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A STUDY OF SEMISTERILITY AND ITS LINKAGE RELATIONSHIPS IN TRANSLOCATION STOCKS OF BARLEY

by

Horace Marr Waddoups

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

PLANT BREEDING

1949

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Logan, Utah

Appreciation is expressed to

Dr. R. W. Woodward

who furnished the material for this study,

and

made many helpful suggestions during the

preparation of the manuscript.

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A STUDY OF SEMISTERILITY AND ITS LINKAGE RELATIONSHIPS IN TRANSLOCATION STOCKS OF BARLEY

INTRODUCTION

Barley (Hordium sp.) is the most important spring sown cereal crop in Utah, both in acreage and in yield of total digestible nutrients per unit area. It also rates high as a feed crop in the United States. For this reason it is important that varieties are available which are high in yield, high in quality, and disease resistant, along with other desirable characteristics. In order to work toward this end most efficiently, it is first necessary that the genetics of the barley plant be worked out.

Barley offers the plant breeders and geneticists a valuable material to use in the study of genetics. The fact that it has many easily distinguishable characters, that it is easy to grow large F_2 populations, and that it has a low chromosome number make it desirable for this type of study. That all interspecific crosses are fertile make it all the more desirable for the plant breeder.

This study is a by-product of the cereal breeding and improvement program being carried on at the Utah Experiment Station.

Recently the study of translocations induced by X-rays and other means has gained wide interests among plant breeders, geneticists, and cytologists alike. Translocations or interchanges consist of the exchange of segments of non-homologous chromosomes. As a result semi-sterility occurs in plants which are heterozygous for the interchange.

The objective of this study is to calculate any linkage which may be found in different crosses involving translocated stocks in barley

in order to determine which linkage groups are involved in the translocation; and to note any characters now linked as a result of a translocation which were not linked in normal barley stocks. The ratios and interactions which occur in any of the characters found in this study will be calculated.

REVIEW OF LITERATURE

According to Brink and Burnham (8), the first case of a structural change (interchange) found in the literature was reported by Bridges (1923) in Drosophila. Belling (5) reports a species of Stizolobium that when crossed with other species of the same genus gives rise to F_1 plants in which half of the pollen and embryo sac mother cells abort. He assumed that 2 genes (L) and (M) are necessary for gamete development and that they are located in non-homologous chromosomes. Belling reported that due to a translocation of segments containing (L) and (M) that half the gametes from the F_1 would contain either (L)(L) or (M)(M) and would be non-viable. Thus, he was first to report semisterility as being due to a translocation. This case was reported in 1914 but was not interpreted until 1925. There was 50 percent abortion observed in both pollen and ovules. The term semisterility seems to have originated with Belling who applied it to the phenomenon in Strizolobium (8, 9).

Brink (7) found the same condition in corn. He reported 1115 normal to 1190 semisterile pollen grains, and 1520 normal to 1154 aborted ovules. He suggested for an explanation of semisterility in maize that a portion of one chromosome has become attached to a member of a non-homologous pair. In this case it was assumed that all spores receiving the "disjoined" section in duplicate or lacking it altogether are abortive.

Morgan, Bridges, and Sturtevant (25) reported in 1925 that cases occur in Drosophila where part of a chromosome is attached to another homologous chromosome. According to Muller (26), the first case in which both genetic and cytological evidence of a translocation was combined in Drosophila was by Stern in 1926. In this case a portion

of the Y chromosome had become attached to the X chromosome.

In 1929 Brink and Burnham (8) found that reciprocal crosses between normal and semisterile maize plants give equal numbers of normal and semisterile offspring. Self-pollination of semisterile individuals likewise produced the same two classes in the same proportion.

Muller (27) reported on a translocation in Drosophila which was designated the "Star-Curly (S Cy) translocation". This translocation was reported to have arisen from a cross of irradiated Curly-winged males with normal females. Later tests showed that the second chromosome containing S and Cy was involved in a translocation with the third chromosome derived from the treated male. The S Cy translocation was later analyzed cytologically, and the cytological and genetic analyses presented by Painter and Muller (30).

Dobzhansky (17) reported finding four translocations involving the second and fourth chromosomes of male Drosophila treated by X-rays. He reported that the translocations manifest themselves by producing an apparent linkage of genes belonging to the second and to the fourth linkage groups. In each case a section of the second chromosome became broken off and reattached to the fourth chromosome. In another paper Dobzhansky (16) reported that most of the translocations described earlier in Drosophila were simple translocations, but later reciprocal translocations were found.

Burnham (10), who was then at Harvard University, reported on three different semisterile lines of corn. He designated them as semisteriles-1,-2, and-3. He reported an association of non-homologous chromosomes at meiosis with a group of four chromosomes plus eight bivalents in each of the three semisterile lines. However, at that

time there was not sufficient evidence to decide whether this was the result of segmental interchange or simple translocation.

In Burnham's study the combination of semisteriles-1 and-2 gave a new class which was somewhat more than 75 percent sterile, and in which two separate groups of four chromosomes occurred plus six bivalents. Neither of the two pairs involved in semisterile-2 was concerned in semisterile-1. The combination of semisteriles-1 and-3 gave a new class which was a little less than 75 percent sterile, and in which there was a group of six chromosomes plus seven bivalents. He concluded that one of the pairs involved in semisterile-3 was probably the same as was concerned in semisterile-1. Later, Burnham (11) and Brink and Cooper (9) obtained evidence to show that there was an interchange involving relatively large sections of the chromosomes. In these cases a ring of four chromosomes was formed at diakinesis. Disjunction of the four chromosomes at anaphase was such that approximately 50 percent of the spores were deficient for relatively large sections of the monoploid complement. This would account for the sterility in these types. In cases reported where one of the interchanged pieces was short, chain configerations were formed at diakinesis. If both pieces were very short, ten "pairs" might be formed regularly, giving no evidence that an interchange had occurred as in a case reported by Clarke and Anderson (15). This would account for genes in different linkage groups showing linkage without semisterility being involved. Brink and Cooper (9) and Anderson (2) found that half of the normal offspring from semisterile plants is of the standard normal type and the other half is of the translocation normal type, and when the two classes were crossed all the hybrids were semisterile.

