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Mutants And Linkage Studies In *Triticum monococcum* and *T. aegilopoides*

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INTRODUCTION

As stated in an earlier publication (Smith, 1936) genetic and cytological studies of *Triticum monococcum* and *T. aegilopoides* were begun in order to lay a foundation of knowledge in these non-polyploid species as a basis for later studies of the effects of polyploidy in existing polyploid species of *Triticum* and in artificially induced amphidiploid hybrids. The present report presents a somewhat fuller, though still brief, description of a larger number of mutants and adds considerably to the linkage information in the previous publication.

There are fewer varieties of einkorn than of the tetraploid and hexaploid species of wheat and there are not enough clear-cut genetic differences for a genetic analysis of the species. X-rays, however, are a ready means of producing heritable variations. From among about 400 mutants found in irradiated material over 80 viable mutants have been saved. The lethals (white and yellow seedlings or other inviable types) and types poorly separable from normal have been discarded.

All the mutations from X-rayed material which have been tested behave as recessives except two (not described) which are possibly cytoplasmic. Fifty-six of the viable mutants are here described. Crosses and comparisons between similar types have made it reasonably certain that no duplicates are included.

The name given a mutant is descriptive of one of its chief characteristics. Mutants which are indistinguishable or separable only with difficulty in segregating populations have been given the same name, with numerals to designate the ones proven not to be duplicates and letters for those not tested. The suffix ''ex'' has been used in the designation of chlorophyll variants which turn green in later growth, types termed ''virescent,'' ''viridis,'' or ''alboviridis'' by others. For example, ''creamex'' indicates a mutant which is cream colored as a seedling but changes to normal green in later development.

The descriptions are brief and mention only the chief similarities and dissimilarities of the mutants. To describe the individual characteristics and their modifications due to changes in environment, particularly in temperature, would require tedious detail, although these minor variations are helpful in classifying the mutants.

Only nine of the genes listed (*B, ba-1, F, g, Gp, P-1, P-2, sg,* and *T*) were found in untreated material. The source of each of these is indicated in the descriptions. All except *sg* are factors which differentiate the existing forms of einkorn and occur in other varieties than those mentioned in this paper. For a recent taxonomic treatment of the varieties of einkorn, see Stranski (1935).

MATERIALS AND METHODS

Dormant seeds of *Triticum monococcum* vars. *vulgare* and *flavescens* were subjected to X-ray treatment of 12,500 *r* units. The X-ray apparatus was operated at 140 K. V. P., 4 m. a. tube current. The seeds, in a single layer, were exposed to unfiltered radiation at 12 inches distance for 97 minutes. Following the method described by Stadler (1930) the irradiated seeds were planted in the field, and the mutants selected in progeny tests of individual heads of the resulting plants.

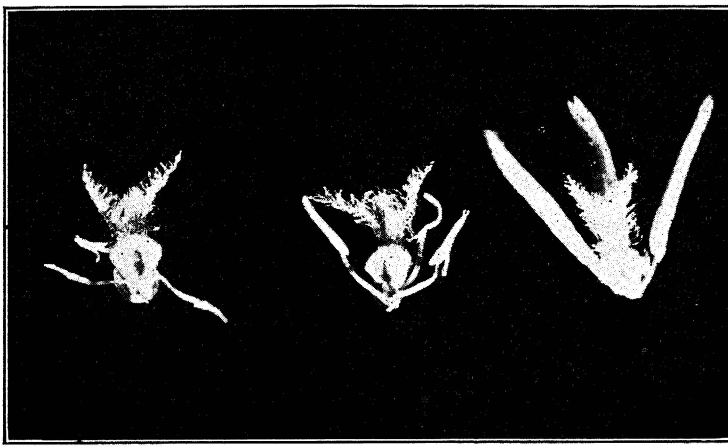
Cytological observations of pollen mother cells and microspores were made on aceto-carmine smear preparations. Anthers which were used had been fixed in the spike in Carnoy's or Farmer's fluid for one to several days. Some preparations were made permanent following the method described by McClintock (1928).

Aceto-carmine smears of root tips gave more reliable counts of chromosomes than did sections. About 1 mm. of the root tip was placed on a slide and smeared in a drop of aceto-carmine with a spear-point needle. The mount was covered and heated over an alcohol lamp. Individual cells were flattened by applying pressure with the point of a dissecting needle while the cell was being observed under the low power of the microscope. Usually the number of chromosomes could be accurately determined in several cells of each tip. Root tips were also sectioned following the method of Randolph (1935).

Photomicrographs were taken with a Leitz Makam camera.

ALPHABETICAL LIST OF GENES AND BRIEF DESCRIPTION OF MUTANTS

*an-1*______Antherless-1 (Fig. 1). Anthers apparently cease development before meiosis is completed. Pachytene is last stage observed. At flowering, anthers still rudimentary in size. Ovules fertile. Classification and viability good.



a b c

Fig. 1.—Antherless mutants: a, sexual organs from antherless–1; b, antherless–2; c, a normal plant. In antherless–1 meiosis is not completed. The anthers are smaller in this mutant than in antherless–2, where meiosis proceeds apparently normally.

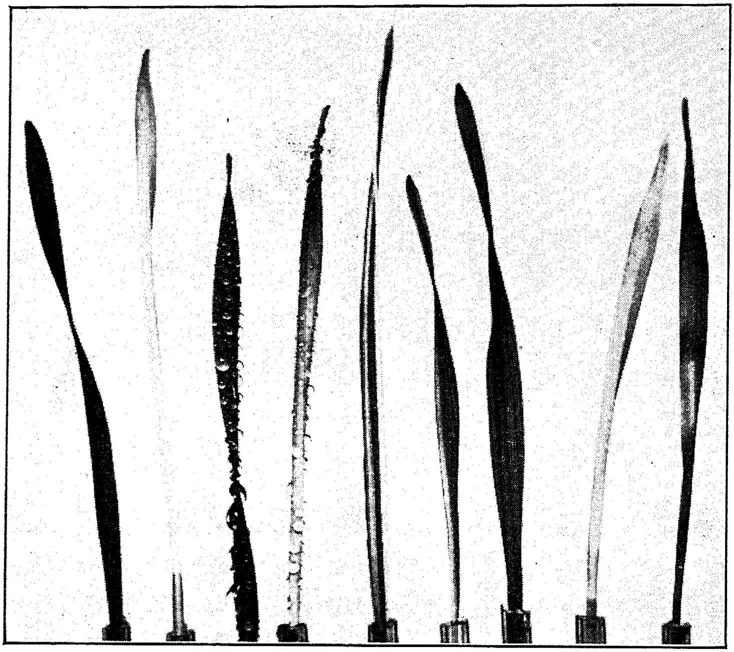
*an-2*______Antherless-2 (Fig. 1). Anthers cease development shortly after meiosis. At flowering, anthers slightly larger than in antherless-1. Ovules fertile. Classification and viability good.

