by McClintock (1950) in maize. Such a gene, though capable of mutation, is of null effect. Mutation consists of the unmasking of the gene, with restoration of its original function and stability. At the virescent locus, this would mean that *v* was the normal allele, that it had been masked to give *V*, and that *v* had been recovered by the unmasking of *V*. This is highly improbable, because *v* is of such deleterious effect that it could scarcely be the normal allele. The instability of *v* suggests that it may have arisen by the masking of *V*, but this possibility must also be ruled out, for complete loss of *V* leads to no chlorophyll abnormality.

The second type of gene seems much more likely to be the type which includes *V*. It is a gene which is duplicated at one or more other loci. In wheat there are presumably many such genes, duplicated on each of two other chromosomes. This kind of gene, though active in the sense of forming a product, shows no dosage effect, because its product is surplus in the presence of the four duplicate genes on the other two pairs of chromosomes. Being non-essential, it is not restricted in mutating by the necessity of continuing to fulfill some vital function.

Since *v* affects chlorophyll primarily, there is some reason to think that *V* may also be concerned in chlorophyll production. That this may be the case is suggested by evidence that chromosome III carries a gene which is essential to chlorophyll production in the absence of one or more of the chromosomes homoeologous to III. The evidence consists of the occurrence of a chlorophyll-deficient sector in a nulli-III plant.

An origin similar to that of virescent seems likely for the hemizygous-ineffective sphaerococcum gene, *s*. The non-sphaerococcum allele, *S*, is indicated by the 0-4 dosage series to be a null allele. As with *V*, it is improbable that it is a deficiency, for the *s* allele is believed to have arisen from it as a mutant (Ellerton, 1939). A reasonable assumption is that the parent *S* gene is one which is duplicated at other loci and hence is non-essential.

Evidence is lacking that the incompletely dominant vulgare gene, *Q* (speltoid-suppressing and squarehead), arose as a mutant of a triplicated, non-essential gene. Indications are that *q* is a null allele, but the full dosage series has not been studied. McFadden and Sears' (1946) suggestion that *q* consists of a short segment intercalated from another species would mean that *q* is actually a deficiency.

Only genes not fully effective when hemizygous have been considered here. There seems to be no reason why this should be the only type of gene to have arisen from triplicated, non-essential genes. Not all mutants arising in this way should fail of expression in single dose.

Translocation of Parts Between Chromosomes

The fact that the 21 chromosomes fall into seven homoeologous groups of three suggests that in the evolution of wheat there has been rather little translocation of parts between chromosomes. On the other hand, it is clear that reciprocal translocation has not been completely suppressed, for several translocations have been found in existing varieties: Chinese and Thatcher differ by a translocation involving chromosomes IV and X, Chinese and Poso by a translocation involving V and VII, and Chinese and Indian by a translocation involving III and VII.

Obviously, translocations between unrelated chromosomes tend to destroy the integrity of the homoeologous series, by creating chromosomes with homologies in two different groups. Thus far no case has been detected in which a chromosome has homology for two groups.* This could mean that the variety used, Chinese Spring, has the primitive chromosome arrangement, from which the various other arrangements have been derived by translocations. On the other hand, it may simply be a consequence of the relative insensitivity of the test used to detect homology.

The lack of sensitivity of the nullisomic-tetrasomic compensation test is due to the following circumstance. Where two chromosomes have a large proportion, say more than half, of their genes in common, it is to be expected that addition of the tetrasome of one chromosome to a plant nullisomic for the other chromosome will cancel most of the nullisomic effects and thereby improve the plant. Not all the nullisomic effects will be canceled, however, so the nullisomic-tetrasomic will not be equal to normal. Now if two chromosomes have only a fraction, say one-tenth, of their genes in common, there will be some canceling of nullisomic effects when the tetrasome is added to the nullisomic; but most of these effects will remain, and to them will be added the deleterious effects of duplication for the other 90 per cent of the genes. The net result may well be a nullisomic-tetrasomic plant which is weaker and less fertile than the simple nullisomic, and the 10 per cent of homology will go undetected.