This agrees with the findings of the other workers.

In 1934 Burnham (12) reported finding about 59 percent of aborted pollen in plants heterozygous for a translocation between chromosome 8 and 9 (previously referred to as semisterile-2) of maize. He also found a comparable degree of ovule abortion in such plants. Counts at diakinesis in plants heterozygous for T8-9 showed about 7 percent of chain configerations, the remainder being rings of four chromosomes. Plants homozygous for the interchange showed normal fertility. Anderson (4) presents data on linkage relations in nine translocations involving chromosome 8 in maize.

In 1940 Pellew (31) reported linkages based on F_2 data with translocation in Pisum. Later, Lamm (24) reported an interchange complex in Pisum in which he compared linkage in the F_2 progeny of a selfed translocation heterozygote with the corresponding data from a backcross progeny. It is of interest to note that Lamm observed the crossing over values are rather reduced in the translocation heterozygote when compared with the standard structural type. This reduction in crossing over occurred between two loci (St-B) near the point of interchange.

The first reciprocal translocation found in the literature in barley was reported by Smith (35) in which limited observations indicated that in about 60 percent of the pollen mother cells segregation of the chromosomes were disjunctional. Fertility was about 65 percent perfect in three ring-forming plants.

Burnham (14), now at Minnesota, has shown the naturally occurring semisterile-3 line was heterozygous for an interchange between chromosomes 1 and 7. Pollen counts on plants heterozygous for T1-7a averaged

48 percent. Homozygous stocks for the interchange had normally filled ears and normal pollen. In crosses with normals a ratio of 1 normal and 1 semisterile plant was observed as in the other cases reported earlier. It was found that a piece including approximately 84 percent of the long arm of chromosome 7 exchanged positions with a piece including about 60 percent of the longer arm of chromosome 1. The previously reported semisterile-1 line was found to be an interchange between chromosomes 1 and 2; therefore, the former assumption that semisterile-1 and-3 involved a common chromosome has been verified.

Anderson (1) found an interchange in maize following X-ray treatment. The interchanged chromosomes were identified as numbers 6 and 9. The chromosomes opened out to form a ring at diakinesis and the resulting plant was partially sterile. Like the other interchanges reported in maize, this one was viable in homozygous condition giving normal vigorous plants which are fully fertile. In another paper Anderson (2) reports that the spores which receive one normal and one interchanged chromosome are deficient for a portion of a chromosome and have a duplication for another portion so form abortive grains. He observed that crossovers may take place between an interchanged chromosome and its normal homolog at any point. Therefore, the interchange may be followed in linkage tests by means of the semisterility, which behaves in out-crosses like a dominant gene at the locus of the interchange in both linkage maps. In this paper Anderson describes the cytological examination as follows:

> Cytological examination shows a cross-shaped figure at mid-prophase with a change of partners at the cross or point of interchange. At all points homologs are paired as in normal chromosomes. The chromosomes begin separating at late pachytene or diplotene, continuing separation until

at diakinesis only the ends remain joined. By this stage the chromosomes have also shortened and thickened, giving the typical ring configerations characteristic of interchanges. At anaphase these rings separate or are pulled apart, two chromosomes going normally to each pole.

In 1947 Joachim (21) reported on the product method of calculating linkage from F_2 data involving semisterility and its application to a barley translocation. She made crosses with Smith's translocation A stock and calculated the linkages with semisterility. The translocation stock was found to have a ring of four chromosomes plus five pairs which is in agreement with Smith's findings. Semisterility was found to be linked with the character pair two-row vs. six-row (Vv) in linkage group I, the recombination value for F_2 data in repulsion by the product method being 7 $\pm$ 3.9 percent. The second linkage group involved was not identified. In Joachim's study semisterility showed independence with the following characters: black vs. white pericarp and lemma (Bb), hooded vs. awned (Kk), long vs. short haired rachilla (Ss), and covered vs. naked caryopsis (Nn).

Similar results have been reported in animals. Koller (22) reported three semisterile lines of mice with fertility from 30-50 percent. Cytological analysis showed that differences in fertility were correlated with corresponding differences in the frequencies of a non-disjunctional co-orientation of chromosomes in the ring of four.

As to the effect of X-rays upon the chromosomes, Muller and Painter (29) reported in 1929 that X-rays may definitely cause translocations. In Drosophila, translocations involving groups II and III have been the most numerous. The frequency of translocations following heavy irradiation by X-rays was found by Muller and Altenburg (28) to be surprisingly high. He found the percentage of breaks and reattachments to a non-homologous chromosome to be at least 7 percent in a

total of 883 fertile cultures derived from irradiated F_1 males.

Anderson (2) reports the frequency at which chromosomes in maize become involved in translocations following X-ray treatment is in close proportion to the lengths of the different chromosomes. The ratio of X-ray dose to neutron dose, required to produce an equivalent effect has been reported by Thoday and Lea (36). They found the ratio is not the same for several types of aberrations: 2.4 for chromatid breaks, 3.6 for isochromatid rejoins, 4.5 for chromosome breaks, and between 5 and 10 for interchanges.