*ar-a*______Argentia-a (*ar*)*. Seedlings have longitudinal white stripes which are somewhat variable in width. Some seedlings white. Older plants normal green with streaking often noticeable on glumes and necks of emerging heads. Classification (in cool temperatures) good. Viability fair.

*ar-b*______Argentia-b (Fig. 2). Similar to argentia-a in seedling stage, though a more conspicuous mutant. Older plants have distinct white stripes.

*In revising and adding to the list of mutants already published (Smith, 1936) some changes in names have been made. These changes are indicated by giving in parenthesis following the name of the mutant the gene symbol previously applied.

*ar-c*______Argentia-c. Similar to argentia-a in seedling stage. Sheaths and culms of older plants argentia to almost white. Some fine, white stripes on older leaves. Classification and viability good.



a b c d e f g h i

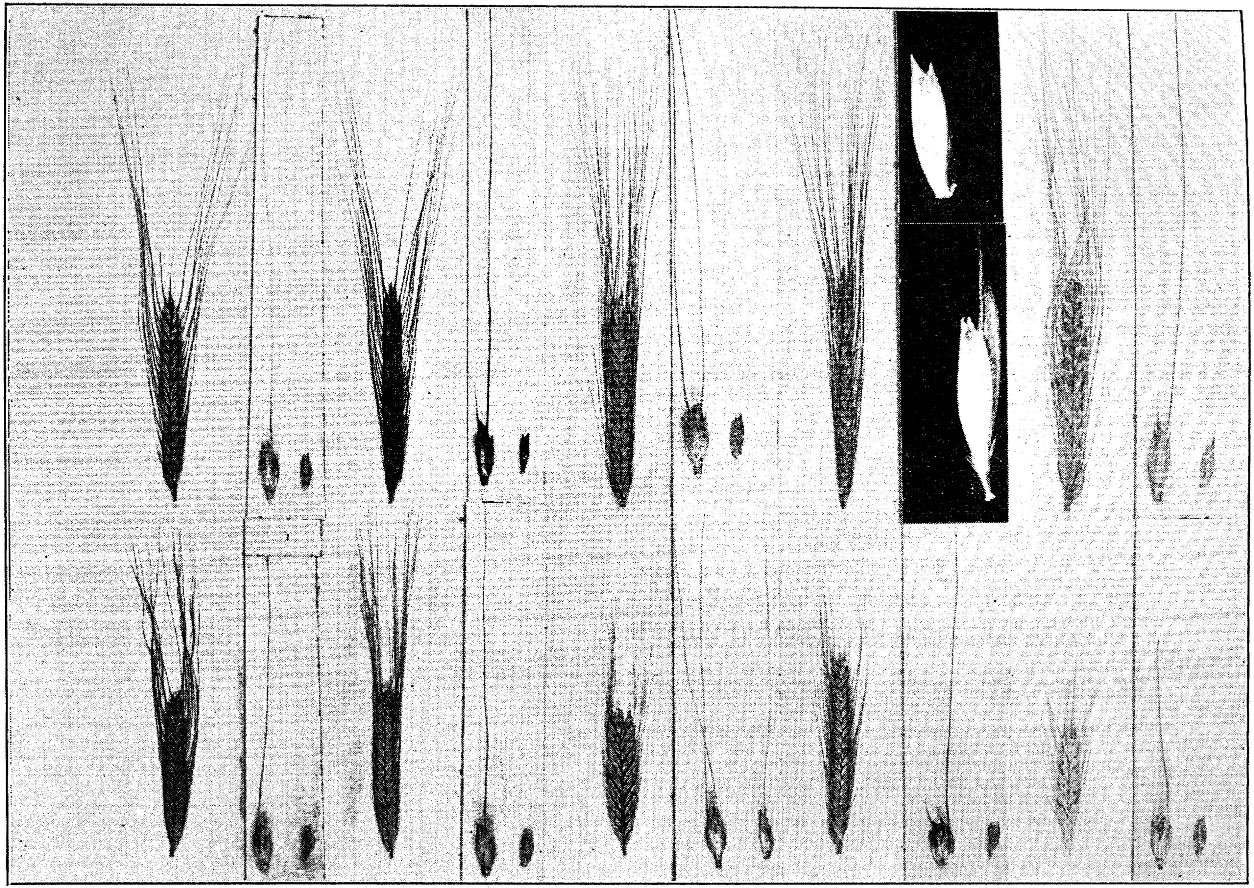
Fig. 2.—Seedling mutants; a, normal; b, creamex–1; c, glossy–1; d, glossy creamex; e, argentia-b; f, japonica; g, jadestripe; h, yellow; i, yellow zoned. c and d had been sprayed with water.

*B*________Black (Fig. 3). Pigment in the mature spike, causing the head to appear black. Dominant factor occurs in *T. aegilopoides* vars. *baidaricum, stramineonigrum,* and *pancici;* recessive in *T. monococcum* vars. *hornemanni, vulgare, pseudo-vulgare, flavescens,* and *laetissimum.* Classification fair. Viability normal.

*ba-a*______Biaristate-a. A well developed awn on the lemma of each of the two florets of a spikelet. Present in *T. aegilopoides* var. *baidaricum.* Classification fair. Viability good.

*ba-b*______Biaristate-b (ba_1) (Fig. 3). Similar to *ba-a.*

*c-1*_______Compact-1 (Fig. 3). Rachillae shortened. Heads about one-third shorter than normal heads with the same num-



a b c d e
f g h i j

Fig. 3.—Heads, spikelets, and outer glumes of head types. a, normal; b, black; c, biaristate–b; d, glume pubescence; e, glume toothed; f, compact–1; g, compact–2; h, glume awned; i, short glume; j, wiry.

ber of spikelets. Mature plants also somewhat dwarfish with thick, brittle culms. Classification and viability good.

c-2.......Compact-2 (Fig. 3). Similar to compact-1.

cx-1......Creamex-1 (*cx*) (Fig. 2). Seedlings virescent cream. Older leaves normal green or occasionally show yellow green streaks. Readily classifiable to near maturity. Viability fair.

cx-2......Creamex-2 (*px*). Similar to creamex-1, except changing to normal green more quickly in high temperatures. Classification and viability good.