Since translocated segments consist of only a part of one chromosome arm, they will usually include considerably fewer than half the genes of the chromosome concerned. Most instances of inter-group homology due to translocation may therefore fail of detection by the nullisomic-tetrasomic compensation test. It is thus possible that a part of the heterogeneity observed in some of the homoeologous groups may be the result of inter-group translocation and that Chinese does not have as primitive an arrangement

*See footnote on page 4 for an exception to this statement.

of chromosome parts as does some other variety. If the aneuploids had been obtained in another variety, the seven homoeologous groups might have been more clear-cut than they are in Chinese.

Although a few translocations might occur between chromosomes of different homoeologous groups without greatly affecting the integrity of the groups, the groups would inevitably be destroyed if many such translocations occurred. The fact that homologies within groups are of an entirely different order from homologies between groups clearly shows that the groups are essentially intact and that relatively few translocations can have occurred.

Practical Value of the Aneuploids

From the descriptions and figures of the nullisomics, it is clear that none of these is sufficiently vigorous and fertile to have an agronomic advantage over the normal. Monosomics and trisomics, though more nearly normal, do not breed true. Since some of the tetrasomics are nearly normal in vigor and fertility, these could be useful in special instances where it was desired to double the normal dosage of a particular gene, such as one for disease resistance. However, tetrasomics, though more stable than monosomics and trisomics, tend to produce some trisomic offspring (Table 8), and would revert in a few generations to the disomic (normal) type. One way of overcoming this difficulty would be to combine the tetrasome with one of the two homoeologous nullisomes, so that selection would favor the tetrasome and tend to eliminate any non-tetra (or-tri) plants which appeared. A few of the nulli-tetra combinations are vigorous and fertile, but insufficient tests have been made to show whether any of them could compete agronomically with normal material.

Although there is apparently no possibility that any nullisomic will have practical value (except if compensated for by a homoeologous tetrasome), there is a chance that deficiency for a particular chromosome arm might not be deleterious or might even be beneficial. It has been pointed out that the short arms of chromosomes V, IX, and XVIII have little effect on the plant, and that one arm of chromosome VII actually seems to have a deleterious effect. However, there is little reason to believe that plants deficient for the short arm of V, IX, or XVIII would come up to normal in yielding ability; and there is no evidence yet that the loss of the one arm of VII would improve yielding ability. Even if a higher-yielding type could be obtained with a pair of telocentrics, there would presumably be some difficulty in maintaining the purity of the line, since telocentric chromosomes are particularly subject to somatic aberration and loss (Rhoades, 1940; Sears, 1952b). Natural selection, however, might keep a vigorous line with a pair of telocentrics reasonably constant.

The fact that certain individual arms of chromosomes can be dispensed with without much if any deleterious effect, whereas no entire chromosome is readily dispensable, suggests that still smaller deficiencies might be beneficial, perhaps resulting in increased yielding ability. The same conclusion can be reached from a consideration of the fact that most genes of wheat are present in duplicate or triplicate, and that these dosages may in some cases be beyond the optimum. Certainly some genes have dosage effects at levels of four to six, and it would be very surprising if every such gene had its optimum effect at six doses rather than four. Evolution would of course result in the accumulation of deficiency mutations at these loci, thereby reducing the dosage; but hexaploid wheat is believed to be a young species, on which evolution has had relatively little time to work. Since deficiencies are readily induced by x-rays and other ionizing radiations, it follows that a chance may exist for picking up mutations to greater yielding ability from x-ray and neutron experiments such as Mac Key (1954) has undertaken.

Whether mutations to such characters as disease resistance can be obtained by use of x-rays (or neutrons) should be determinable simply by test of the nullisomics. The large majority, or possibly all, of the induced mutants will presumably be deficiencies (Stadler and Roman, 1948), and each nullisomic will show whether deficiency for any part of the chromosome concerned brings about increased disease resistance.

As indicated in a previous paper (Sears, 1953), the monosomics and nullisomics can be used in various ways to locate genes on particular chromosomes. Already these methods are being used by a number of wheat cytogeneticists, and a good start has been made toward mapping the chromosomes. Several genes for disease resistance, as well as some for morphological characters, have been located. The value for wheat improvement of a thorough knowledge of the genetic make-up of wheat is obvious.