The corn linkage studies with semisterility due to a reciprocal translocation as reviewed here have been based mostly on backcross data. In barley a plant which is normally self-fertilized, it is not feasible to make backcross studies due to the amount of labor that would be involved. Since semisterility in F_2 populations does not behave as a Mendelian character, special formulae are necessary for calculating the linkage intensities. A table to facilitate use of the product method in calculating the percentage of recombination from F_2 data involving semisterility and a simple inherited character pair has been worked out by Joachim (21). A column containing factors to facilitate calculation of the standard error is also given.

Joachim calculated the proportions of male and female gametes and the F_2 phenotypes as follows:

> In an F_2 linkage test involving a simply inherited character pair (Aa) and semisterility due to chromosomal interchange vs. normal (designated Bb) the Aa pair will segregate in a 3:1 ratio, while the Bb pair will segregate in a special 1:1 ratio of semisteriles (Bb) to normals, the normals being of two equally frequent types either standard (bb) or homozygous interchange (BB) normals. Assuming no difference in crossing over between the two sexes, p being the recombination value in repulsion, the four classes of male and female gametes for

repulsion (where semisterility entered the cross with the aa parent) will be:

AB	Ab	aB	ab
$\frac{p}{2}$	$\frac{1-p}{2}$	$\frac{1-p}{2}$	$\frac{p}{2}$,

and the frequencies of the F_2 phenotypes are as follows:

A Phenotypes		a Phenotypes	
Semisteriles	Normals	Semisteriles	Normals
$\frac{(2-2p+2p^2)}{4}$	$\frac{(1+2p-2p^2)}{4}$	$\frac{(2p-2p^2)}{4}$	$\frac{(1-2p+2p^2)}{4}$

As to the use of translocations in genetic studies in the future, Anderson (3) reports the following:

> Chromosomal interchanges or reciprocal translocations are excellent tools for the exploration of portions of chromosomes where no known genes are available. For most cases it is only necessary to cross any new or unplaced gene with the translocation stock, backcross with the new gene if recessive or with normal stock if dominant. Classification of the gene character under consideration and semisterility will give a direct linkage test with a known point on the chromosome.

The genetics and linkage studies of barley has been summarized by Robertson (32), Robertson, Wiebe, and Immer (33), Immer and Henderson (20), and Robertson, Wiebe, and Shands (34). The descriptions and symbols of the characters in the different linkage groups studied in this problem are presented in Table 1. The characters involved in this study are arranged in diagram form in Fig. 1. The average linkages between factors found in the above literature are given.

Table 1. Descriptions and symbols of the characters studied in the seven linkage groups.

Linkage Group	Description of Character	Symbol
I	Normal vs. long awned glumes	Ee
I	Dense vs. lax heads	Ll
I	Non-six row vs. six-row	Vv
I	Deficiens vs. six-row	$V^{t}v$
I	Purple vs. white glumes	Prpr
II	Black vs. white lemma and caryopsis	Bb
III	Hulled vs. naked caryopsis	Hn
IV	Hooded vs. awned	Kk
V	Rough vs. smooth awns	Rr
V	Long vs. short haired rachilla	Ss
VI	Normal vs. albino seedlings	Anan
VI	Normal vs. xantha seedlings	Xexe
VII	Normal vs. brachytic growth	Brbr
*	Normal vs. semisterility	Ner.SS
**	Length of glume hairs	$l_1 l_2 l_3$
**	Glossy vs. non-glossy head	Gegg
**	Non-glossy vs. glossy stem	Gsgs
**	Normal vs. male sterility	Msms

* Semisterility may be linked with factors in any linkage group depending upon the point of interchange between segments of chromosomes.

** The linkage group for these characters has not yet been established.

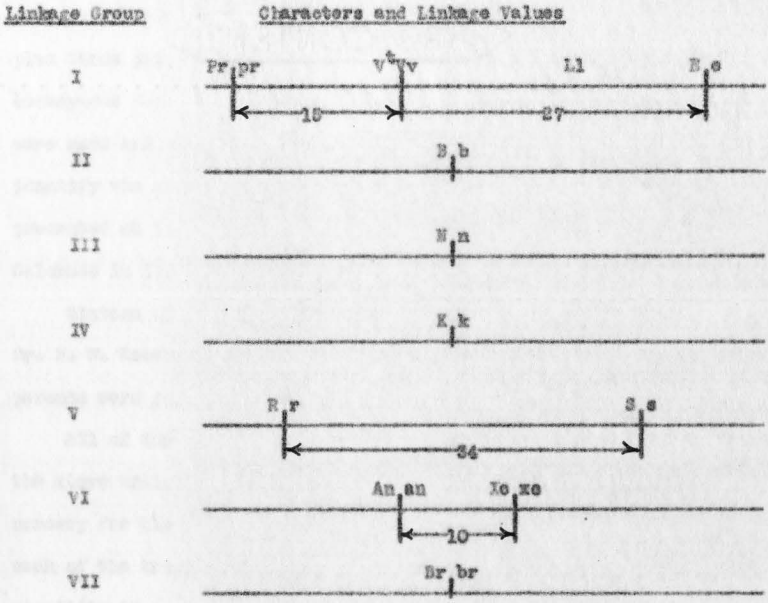

Fig. 1. The location of the various characters studied in this problem in relation to the 7 linkage groups.

MATERIALS

Dr. C. R. Burnham, at Minnesota, had seed of Mars barley X-rayed by Dr. L. J. Stadler. Head progenies of this X-rayed seed were grown by Burnham. From this lot of seed, twenty-seven lines had a ring of four chromosomes plus five pairs, one had two separate rings of four plus three pairs, and the remainder had seven pairs. Seventeen lines homozygous for the translocation have been identified. Intercrosses were made and examined cytologically to establish a set of testers to identify the seven chromosomes. A summary of this work to date was presented at the American Society of Agronomy meetings at Fort Collins, Colorado in 1948 by White and Burnham (37).