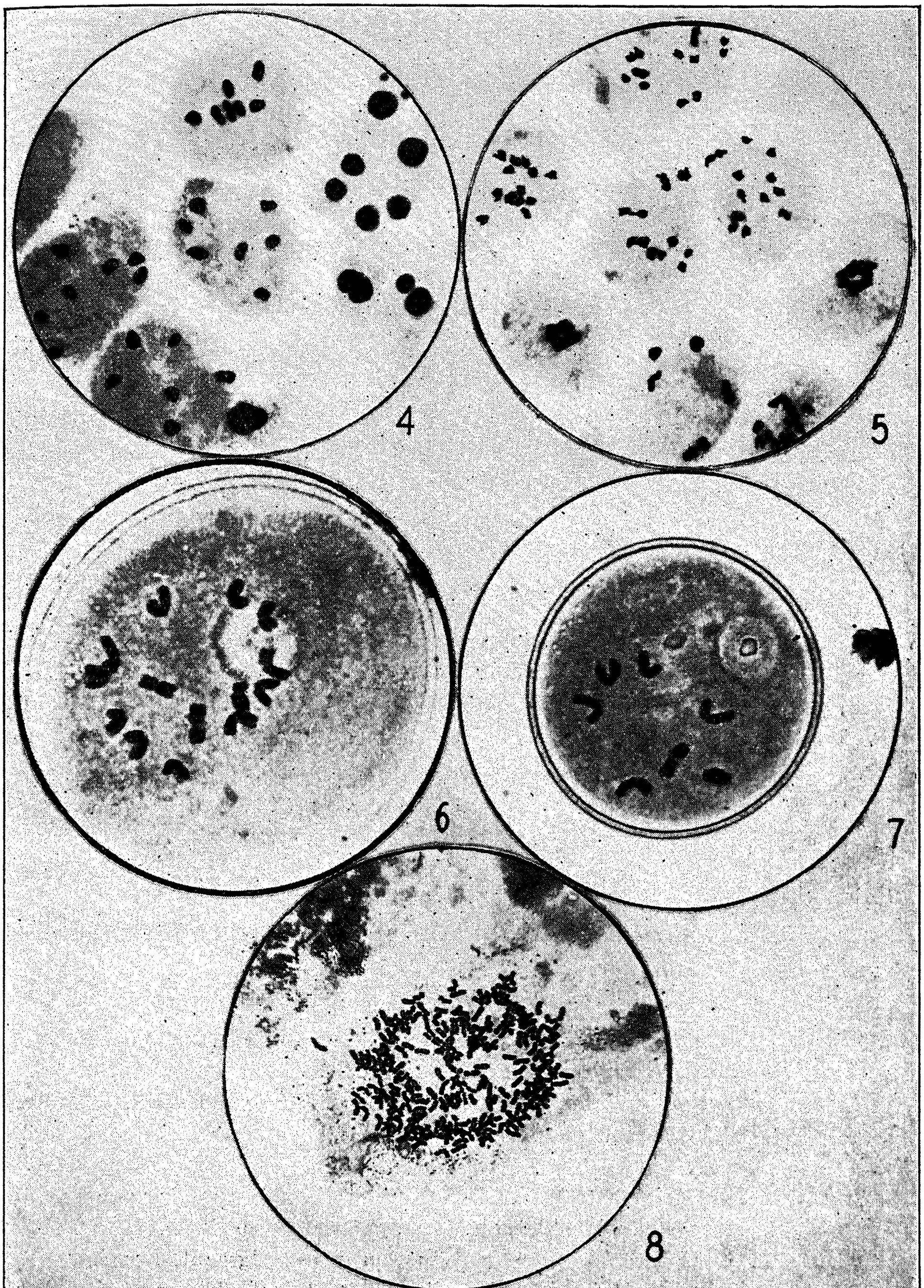
cx-3......Creamex-3. Seedlings and young leaves of older plants virescent cream, changing to light or normal green. Classification and viability good.

ds........Diploid spores (Figs. 4 to 8). Reductional division frequently fails to occur and two diploid, instead of four haploid, microspores are formed. Occasionally microspores with other than 7 or 14 chromosomes are produced. Fertility about one-third, height about three-fourths that of normal plants. Progeny consist of three types: (1) Diploids with regular meiosis (presumably resulting from outcrosses); (2) Diploids which are *ds ds;* (3) Small, thick-leaved plants which die in the seedling stage. These plants are most numerous and have characteristically 28 chromosomes, though the number varies (apparently in the main geometrically) in different cells of the root tip up to as many as about 224 (Fig. 8). Classification (macro-and microscopically) and viability good.

e-1.......Early-1. Growth period shortened about three weeks in field and considerably more in the fall greenhouse crop, where *e-1 e-1* plants head in about two months while plants of the parent variety (*T. monococcum* var. *vulgare*) require about five months to reach the heading stage under similar conditions. Classification and viability good.

e-2.......Early-2. Similar to early-1, but more vigorous and about one to two weeks later in the field or greenhouse. Classification good, except in late spring plantings. Viability good.

Figures 4 to 8.—Diploid Spores: Fig. 4. Left, four pollen mother cells at first metaphase. At right, tapetal cells. x 500. Fig. 5. Several pollen mother cells from metaphase to telophase showing that, in some cells, all the chromosomes gather into one group at telophase. x 500. Fig. 6. Diploid spore. x 1050. Fig. 7. Haploid spore from same anther as Fig. 6. x 1050. Fig. 8. Root tip cell from an offspring of *ds ds* plant. There are about 224 chromosomes in this cell. x 450.


4
5
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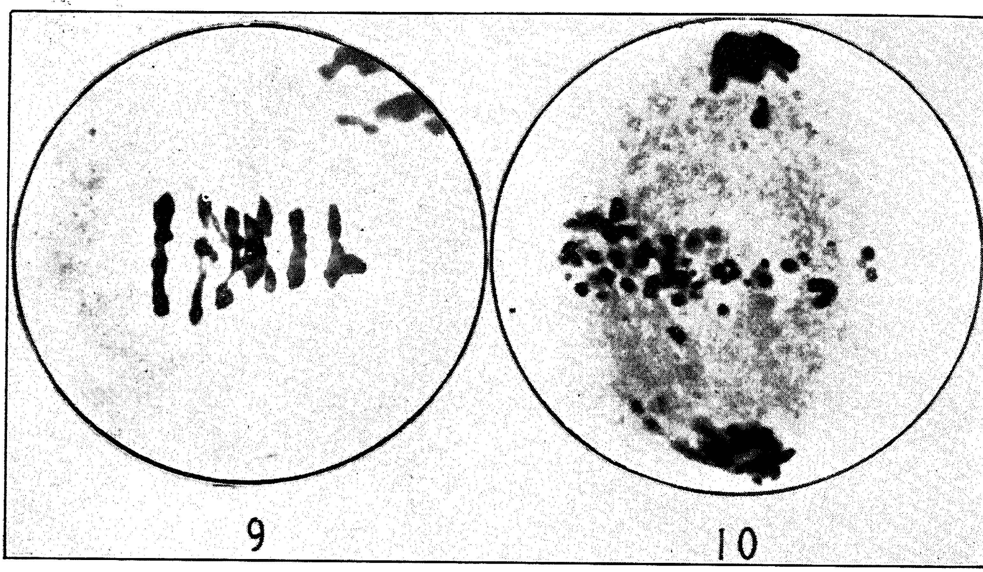
7
8

F--------Fragile. Head fragile, rachis disarticulating at maturity. Dominant factor present in varieties of *T. aegilopoides* mentioned under *B*. Classification difficult.

fr--------Fragmentation (Figs. 9 and 10). First meiotic metaphase in pollen mother cells more or less normal with only occasional chromatin fragments present. At first anaphase several to over 70 fragments observed. Chromatin bridges common, particularly at second anaphase. Micronuclei and microcytes numerous. No division occurs in the microspores. All pollen grains devoid of starch. Ovules fertile. Classification and viability good.