Another promising avenue through which the work with aneuploids may contribute to wheat improvement is the substitution of a pair of chromosomes from one variety into another. This can readily be done, using the nullisomics and monosomics (Sears, 1953), and it is entirely possible that some of the substituted lines will be better than the host lines. This would be a type of hybrid vigor in which the increased vigor was due to interaction between genes at different loci.

O'Mara (1947) found that when a pair of hairy-neck chromosomes from rye was substituted for the chromosome-IX pair of wheat a much more nearly normal plant was obtained than when the rye pair was simply added to the entire wheat complement. It is possible that certain other chromosomes from rye or from other genera related to wheat might advantageously be substituted for specific wheat chromosomes. This can be done using the nullisomics and monosomics. First, an addition line is obtained which has

the full 21 wheat pairs plus the desired pair from the foreign species (see O'Mara, 1940, for the technique of making such additions). This addition line is then crossed with a particular nullisomic or monosomic. F_1 plants are monosomic for both the wheat chromosome concerned and the foreign chromosome. In F_2 the desired substitution type, nullisomic for the wheat chromosome and disomic for the foreign chromosome, may be obtained; or the F_1, as the female parent, may be backcrossed to the 22-pair line, and B_1 individuals selected which are monosomic for the wheat chromosomes and disomic for the foreign chromosome. Following selfing, these monosomic-disomic plants should produce some nullisomic-disomic offspring, particularly if the foreign chromosome tends to compensate for the missing wheat chromosome. Whether obtained in F_2 or following backcrossing, the nullisomic-disomics will ordinarily be distinguishable from other 21-pair plants by the genetic effects of the foreign chromosome.

SUMMARY

All of the 21 possible monosomics and trisomics, together with their nullisomic and tetrasomic derivatives, have been obtained in the common-wheat variety, Chinese Spring. The monosomics and trisomics were chiefly obtained from haploids and from partially asynaptic nullisomic III. More than 200 monosomes and 35 trisomes were identified.

The chromosomes of the *AB* (emmer) genomes are numbered I to XIV, and those of the *D (Aegilops squarrosa)* genome XV to XXI. On the basis of genetic relationships indicated by the ability of tetrasomes to compensate for nullisomes, the 21 chromosomes fall into seven homoeologous groups of three chromosomes each.

Most monosomics and trisomics differ little from normal. Nullisomics are mostly of greatly reduced vigor and fertility, but all survive to maturity and are at least partly fertile either as male or female or both. Most have distinctive plant and spike characteristics. Tetrasomics tend to differ from normal in the opposite direction from the corresponding nullisomics but to a smaller extent in most but not all cases. Every tetrasomic has both female and male fertility.

Measurements of monosomes at second telophase of meiosis showed greater length differences than at first metaphase. Even at second telophase, however, few monosomes could be identified with certainty.

Frequencies of nullisomic offspring from monosomic plants ranged from 7.6 per cent to 0.9 per cent. These frequencies are believed to depend on about 25 per cent female transmission of monosomes, together with male transmission of from about 90 per cent to almost 99 per cent.

The various trisomics produced from 0.5 to 12.5 per cent tetrasomics, with an average of 3.3 per cent. Since female transmission of the extra

chromosome is about 45 per cent, male transmission averaging about 7 per cent is indicated.

Nullisomics that were fertile bred reasonably true, except for partially asynaptic nulli-III. Tetrasomics were less constant, tending in particular to produce trisomic offspring.

Either a telocentric or an isochromosome or both has been obtained for each of the 21 monosomes. They have appeared in high frequency (3.0 per cent telos and 1.2 per cent isos for the eight chromosomes, exclusive of IX, for which suitable data are available). On the female side monotelo- and mono-isosomics are evidently transmitted in frequencies similar to those of ordinary monosomics, with the possible exception of iso-X. Through the pollen, transmission of monotelos and particularly mono-isos tends to be less than of the corresponding intact monosomes, with the result that more nullisomic offspring are recovered. The monotelo- and mono-isosomics show which chromosome arms carry various genes.

Chimeras have been found which involved loss or duplication of one or more chromosomes. Such loss or duplication is more likely to have a detectable effect in aberrant material, such as nullisomics, where duplication of a homoeologous chromosome may produce a more nearly normal plant, and loss of such a chromosome may increase the abnormality.