Sixteen of the above translocation stocks are grown here by Dr. R. W. Woodward. It is from these stocks that the translocation parents were obtained for this thesis.

All of the crosses in this study were made by Dr. Woodward, using the above translocations for one parent and stocks from his genetic nursery for the other parent. A list of the crosses with parents in each of the translocation and standard normal lines and the F_1 pollen sterility is presented in Table 2. It was from the F_1 seed from these crosses that this study began.

Table 2. Barley translocation lines and genetic strains used as parents in crosses for inheritance studies and the F_1 pollen sterility.

Cross Number	Parents*	F_1 Pollen Sterility (%)
Translocation line c1483-6		
B243	c1483-6 SS x Xexe	20-50
B245	c1483-6 SS x Hooded Club	35-40
B248 Family I & II	c1483-6 SS x Black Deficiens	40-50
B250 Family II	c1483-6 SS x AnAn	30-40
B252	c1483-6 SS x Glossy Uns	15-25
Translocation line c1483-4		
B257	c1483-4 x White Deficiens	no data
Translocation line c1462-2		
B281	c1462-2 x Hooded Uns Ab 1379	10-15
Standard normal lines		
B248 Family III	c1483-6 SS x Black Deficiens	
B249	c1483-6 SS x Anan	
B250 Family I	c1483-6 SS x AnAn	
B259	c1483-5 N x White Deficiens	
B266	c1462-1 N x Black Deficiens	
B272	c1462-2 SS x Black Deficiens	
B279	c1483-6 N x Black Deficiens	
B283	Brachytic B_4 x c1462-2	

* The translocation lines are indicated by c, and the female parent is listed first in each case.

METHOD OF PROCEDURE

The material for this thesis was grown on the experimental farm at North Logan. Seed bed preparation was done in the regular manner for spring sown cereals. The rows were marked 12 inches apart except for every fourth row which was 16 inches apart to permit cultivation with a tractor. Furrows for planting were made with a hand cultivator at the time of seeding. The F_2 seed was hand-spaced approximately 2 inches apart in the row and covered with a hoe. Cultivation was done 4 rows at a time with a tractor as stated above. The plot was irrigated along with the yield nursery.

Plants with characters which were hard or impossible to distinguish in the mature stage, such as male sterility, glossy heads, and purple glumes were tied with colored string at the time they could be most easily detected. When the plants were mature each family or cross was pulled, tied, and labeled with the same tags used for identification throughout the season. The bundles were then placed in a steel shed for storage until classified.

In classifying the F_2 families, symbols representing the segregating characters for each plant were recorded separately. Chi-square, a test for goodness of fit, was calculated for each segregating character pair and for every possible dihybrid combination of character pairs.

To calculate linkages, the product method (18, 19, 21) was used when four classes were involved, and the maximum likelihood method (23) when one of the four classes were missing.

All crosses in which poor fits resulted were grown in the F_3, especially if there was doubt as to the F_2 classification of linked characters.

PRESENTATION AND ANALYSIS OF DATA

Crosses Involving Translocation Lines

The presentation and analysis of data will be discussed by crosses. The first crosses to be presented will be those involving translocation line c1483-6 as one of the parents. These include the following crosses: B243; B248, Family I + II; B250, Family II; and B252.

In cross B243 all the monohybrid pairs fit the expected ratios. All observed segregation of characters for monohybrid ratios are presented in Table 3. There was a significant linkage with length of glume hairs (#1#2#3) in relation to normal vs. semisterility with a crossover value of 21.0 ± 5.8 percent. A summary of the linkage data between normal vs. semisterility and various character pairs in crosses with line c1483-6 is presented in Table 4. More detailed data for each dihybrid segregation in all crosses are presented in the Appendix. There was no linkage between rough vs. smooth awns (Rr) and long vs. short rachilla hairs (Ss) as was to be expected if the lines used for parents were both normal; however, there are several factors for smooth awns so another factor may be involved in this case. A summary of observed segregation for qualitative character pairs in the F_2 progeny of crosses with line c1483-6 involving semisterility is presented in Table 5. Crossover values where both monohybrids segregated in the ratio 3:1 were calculated by the product method (18, 19).

Cross B245 was interesting in view of the fact that two new linkage groups were brought together, presumably due to a translocation. Hulled vs. naked caryopsis (Nn) in linkage group 3, and rough vs. smooth awns (Rr) in linkage group 5 showed a recombination value of 38.4 ± 7.0 percent. Both hulled vs. naked caryopsis (Nn) and rough vs. smooth awns (Rr)

Table 3. Summary of observed segregation of characters for monohybrid ratios in all crosses. Calculated values, ratios, X^2, and P values are included.