9 10

Figures 9 and 10.—Fragmentation: Fig. 9. First metaphase. Fig. 10. First telophase.

fs-a------Finestripe-a (*fs*). Fine, white, longitudinal stripes on seedlings and mature plants in cool temperatures. Classification good at low temperatures to near maturity. In high temperatures striping is reduced or absent. Viability good.

fs-b------Finestripe-b (*si*). Similar to finestripe-a in seedling stage. More white in older plants. Somewhat less viable.

g--------Green base. Absence or reduction of red pigment, especially apparent in the coleoptile and first leaf. The recessive *g* occurs in *T. monococcum* vars. *flavescens* and *laetissimum*. In low temperatures *g g* seedlings develop red color; in high temperatures *G G* or *G g* seedlings are non-red base. Classification good at 50° to 70° F. Viability normal.

ga------- Glume awned (Fig. 3). Awn on both outer glumes in addition to awn on lemma. Awn on lemma reduced. The glumes are also softer and the seeds less tightly enclosed, making shelling easier. Classification and viability good.

gl-1------ Glossy-1 (Fig. 2). Leaves of young seedlings dark green and with glossy surfaces to which water, when sprayed on, adheres in fine droplets. Classification and viability good.

gl-2------ Glossy-2. Similar to glossy-1.

glx------- Glossy creamex (Fig. 2). Seedlings both virescent and glossy. These two characteristics may be due to different genes rather than to two effects of the same gene, but if this is true, the genes are quite closely linked as no crossover was found among 910 F_2 individuals from coupling crosses. Classification good. Viability poor to fair in greenhouse; inviable in field.

go------- Golden. Seedlings normal green. Older plants light yellow green. Classification usually good near maturity. Viability good.

Gp------- Glume pubescence (*Gs*) (Fig. 3). Fine pubescence on glumes. Occurs in *T. aegilopoides* var. *stramineonigrum*. Classification and viability good.

gt------- Glume toothed (Fig. 3). Tooth on outer glumes 3 to 4 times normal length. Entire plant coarse. Fertility reduced. Classification and viability good.

gv------- Green veins. Midribs and veins of leaves conspicuously darker green than intervascular spaces. Classification good. Inviable in field, poor in greenhouse.

j--------- Japonica (Fig. 2). Seedling and mature plant leaves have narrow to broad, yellow green stripes. Classification good. Viability fair in greenhouse; poor in field.

js-------- Jadestripe (Fig. 2). Similar to green veins except plants vigorous and difference in color between the veins and intervascular spaces not so marked. Classification good in first leaf over a wide range of temperatures, more difficult later. Viability good.

lg-------- Light green (*cg*). Seedlings and older plants light green. Older leaves develop necrotic patches. Classification and viability fair.

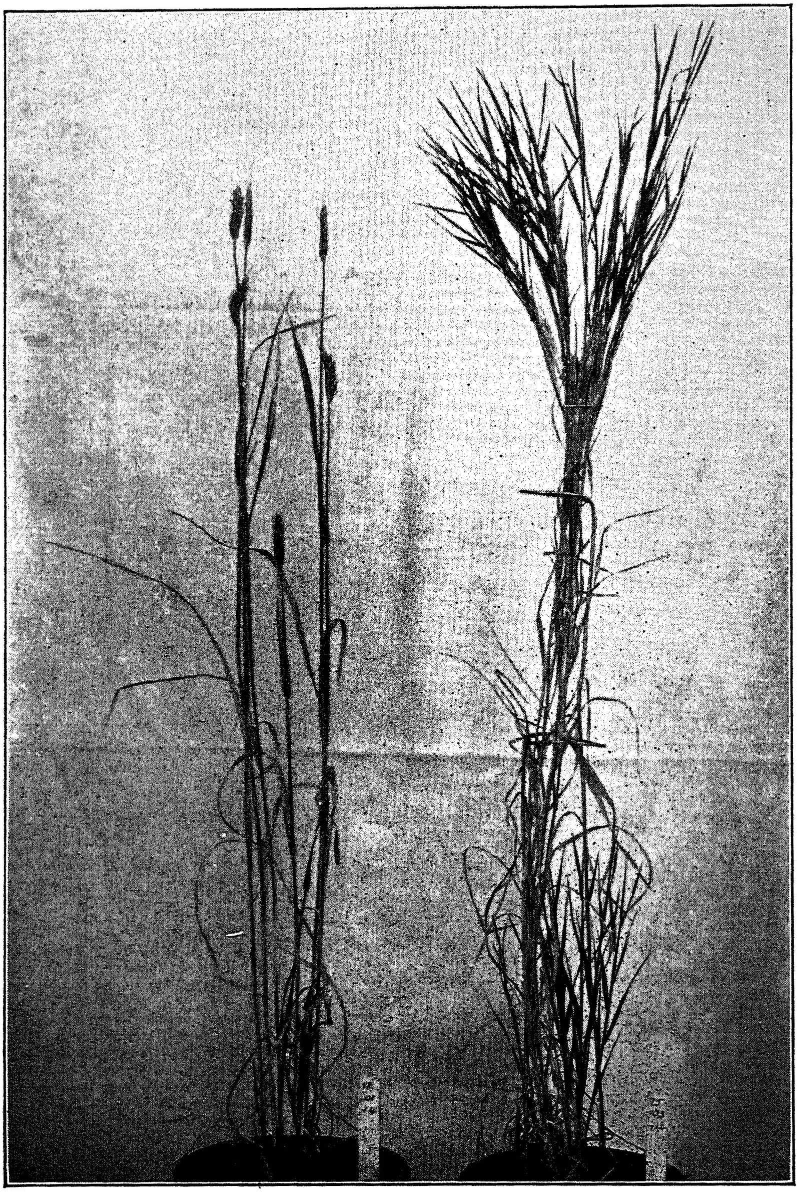


Fig. 11.—Many internodes. A many-internode plant (right) and normal for comparison. Above the top wire support on the *mi mi* plant are heads containing several seeds. The surmounting flare of potentially fruiting shoots arose from the nodes just below the heads.

ls........ Light stripe. Seedlings and older plants have light yellow green or virescent yellow green stripes. Classification fair. Viability good.

lx........ Lightex (*pa*). First leaf distinctly light green on emergence. Later all leaves indistinctly pale green or normal. Classification good on first or second day of emergence (longer in cool temperatures). Viability good.

ma....... Maple. Seedlings and young tillers normal green. Older leaves become yellow green. Classification near maturity good. Viability good.

mi....... Many internodes (Fig. 11). Internodes short and increased in number. Leaves also somewhat narrow and dainty. Seed production low in greenhouse. Homozygous *mi mi* plants rarely head in field. Classification good from late seedling stage to maturity. Viability good.

pa-a...... Pollen abortion-a. Meiosis normal but mature pollen devoid of starch. Ovules fertile. Classification and viability good.

pa-b...... Pollen abortion-b. Similar to pollen abortion-a.

pa-c...... Pollen abortion-c. Similar to pollen abortion-a, except some mature microspores occasionally contain starch.