The characteristics of nullisomics are believed largely due to reduction in dosage of triplicate genes, the genes concerned being relatively few in number.

Evidence is presented for the origin of certain genes in wheat through mutation at loci that are non-essential because of being duplicated on other chromosomes.

Translocations have been observed between varieties of wheat, and these translocations must tend to destroy the integrity of the homoeologous groups. They have failed to do so, however, presumably because there have been relatively few of them.

The aneuploids of wheat are making possible a thorough genetic analysis, through which they contribute greatly to wheat improvement. Other practical possibilities include balanced nullisomic-tetrasomic combinations, deficiencies for parts of chromosomes, and substitutions of entire chromosomes from other varieties and genera.

GLOSSARY

Aneuploid, an individual with other than an exact multiple of the haploid complement of chromosomes.

Asynaptic, used loosely here to denote the presence of unpaired homologous chromosomes at first meiotic metaphase. In a stricter sense, would exclude cases of desynapsis, where pairing occurs in prophase but is not maintained until metaphase.

Culm, the jointed stem of grasses.

Di-isosome, a pair of isochromosomes.

Diploid, an individual or species with twice the basic complement of chromosomes. Also, in allopolyploid species an ordinary individual having each chromosome present in duplicate, in distinction from the haploids and triploids that also occur.

Disome, a chromosome present in two doses, the normal number for a diploid organism.

Ditelosome, a pair of telocentric chromosomes.

Euhaploid, a true haploid, in contrast with individuals deficient or duplicated for one or more whole chromosomes.

Euploid, an individual with an exact multiple of the haploid complement of chromosomes.

Genome, strictly speaking, the entire genic complement of an organism; but commonly used in literature dealing with wheat to denote the separate sets of chromosomes derived through polyploidy from different ancestral diploid species. Thus, 21-pair hexaploid wheat has genomes A, B, and D, each consisting of 7 pairs of chromosomes.

Glumes, the bracts enclosing the flowers of grasses. In wheat each spikelet is enclosed in a pair of outer, or empty, glumes, and each separate floret is enclosed by a lemma, or flowering glume, and a palea.

Haploid, an individual having only one of each kind of chromosome.

Hemizygous, a term applied to a gene which is present in only one dose with no accompanying allele. Every gene on a monosome is hemizygous.

Heterobrachial, having one arm longer than the other.

Hexaploid, an individual or species having six times the basic number of chromosomes. In an autohexaploid all six sets are the same, while in an allohexaploid, like wheat, three different sets are represented.

Homoeologous, as applied to chromosomes, homologous in part (see Huskins, 1941).

Idiogram, a diagram showing the relative lengths and centromere positions of the different chromosomes of an organism.

Isochromosome, a chromosome with identical arms. Herein frequently shortened to "iso." Iso-IV = an isochromosome for one arm of chromosome IV.

Lemma, the flowering glume, which, together with the palea, encloses the individual flower of grasses.

Misdivision, crosswise instead of longitudinal division of a centromere. Only known to affect univalent chromosomes. May occur at either first or second division of meiosis. Gives rise to isochromosomes and telocentrics.

Mono-isosome, an isochromosome present in single dose.

Monosome, a chromosome present in single dose. Mono-IV = either monosome IV (*i. e.,* chromosome IV present in single dose) or monosomic IV (*i. e.,* a plant which carries monosome IV).

Monotelosome, a telocentric chromosome present in single dose.

Nullisome, a chromosome altogether lacking. Nulli-IV = either the deficiency for chromosome IV, or a plant nullisomic for chromosome IV.

Polyploid, an individual or species having more than twice the basic number of chromosomes.

Telocentric chromosome, a chromosome with only one arm and hence a terminal centromere. Herein frequently shortened to "telo."

Tetrasome, a chromosome present in four doses. Tetra-IV = either the tetrasome involving chromosome IV or a plant carrying tetrasome IV.

Triploid, an individual having each chromosome present in triplicate. Also used to designate individuals with three chromosome sets which are not necessarily homologous, as in hybrids between tetraploid and diploid species of wheat. These hybrids have two more or less homologous sets and one with no homologue.

Trisome, a chromosome present in three doses. Tri-IV = either trisome-IV or trisomic-IV.

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