Character	Observed	Calculated	Total	Ratio	X^2	P Value
Cross B245						
S	115	111		3		
s	33	37	148	1	0.577	.48
K	118	111		3		
k	30	37	148	1	1.765	.19
#1	43	37		1		
#2	67	74		2		
#3	38	37	148	1	1.662	.45
R	26	22.5		3		
r	4	7.5	30	1	2.178	.15
XcXc	51	49.33		1		
Xcxc	97	98.67	148	2	0.085	.78
Normal	69	74		1		
SS	79	74	148	1	0.676	.45
Cross B246						
N	204	206.25		3		
n	71	68.75	275	1	0.099	.76
R	56	48.75		3		
r	9	16.25	65	1	4.311	.04
l	189	206.25		3		
L	86	68.75	275	1	5.773	.02
F3						
e 74	188	206.25		3		
E 201	87	68.75	275	1	6.459	.01
K	210	206.25		3		
k	65	68.75	275	1	0.273	.62
Pr	210	206.25		3		
pr	65	68.75	275	1	0.273	.62
Normal	117	137.5		1		
SS	158	137.5	275	1	4.804	.03
Cross B248, Family I + II						
V^tV^t	35	35.75		1		
V^tv	67	71.50		2		
vv	41	35.75	143	1	1.070	.48

Table 3. (continued)

Character	Observed	Calculated	Total	Ratio	X^2	P Value
Cross B248 (cont.)						
B	109	107.25		3		
b	34	35.75	143	1	0.114	.73
#3	74	71.5		1		
#2	69	71.5	143	1	0.175	.68
R	115	107.25		3		
r	28	35.75	143	1	2.240	.14
N	103	107.25		3		
n	40	35.75	143	1	0.674	.35
Normal	86	71.5		1		
SS	55	71.5	143	1	7.615	.01-
Cross B248, Family III						
$y^t y^t$	11	15.5		1		
$y^t y$	30	31		2		
yy	21	15.5	62	1	3.290	.19
B	41	46.5		3		
b	21	15.5	62	1	2.602	.11
#3	42	46.5		3		
#2	20	15.5	62	1	4.364	.13
R	53	46.5		3		
r	9	15.5	62	1	3.634	.06
N	49	46.5		3		
n	13	15.5	62	1	0.538	.48
Cross B249						
VV	26	23.5		1		
Vv	50	47		2		
vv	18	23.5	94	1	1.745	.65
B	69	70.5		3		
b	25	23.5	94	1	0.128	.71
R	77	70.5		3		
r	17	23.5	94	1	2.397	.12
N	78	70.5		3		
n	16	23.5	94	1	3.192	.06

Table 3. (continued)

Character	Observed	Calculated	Total	Ratio	X^2	P Value
Cross B249 (cont.)						
S	64	70.5		3		
s	30	23.5	94	1	2.397	.12
AnAn	35	31.33		1		
Anan	59	62.67	94	2	0.821	.35
Cross B250, Family I						
VV	41	36.75		1		
Vv	75	73.50		2		
vv	31	36.75	147	1	1.422	.26
B	114	110.25		3		
b	33	36.75	147	1	0.510	.48
#3	82	73.5		1		
#2	65	73.5	147	1	1.966	.18
R	112	110.25		3		
r	35	36.75	147	1	0.111	.74
N	118	110.25		3		
n	29	36.75	147	1	2.179	.15
S	115	110.25		3		
s	32	36.75	147	1	0.819	.35
Cross B250, Family II						
B	89	93		3		
b	35	31	124	1	0.688	.40
R	95	93		3		
r	29	31	124	1	0.172	.65
VV	34	31		1		
Vv	59	62		2		
vv	31	31	124	1	0.436	.80
N	86	93		3		
n	38	31	124	1	2.108	.15
S	91	93		3		
s	33	31	124	1	0.172	.65
#3	92	93		3		
#2	32	31	124	1	0.045	.85
Normal	62	62		1		
SS	62	62	124	1	0.000	1.00

Table 3. (continued)

Character	Observed	Calculated	Total	Ratio	X^2	P Value
Cross B252						
VV	69	68		1		
Vv	132	136		2		
vv	71	68	272	1	0.265	.88
R	195	204		3		
r	77	68	272	1	1.588	.21
Gs	207	204		3		
gs	65	68	272	1	0.167	.68
Normal	198	204		3		
SS	74	68	272	1	0.706	.40
Cross B257						
V^tV^t	85	96		1		
V^tv	212	192		2		
vv	87	96	384	1	4.167	.12
Ge	291	288		3		
ge	93	96	384	1	0.125	.72
R	298	288		3		
r	86	96	384	1	1.389	.25
Pr	224	216		9		
pr	160	168	384	7	0.677	.45
Normal	194	192		1		
SS	190	192	384	1	0.042	.84
Cross B259						
Pr	234	227.25		9		
pr	170	176.75	404	7	0.506	.48
Ge	273	303		3		
ge	131	101	404	1	11.888	.01-
V^tV^t	103	101		1		
V^tv	216	202		2		
vv	85	101	404	1	3.545	.06
R	327	303		3		
r	77	101	404	1	7.600	.01-

Table 3. (continued)

Character	Observed	Calculated	Total	Ratio	X^2	P Value
Cross B266						
V^tV^t	40	35		1		
V^tv	62	70		2		
vv	38	35	140	1	1.886	.41
N	99	105		3		
n	41	35	140	1	1.372	.25
B	105	105		3		
b	35	35	140	1	0.000	1.00
Cross B272						
V^tV^t	11	17.5		1		
V^tv	34	35.0		2		
vv	25	17.5	70	1	5.657	.06
N	51	52.5		3		
n	19	17.5	70	1	0.172	.68
B	57	52.5		3		
b	13	17.5	70	1	1.200	.28
Cross B279						
V^tV^t	44	50		1		
V^tv	105	100		2		
vv	51	50	200	1	0.990	.55
B	153	150		3		
b	47	50	200	1	0.240	.62
N	143	150		3		
n	57	50	200	1	1.307	.25
R	164	150		3		
r	36	50	200	1	5.227	.02
Cross B281						
VV	35	31		1		
Vv	54	62		2		
vv	35	31	124	1	2.065	.35
K	91	93		3		
k	33	31	124	1	0.172	.68
Ms	89	93		3		
ms	35	31	124	1	0.688	.45
Normal	38	44.5		1		
SS	51	44.5	89	1	1.899	.09

Table 3. (continued)

Character	Observed	Calculated	Total	Ratio	X^2	P Value
Cross B283						
VV	16	19.5		1		
Vv	43	39		2		
vv	19	19.5	78	1	1.051	.29
N	57	58.5		3		
n	21	19.5	78	1	0.154	.69
R	65	58.5		3		
r	13	19.5	78	1	2.889	.09
#2	55	58.5		3		
#3	23	19.5	78	1	0.538	.36
Br	61	58.5		3		
br	17	19.5	78	1	0.427	.52

Table 4. Observed segregation and linkages between normal vs. semisterility and various character pairs designated Y vs. y in crosses with line cl483-6. P values for the X^2 tests for independence and crossovers plus or minus standard error values are included.