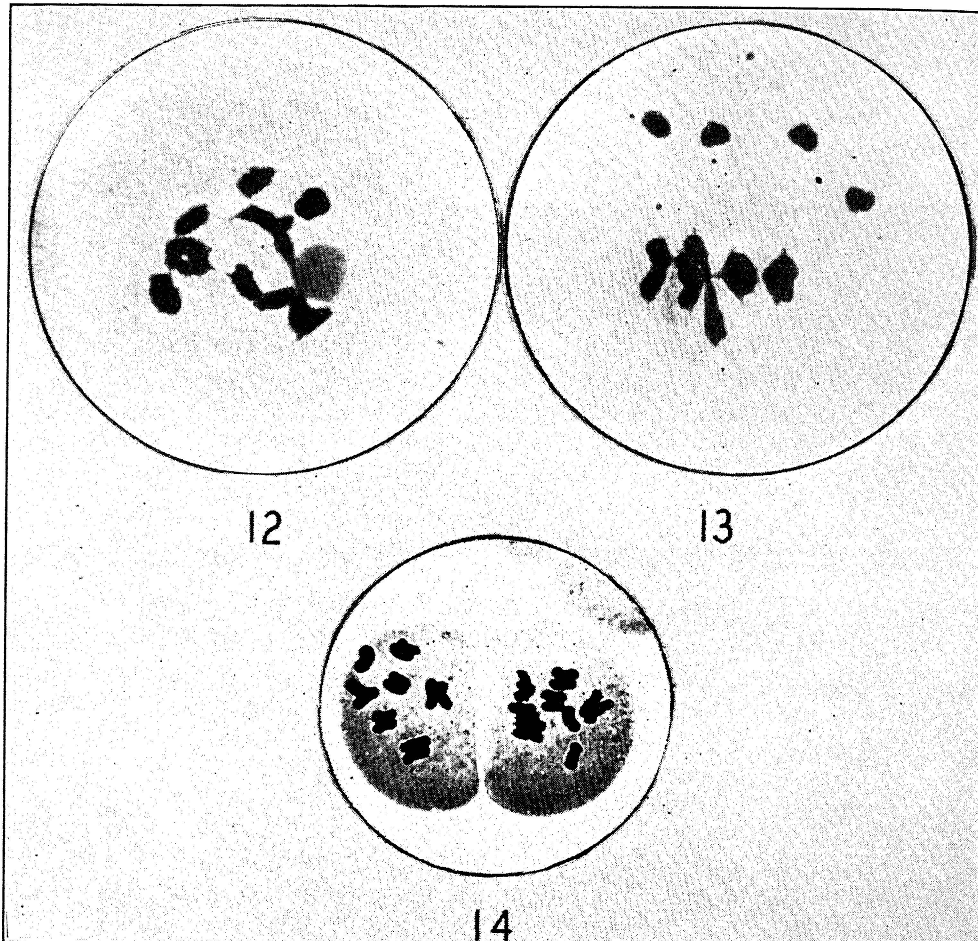
P-1 P-2... Pubescence (S_1S_2). Complementary factors for pubescence on leaves. Pubescence best developed in varieties of *T. aegilopoides*. Classification variable, probably due to modifying factors. Viability good.

pd....... Prolonged diakinesis (Figs. 12-14). Diakinesis in pollen mother cells prolonged and univalents common. No division occurs in the microspores. Mature pollen devoid of starch. Ovules fertile. Near maturity in field *pd pd* plants appear glossy. Classification and viability good.

pu-1..... Partial univalence-1 (Fig. 15). Number of bivalents varies in different pollen mother cells and many pairs attached at only one end. Number of chromosomes in microspores variable. Fertility low, even when pollinated by pollen from a normal plant. Some off-spring normal at meiosis (from outcrosses?); some *pu-1 pu-1;* some trisomic. Classification and viability good.

pu-2...... Partial univalence-2. Similar to partial univalence-1.

pu-3..... Partial univalence-3. Similar to partial univalence-1 at meiosis, though perhaps less abnormal, i. e., fewer univalents. Affected plants more fertile and most of progeny *pu-3 pu-3*.



Figures 12 to 14.—Prolonged Diakinesis: Fig. 12. Diakinesis. x 1050. Fig. 13. First metaphase. x 1050. Fig. 14. Second metaphase. x 850. The chromosomes are unusually condensed and univalents are common in this type.

sg------- Short glume (Fig. 3). Outer glumes shortened. Awns and glume tooth also reduced in length. Plants somewhat dwarfish. Found in an untreated population of *T. monococcum* var. *flavescens*. Classification at emergence fair, at heading good. Viability good.

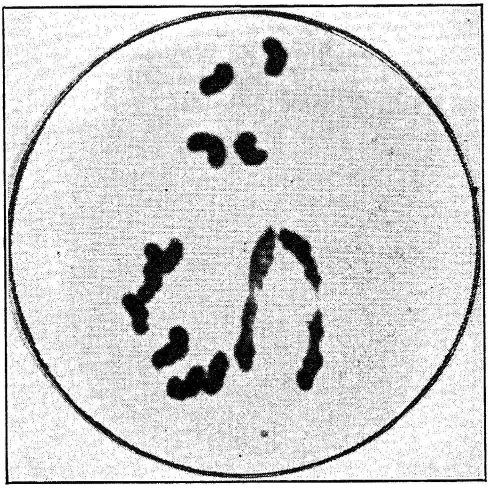
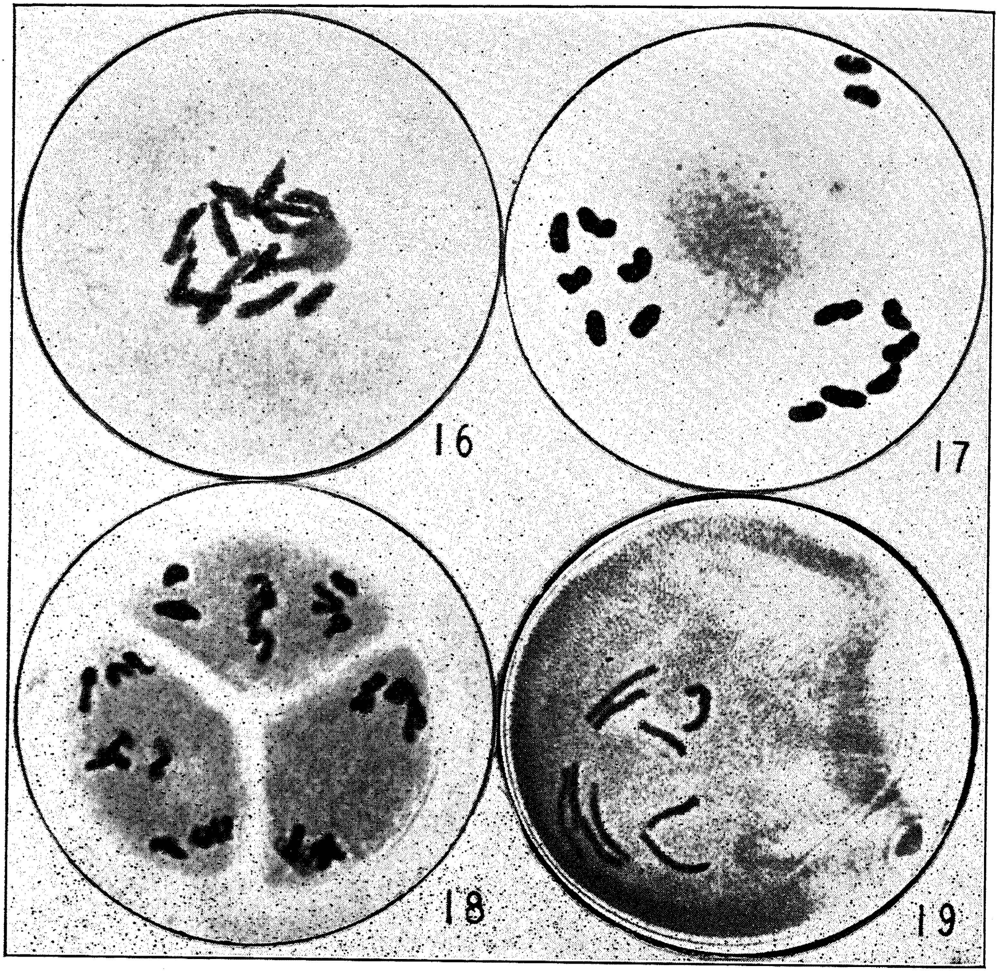


Fig. 15.—Partial univalence-1. First meiotic metaphase showing two pairs and ten univalents. The number of pairs is highly variable. Other stages are similar to those shown for "univalence" (Figs. 16 to 19) except in frequency of abnormalities. x 1050.

sk------- Streak. Young seedling leaves usually normal green, though some fine white streaks may be present. Near base of 3rd or 4th and later leaves, particularly near the midrib and on the sheaths, find white streaks are present. Classification at about 5th leaf stage and later good. Viability good.

T--------Tuft. Tuft of hairs on rachilla at base of spikelet. Especially well developed in certain varieties of *T. aegilopoides*, though not entirely absent in varieties of *T. monococcum*. Classification variable, often poor in F_2. Viability normal.

un-1----- Univalence-1 (Figs. 16-19). No bivalents at diakinesis or first metaphase in pollen mother cells. Extra cells and micronuclei common at quartet stage. Most microspores have no mitotic division and number of chromosomes variable among those that do. Few pollen grains contain starch. Fertility low, even when pollinated with pollen from normal plants. Classification and viability good.



Figures 16 to 19.—Univalence: Fig. 16. Diakinesis, showing all univalents. Fig. 17. First anaphase, showing chromosomes in three groups. Fig. 18. Second anaphase in three daughter cells resulting from the first division. There are three chromosomes lagging on the spindle of each of two of the cells. Split halves of three of the univalents presumably separated in the first division. Fig. 19. Microspore with 10 chromosomes.

un-2 ----- Univalence-2. Similar to univalence-1, except plants are also distinguishable macroscopically by a lax head, long tooth on outer glume, and other characteristic modifications in morphology.

wi ------- Wiry (Fig. 20). Leaves of plants a few weeks old or older narrow and stiff. Homozygous *wi wi* plants rarely head in field, fairly fertile in greenhouse. Classification and viability good.

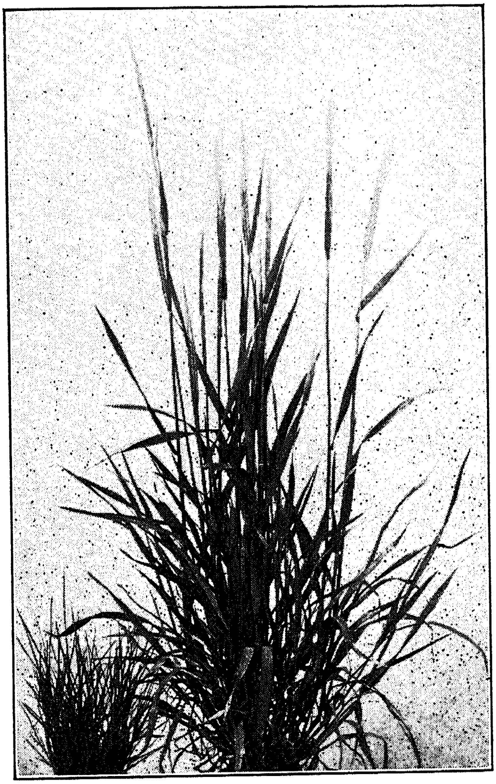


Fig. 20.—Wiry. A "wiry" plant (left) and a normal sib. This mutant usually does not head in the field, but is fairly fertile in the greenhouse.

y ------- Yellow (Fig. 2). Plants conspicuously yellowish from emergence to maturity. Classification good. Viability fair in greenhouse; poor in field.

yg ------ Yellow green. Plants yellow green from early seedling stage to maturity. Less yellow than *y y*. Classification and viability good.

yx-1 ----- Yellowex-1 (lx_1). A virescent yellow green. Distinguishable from emergence of first leaf to near maturity. Classification good. Viability poor in field, fairly good in greenhouse.

yx-2 ----- Yellowex-2 (*vn*). Similar to yellowex-1, except plants more vigorous.

yz ------- Yellow zoned (Fig. 2). Seedling leaves have transverse yellow green bands. Older plants sometimes yellow green. Classification good. Viability fair.

LINKAGE STUDIES

A considerable number of crosses between the mutants described above have been made and 106 combinations have been sufficiently tested in F_2, and a few in F_3, to indicate the presence or absence of linkage. These combinations are summarized in Figure 21.

Nine pairs of factors showed strong linkage. The data from populations segregating these factor pairs are presented in Tables 1 to 5. In calculating the crossover values the formulae of Immer (1930, 1934) were used. Where no crossover was observed a crossover value is enclosed in parentheses following the observed percentage with a "$<$" symbol which represents the value that would have been obtained had a single crossover been found.

In determining the genotypes of F_2 plants a progeny test of between 20 and 50 F_3 individuals was grown.

Four combinations of factor pairs gave no evidence of crossing over. One of these combinations involves two dominants, black head color and glume pubescence, which occur together in *T. aegilopoides* var. *stramineonigrum* and might, therefore, be due to multiple effects of the same gene. The two characters occur separately, however, in *T. monococcum* var. *hornemanni* (pubescence limited to margin of the lemma) and *T. aegilopoides* var. *baidaricum*, though they are linked (Table 5 RS), which suggests that two genes are involved. The other three combinations involve recessives which are presumably closely linked genes rather than alleles, since the F_1 hybrids are normal.