Cross	Character Yy	Normal Y	Normal y	Semisterile Y	Semisterile y	Total n	P Value	C.O. ± S.E.
B243	Ss	57	12	58	21	148	.45	
	Kk	52	17	66	13	148	.27	
	#2+3#1	42	27	63	16	148	.03	21.0 ± 5.8%
	Rr	15	2	11	2	30	.22	
	Rexo	26	43	25	54	148	.72	
B245	Nn	74	43	130	28	275	.01-	20.0 ± 4.1%
	Rr	32	2	24	7	65	.07	13.5 ± 6.5%
	IL	73	44	116	42	275	.01-	
	eE	74	43	114	44	275	.01-	
	Kk	83	34	127	31	275	.02	28.0 ± 5.9%
	Prpr	85	32	125	33	275	.02	
B248*	$V^t v$	59	29	43	12	143	.01-	
	Bb	66	22	43	12	143	.05	
	#3#2	40	48	34	21	143	.01	
	Rr	79	9	36	19	143	.01-	13.5 ± 4.4%
	Nn	54	34	49	6	143	.01-	12.5 ± 4.1%
B250**	Bb	41	21	48	14	124	.42	
	Rr	52	16	45	11	124	.56	
	Vv	48	14	45	17	124	.94	
	Nn	31	31	55	7	124	.01-	9.0 ± 3.7%
	Ss	46	16	45	17	124	.97	
	#3#2	44	18	48	14	124	.87	
B252	Vv	150	48	51	23	272	.50	
	Rr	142	56	53	21	272	.51	
	Gs gs	144	54	63	11	272	.14	

* Only Families I and II segregated for semisterility.
** Only Family II segregated for semisterility.

Table 5. Observed segregation for qualitative character pairs in the F_2 progeny of crosses involving semisterility in line c1453-3. P values for the X^2 tests for independence and crossovers plus or minus standard error values are included.

Character Pairs	F2 Phenotypes a	b	c	d	Total n	P Value	C.O. ± S.E.
Cross B243							
Ss-Kk	90	25	28	5	148	.45	
Ss-#243#1	79	36	26	7	148	.35	
Ss-Rr	21	4	5	0	30	.32	
Ss-Xexo	43	72	8	25	148	.47	
Kk-#243#1	87	31	18	12	148	.19	
Kk-Rr	--	--	26	4	30	.15	
Kk-Xexo	39	79	12	18	148	.52	
#243#1-Rr	16	2	10	2	30	.14	
#243#1-Xexo	36	69	15	28	148	.72	
Rr-Xexo	10	16	2	2	30	.45	
Cross B246							
Nn-Rr	37	7	19	2	65	.09	38.4 ± 7.0%
Nn-1L	147	57	42	29	275	.01	
Nn-eE	139	65	49	22	275	.09	
Nn-Kk	160	44	50	21	275	.54	
Nn-Prpr	153	51	57	14	275	.75	
Rr-1L	34	22	8	1	65	.01*	
Rr-eE	26	30	2	7	65	.01*	
Rr-Kk	--	56	--	9	65	.04	
Rr-Prpr	45	11	7	2	65	.06	
1L-eE	104	65	84	2	275	.01*	11.8 ± 5.9%
1L-Kk	147	42	63	23	275	.06	
1L-Prpr	135	54	75	11	275	.01*	36.0 ± 5.2%
eE-Kk	160	28	50	37	275	.01	31.2 ± 3.8%
eE-Prpr	153	35	57	30	275	.01*	38.8 ± 3.9%
Kk-Prpr	158	52	52	13	275	.75	
Cross B248*							
V^tv-Bb	78	24	31	10	143	.62	
V^tv-#3#2	47	55	27	14	143	.09	35.0 ± 7.0%
V^tv-Rr	85	17	30	11	143	.19	
V^tv-Nn	73	29	30	11	143	.66	
Bb-#3#2	58	51	16	18	143	.88	
Bb-Rr	68	21	27	7	143	.50	
Bb-Nn	82	27	21	13	143	.32	
#3#2-Rr	57	17	58	11	143	.36	
#3#2-Nn	59	15	44	25	143	.39	
Rr-Nn	76	37	25	5	143	.05	31.5 ± 7.4%

* Only Families I and II segregated for semisterility.