The high proportion of close linkages may be merely accidental or it may be that the factors arose in regions where crossing over is low, as near the spindle fiber regions in *Drosophila* (Beadle, 1932; Offerman and Muller, 1932; Sturtevant and Beadle, 1936; et al.) or in regions which are especially mutable. Since eight of the nine linkages involve genes found in heavily irradiated material, gross chromosomal changes, such as inversions, reciprocal translocations, etc. may have altered the normal linkage relations.

The linkage data are presented graphically in a linkage map in Figure 22. Since the data are rather limited, they should be considered as indicating only roughly the frequency of crossing over between the factor pairs. One or more genes from each group have been tested with one or more genes from each of the other four groups (Figure 21) and have shown independent inheritance (the apparent linkage between *fs-a* and *j* (35 ± 6) is of doubtful significance since *c-1* and *j* were closely linked but *c-1* and *fs-a* were unlinked in the same populations), but since the crossover intervals involved are short, some of the groups may be on the same chromosome.

ar-a	B	c-1	c-2	cx-1	cx-2	cx-3	e-1	e-2	fs-a	g	ga	gl-1	gl-2	glx	Gp	j	js	lg	lx	sg	wi	y	yg	yx-1	yx-2
	.....	.....	.....	....	*54±5*	.....	.....	*41±5*	*47±6*	*51±2*	.....	*50±3*	.....	.....	.....	.....	.....	.....	*60±5*	*50±4*	.....	*46±2*	*50±3*	*46±4*	*44±6*
ar-a	.....	0	.....	.....	.....	.....	.....	44±5	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
		.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	B	.....	.....	.....	.....	.....	.....	51±4	.....	42±3	.....	.....	.....	.....	0	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
		.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
			.....	.....	.....	.....	*51±2*	*44±6*	.....	*49±8*	*47±4*	*51±7*	.....	.....	.....	.....	*54±6*	.....	*59±4*	*47±4*	.....	*56±3*	*53±3*	*45±3*	.....
		c-1	.....	.....	.....	.....	49±4	50±2	53±2	49±3	.....	.....	.....	.....	52±3	0	.....	.....	.....	.....	.....	53±5	59±4	.....	.....
			.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
				.....	.....	.....	.....	.....	.....	.....	.....	*49±7*	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
			c-2	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
				.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
					.....	.....	.....	.....	*55±4*	.....	.....	.....	.....	*50±5*	.....	.....	.....	.....	.....	.....	.....	.....	*57±5*	*48±6*	.....
				cx-1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	0	.....	.....	.....
					.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
						.....	.....	.....	.....	.....	.....	.....	*60±5*	.....	.....	.....	*47±6*	.....	.....	.....	.....	*56±5*	*47±4*	.....	.....
					cx-2	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
						.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
							.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	*49±5*	.....
						cx-3	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
							.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
								.....	*39±4*	.....	.....	.....	.....	.....	*51±3*	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
							e-1	.....	59±4	.....	.....	.....	.....	.....	54±6	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
								.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
									51±5	*50±4*	*59±4*	*45±3*	*46±5*	.....	*52±3*	.....	*51±4*	.....	*45±6*	*45±4*	.....	.....	.....	*45±2*	.....
								e-2	54±4	48±3	.....	.....	.....	.....	51±5	.....	.....	.....	.....	58±3	.....	.....	0	.....	.....
									.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	65±18	.....	.....	.....
										47±4	.....	.....	*56±5*	.....	.....	.....	*45±5*	*45±6*	*47±4*	*55±3*	.....	*51±3*	*55±4*	*51±2*	*51±7*
									fs-a	.....	.....	0	.....	.....	41±6	.....	.....	.....	.....	.....	0	.....	49±2	.....	.....
										.....	.....	.....	.....	.....	.....	35±6	.....	.....	.....	.....	.....	.....	.....	.....	.....
											.....	.....	.....	.....	*50±5*	.....	.....	.....	.....	.....	.....	*50±4*	*48±5*	*55±2*	.....
										g	.....	47±3	49±5	.....	45±2	.....	51±3	.....	.....	45±3	.....	49±3	44±4	57±5	.....
											.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
												.....	*46±7*	.....	.....	.....	.....	.....	.....	.....	.....	.....	*48±5*	.....	.....
											ga	.....	.....	.....	.....	.....	0	.....	.....	.....	.....	.....	.....	.....	.....
												.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
													.....	.....	.....	.....	*52±4*	.....	*51±5*	*56±6*	.....	*52±4*	*53±2*	*59±5*	.....
												gl-1	.....	.....	50±7	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
													.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....

	glx	Gp	j	js	lg	lx	sg	wi	y	yg	yx-1	yx-2
	.....	.....	.....	.....	.....	[illegible]	.....	.....	[illegible]	[illegible]	.....	.....
gl-2	.....	42±6	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
		.....	.....	.....	.....	.....	.....	.....	.....	.....	*50±5*	*46±4*
glx		.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
		.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
			.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Gp			.....	56±7	.....	.....	.....	.....	.....	.....	.....	.....
			.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
				.....	.....	.....	.....	.....	.....	.....	.....	.....
j				.....	.....	.....	.....	.....	.....	.....	.....	.....
				.....	.....	.....	.....	.....	.....	.....	.....	.....
					.....	.....	.....	.....	.....	*48±4*	.....	.....
js					.....	.....	.....	.....	0	.....	.....	.....
					.....	.....	.....	.....	.....	.....	.....	.....
						.....	.....	.....	.....	.....	.....	.....
lg						.....	.....	.....	.....	.....	.....	.....
						.....	.....	.....	.....	.....	.....	.....
							.....	.....	*60±4*	*48±4*	.....	.....
lx							.....	.....	.....	.....	.....	.....
							.....	.....	.....	.....	.....	.....
								.....	.....	*47±4*	*60±4*	.....
sg								.....	.....	.....	.....	.....
								.....	.....	.....	.....	.....
									49±6	*51±5*	*41±4*	*51±5*
wi									.....	.....	.....	.....
									.....	.....	.....	.....
										.....	*51±5*	*43±5*
y										.....	.....	.....
										47±9	.....	.....
											.....	.....
yg											.....	.....
											.....	.....
												.....
yx-1												.....
												.....
yx-2												

FIGURE 21.—A Chart Summarizing the Linkage Studies.

The figures are the crossover percentages with their standard errors. The top line in each combination is for F_2 repulsion; the second for coupling; and the bottom line for F_3 data. Several percentages deviate from 50% by more than two times the standard error but these are about equally distributed above and below that value. The "0"s indicate linkages. The data for these combinations are given in Tables 1 to 5.

TABLE 1.—Data on Crossing Over between Linked Factors *ar-a*, *c-1*, and *j*.

Genes X	Genes Y	Generation[1]	Constitution of Plants[2]						Total	Crossover Value (%)
Ar-a	C-1	F_2 RS	XY 376	Xy 169	xY 114	xy 3	.....	.....	662	16.5±3.8[3]
"	"	F_3 RS	.....	.....	.....	.....	XXyy 67	Xxyy 19	86	12.5±2.8
C-1	J	F_2 RS	XY 110	Xy 14	xY 54	xy 0	.....	.....	178	0 (<25.0±6.9[4])
"	"	F_3 RS	XX or XxYY 3		XX or XxYy 67		xxYY 18	xxYy 1	89	2.5±2.6[5]

1. RS Selfed progeny from a repulsion cross.
2. Phenotypes in F_2; genotypes in F_3 tests.
3. Standard error.
4. Obtained by assuming a single crossover.
5. Only the xY phenotypes were used in calculating these values.

TABLE 2.—Data on Crossing Over between Linked Factors *fs-a*, *gl-1*, and *wi*.

Genes X	Genes Y	Generation	Constitution of Plants								Total	Crossover Value (%)
Fs-a	Gl-1	F_2 RS	XY 546	Xy 234	xY 235	xy 1	.....	.....	.....	.....	1016	7.0±3.1
"	"	F_3 RS	XXYY 0	XXYy 10	XXyy 38	XxYY 13	XxYy 75	Xxyy 6	xxYY 28	xxYy 1	171	12.5±2.6[1]
Fs-a	Wi	F_2 RS	XY 463	Xy 212	xY 224	xy 8	.....	.....	.....	.....	907	19.0±3.2
"	"	F_3 RS	XXYY 0	XXYy 1	XXyy	XxYY 3	XxYy 24	Xxyy	xxYY 9	xxYy 0	37	7.5±3.7[1]

1. Only the XY phenotypes were used in obtaining these values.

TABLE 3.—Data on Crossing Over between Linked Factors *e-2* and *yg*.

Genes X	Genes Y	Generation	Constitution of Plants								Total	Crossover Value (%)
E-2	Yg	F_2 CS[1]	XY	Xy	xY	xy	.....	.....	.....	.....		20.0±2.9
			170	23	21	36	.....	.....	.....	.....	250	
"	"	F_2 RS	XY	Xy	xY	xy	.....	.....	.....	.....		7.0±3.3
			478	221	211	1	.....	.....	.....	.....	911	
"	"	F_3 RS	.....	.....	.....	.....	.....	.....	xxYY	xxYy		16.5±4.6
			.....	.....	.....	.....	.....	.....	33	13	46	

1. CS Selfed progeny from a coupling cross.

TABLE 4.—Data on Crossing Over between Linked Factors *cx-1*, *ga*, *js*, and *y*.

Genes X	Genes Y	Generation	Constitution of Plants								Total	Crossover Value (%)
Cx-1	Y	F_2 RS	XY	Xy	xY	xy	.....	.....	.....	.....		0 ($<7.5\pm4.1$)
			274	156	148	0	.....	.....	.....	.....	578	
"	"	F_3 RS	XXYY	XXYy	XXyy	XxYY	XxYy	.....	.....	.....		0 ($<1.5\pm1.6$[1])
			0	0	1	0	30	.....	.....	.....	31	
Ga	Js	F_2 RS	XY	Xy	xY	xy	.....	.....	.....	.....		0 ($<19.0\pm11.4$)
			31	22	18	0	.....	.....	.....	.....	71	
"	"	F_3 RS	XX or XxYY		XX or XxYy		Xxyy		xxYY	xxYy		0 ($<5.0\pm4.9$[2])
			0		31		.....		10	0	41	
Js	Y	F_2 RS	XY	Xy	xY	xy	.....	.....	.....	.....		0 ($<13.5\pm6.1$)
			141	56	63	0	.....	.....	.....	.....	260	
"	"	F_3 RS	XXYY	XXYy	XXyy	XxYY	XxYy	Xxyy	xxYY	xxYy		0 ($<0.6\pm0.6$[1])
			0	0	.....	0	82	.....	41	0	123	

1. Only the XY phenotypes were used in calculating these values.
2. Only the xY phenotypes were used in calculating these values.

TABLE 5.—Data on Crossing Over between Linked Factors *B* and *Gp*.

Genes X	Genes Y	Generation	Constitution of Plants				Total	Crossover Value (%)
B	Gp	F_2 RS	XY 100	Xy 52	xY 66	xy 2	220	16.5±6.5[1]
"	"	F_2 CS	XY 559	Xy 0	xY 0	xy 227	786	0 ($<$0.5±0.3)

1. *B* is often difficult to classify and there is some reason to doubt that two individuals were actually double recessives.

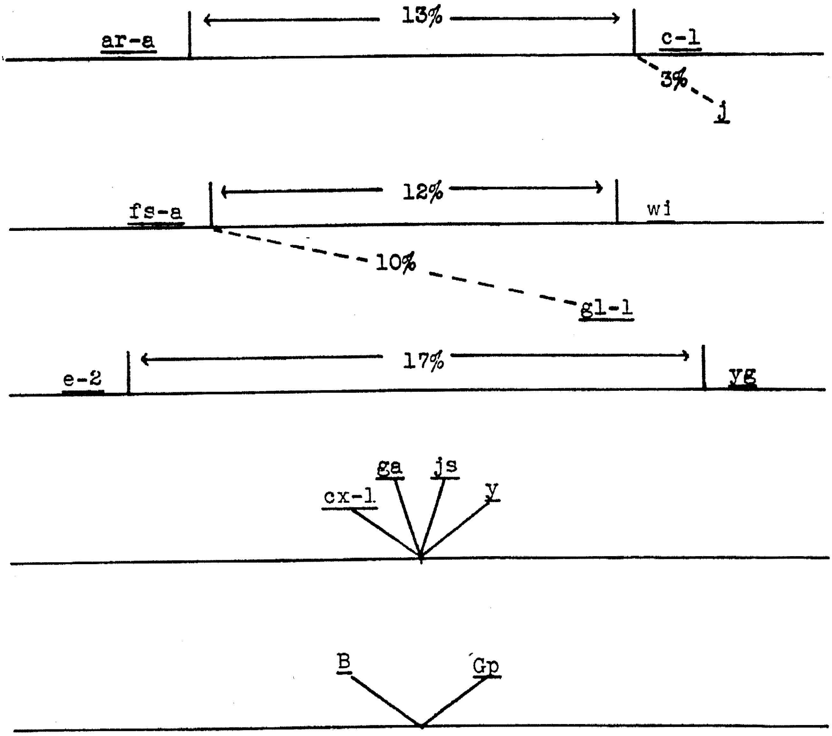


Fig. 22.—Linkage map. The graph indicates the factors which are known to be linked, and approximately their crossover distances apart.

SUMMARY

1. 56 Viable mutants (mainly from X-rayed material) are described.
2. 97 combinations of factors have indicated absence of linkage.
3. Nine pairs of factors are linked, four (involving six genes) closely, or completely.

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