Table 5. (continued)

Character Pairs	F_2 Phenotypes a	b	c	d	Total n	P Value	C.O. ± S.E.
Cross B250*							
Bb-Rr	68	21	27	8	124	.82	
Bb-Vv	64	25	29	6	124	.48	
Bb-Hn	60	29	26	9	124	.35	
Bb-Ss	69	20	22	13	124	.26	
Bb-fs#2	67	22	25	10	124	.62	
Rr-Vv	69	26	24	5	124	.72	
Rr-Hn	67	28	19	10	124	.46	
Rr-Ss	64	31	27	2	124	.05	25.4 ± 8.3%
Rr-fs#2	70	25	22	7	124	.96	
Vv-Hn	65	28	21	10	124	.53	
Vv-Ss	70	23	21	10	124	.83	
Vv-fs#2	73	20	20	11	124	.50	
Hn-Ss	62	24	29	9	124	.47	
Hn-fs#2	70	16	22	16	124	.01	34.5 ± 5.5%
Ss-fs#2	68	23	24	9	124	.96	
Cross B252							
Vv-Rr	154	47	41	30	272	.01-	38.0 ± 3.9%
Vv-Gsgs	148	53	59	12	272	.40	
Rr-Gsgs	145	50	62	15	272	.40	

* Only Family II was translocation normal.

showed linkage with normal vs. semisterility with crossover values of 20.0 ± 4.1 and 13.5 ± 6.8 percent respectively. In this cross hoods vs. awns (Kk) also showed linkage with normal vs. semisterility with a crossover value of 28.0 ± 5.9 percent. Crossover values involving semisterility were calculated by the product method from Joachim's (21) tables. Some of the monohybrid ratios in this cross showed poor fits to the Mendlian ratios. This may be due to the inability to classify the plants for the characters accurately in F_2. In the case of normal vs. long awned glumes (Ee) and dense vs. lax heads (Ll), the heterzygous plants must have been classified with the double recessive. A F_3 row will be grown for each F_2 plant in order to clear up the discrepancies between these two characters. In this cross dense vs. lax heads (Ll) were found to be linked with normal vs. long awned glumes (Ee) with a crossover value of 11.8 ± 5.9 percent. A linkage between these two characters was not found in the literature. This cross also showed linkage of dense vs. lax heads (Ll) with purple vs. white glumes (Prpr), of normal vs. long awned glumes (Ee) with hooded vs. awned (Kk), and normal vs. long awned glumes (Ee) with purple vs. white glumes (Prpr), with recombination values ranging from 31 to 38 percent. These last three crossovers are probably not significant because of the fact that both dense vs. lax heads (Ll) and normal vs. long awned glumes (Ee) did not fit the expected 3:1 ratios. The F_3 rows which will be grown for each plant in this cross should clear up these discrepancies.

There were three families in cross B248, the first two of which segregated for semisterility and were added together for calculations. The third did not segregate for this character so will be discussed under the standard normal crosses. All monohybrids fit the expected

ratio with the exception of normal vs. semisterility. In this case there were more normals than would be expected for a 1:1 ratio. In this cross, as in cross B245, hulled vs. naked caryopsis (Nn) and rough vs. smooth awns (Rr) were found to be linked. The crossover value was 31.5 ± 7.4 percent. Both hulled vs. naked caryopsis (Nn) and rough vs. smooth awns (Rr) were again linked with normal vs. semisterility with crossover values of 12.5 ± 4.1 and 13.5 ± 4.4 percent respectively. Two-row vs. six-row (Vv) showed a linkage with #3 vs. #2 glume hairs with a crossover value of 35.0 ± 7.0 percent in this cross. All other factors segregated for the expected ratios.

All monohybrids fit the expected ratios in cross B250. Hulled vs. naked caryopsis (Nn) again showed linkage with normal vs. semisterility with a crossover value of 9.0 ± 3.7 percent, but rough vs. smooth (Rr) awns showed independence with normal vs. semisterility. Since in all the above crosses the same translocation line was used as one of the parents, it would be expected that all the characters in these crosses would segregate the same. Rough vs. smooth awns (Rr) and long vs. short rachilla hairs (Ss) showed linkage in this cross as would be expected when two normal lines are crossed. A linkage was observed between hulled vs. naked caryopsis (Nn) and #3 vs. #2 glume hairs. However, it could not be certain whether a crossover this wide is significant when glume hairs show possible linkage with several linkage groups as it did in this study. The standard normal parent in this cross was from a line segregating for normal vs. albino seedlings (Anan) which is lethal when in the homozygous albino (anan) condition. There was a 2 to 1 chance that the plant used would carry the albino factor, but in this case the plant was probably homozygous for normal seedlings.

Cross B252 segregated for two-row vs. six-row (Vv), rough vs. smooth awns (Rr), and non-glossy vs. glossy stems (Gsgs) in addition to normal vs. semisterility. In this cross normal vs. semisterility did not segregate for the expected 1:1 ratio. It did, however, fit a 3:1 ratio with a P value of .40. It is suspected in this case that a family of standard normals got mixed with a translocation normal family. Therefore, the X^2 values for dihybrids involving semisterility were calculated for the 9:3:3:1 ratio. All dihybrids fit the expected ratio except two-row vs. six-row (Vv) in relation to rough vs. smooth awns (Rr) which showed a crossover value of 38.0 ± 3.9 percent. Inasmuch as two-row vs. six-row (Vv) and rough vs. smooth awns (Rr) has segregated independently in other crosses with line cl483-6, this crossover is probably not significant. It is likely that there was no linkage between the other characters with normal vs. semisterility in this cross as indicated by the P values.

The next cross discussed will be one with line cl483-4. Cross B257 segregated for deficiens vs. six-row (V^tv), glossy vs. non-glossy heads (Gegs), rough vs. smooth awns (Rr), and purple vs. white glumes (Prpr), in addition to normal vs. semisterility; all of which fit the expected monohybrid ratios. In this cross purple vs. white glumes (Prpr) segregated in a ratio of 9:7. As far as is known, this is the first time this ratio has been observed for this character. There evidently must be complementary factors for purple as this ratio was observed in two crosses. All of the characters showed independent inheritance with normal vs. semisterility. A summary of the linkage data between normal vs. semisterility and the character pairs with line cl483-4 is presented in Table 6.

Table 6. Independent inheritance and linkage relationships between normal vs. semisterility and various character pairs in lines cl483-4 and cl462-2. P values for the X^2 tests for independence and crossovers plus or minus standard error values are included.

Cross	Character Yy	Normal Y	Normal y	Semisterile Y	Semisterile y	Total n	P Value	C.O. ± S.E.
B257	V^tv	146	48	151	39	384	.55	
	Gegs	146	49	146	44	384	.94	
	Rr	151	43	147	43	384	.68	
	Prpr	114	80	110	80	384	.84	
B281	Vv	28	10	38	13	89	.58	
	Kk	22	16	40	11	89	.03	20.0 ± 7.3%
	Mems	38	--	51	--	89	.19	

All of the dihybrids showed independent inheritance with the exception of deficiens vs. six-row (V^tv) and purple vs. white glumes (Prpr). Linkage was calculated by the product method from Immer's (19) 3:1 and 9:7 table. This linkage was found to be 16.0 ± 3.2 percent. It is suspected that this purple is due to the same factor as has been reported by other workers because it shows approximately the same linkage with deficiens vs. six-row (V^tv). The summary of observed segregation for qualitative character pairs with line cl483-4 is presented in Table 7.

The last cross in this study involving a translocation line is B281 which involves line cl462-2. There were three characters segregating in addition to normal vs. semisterility, all of which fit the expected monohybrid ratios. The character pair, hoods vs. awns (Kk) showed linkage with normal vs. semisterility with a crossover value of 20.0 ± 7.3 percent. Evidently linkage group 4 is one of the groups involved in this translocation. A summary of linkage data between normal vs. semisterility and various character pairs in line cl462-2 is presented in Table 6.

Table 7. Segregation of qualitative character pairs in the F_2 progeny of crosses with lines cl483-4 and cl462-2 involving semisterility P values for the χ^2 tests for independence and crossovers plus or minus standard error values are included.

Character Pairs	F_2 Phenotypes a	b	c	d	Total n	P Value	C.O. ± S.E.
Cross B257							
V^tv-Gege	228	69	62	25	384	.51	
V^tv-Rr	234	63	64	23	384	.32	
V^tv-Prpr	202	95	22	65	384	.01*	18.0 ± 3.2%
Gege-Rr	230	61	68	25	384	.45	
Gege-Prpr	175	116	49	44	384	.32	
Rr-Prpr	163	135	61	25	384	.04	
Cross B281							
Vv-Ek	67	22	24	11	124	.68	
Vv-Mems	66	23	23	12	124	.48	
Ek-Mems	62	29	27	6	124	.52	

The dihybrids in this cross all showed independent inheritance. It should be noted that those plants which were male sterile could not be classified for normal vs. semisterility, but from the data it would appear that they were independent. A summary of the observed segregation of the dihybrids in cross B281 is presented in Table 7.

Crosses Involving Standard Normal Lines

When the crosses were made for this study, the translocation lines had not yet been purified; therefore, there was an equal chance of getting normal or translocation pollen. Consequently, there were eight crosses in which the parent turned out to be standard normal.

A summary of these crosses will be presented for the genetic data which they contain because some of the characters studied have not as yet been located. In cross B248 only Family III was a standard normal. All of the monohybrids fit the expected ratios. In the dihybrids, deficiens vs. six-row (V^tv) shows possible linkage with #3 vs. #2 glume

hairs with a crossover value of 30.5 ± 11.4 percent. All other dihybrid ratios show independent segregation. A summary of the observed segregation for qualitative character pairs of all crosses with standard normal lines is presented in Table 8.

In cross 3249 there was a segregation for six characters all of which fit the expected monohybrid ratios. One of the characters involved was normal green vs. albino seedlings (Anan) which is lethal when in the homozygous recessive condition. Therefore, one-fourth of the population was lost in the seedling stage. To determine linkage or independence with this character, F_3's were grown in the greenhouse to classify the F_2 plants either homozygous and heterozygous green for this seedling character.

In the dihybrid segregations there were three possible linkages observed. Rough vs. smooth awns (Rr) showed linkage in relation to long vs. short rachilla hairs (Ss) with a crossover value of 37.5 ± 8.7 percent. This is in agreement with results reported by other workers between these two character pairs. Other factors which showed possible linkage in this cross were two-row vs. six-row (Vv) in relation to rough vs. smooth awns (Rr) and two-row vs. six-row (Vv) in relation to hulled vs. naked caryopsis (Nn). However, these two indicated linkages are undoubtedly not real linkages because the three factors have definitely been established by previous workers and by other crosses in this study to be in different linkage groups. All other factors in this cross show independent inheritance.

Only Family I was standard normal in cross 3250. All of the six characters which segregated fit the expected monohybrid ratios. In the dihybrid segregations all characters showed independent

Table 8. The observed segregation for qualitiative character pairs in the F2 progeny of crosses with standard normal lines. P values for the X^2 tests for independence and crossovers plus or minus standard error values are included.

Character Pairs	F2 Phenotypes a	b	c	d	Total n	P Value	C.O. ± S.E.
Cross B248*							
V^tv-Bb	26	13	13	8	62	.11	
V^tv-#3#2	24	17	18	3	62	.03	30.5 ± 11.4%
V^tv-Rr	36	5	17	4	62	.09	
V^tv-Nn	34	7	15	6	62	.28	
Bb-#3#2	27	14	15	6	62	.22	
Bb-Rr	36	5	17	4	62	.09	
Bb-Nn	32	9	17	4	62	.32	
#3#2-Rr	34	8	19	1	62	.04	
#3#2-Nn	36	6	13	7	62	.15	
Rr-Nn	42	11	7	2	62	.24	
Cross B249							
Vv-Bb	57	19	12	6	94	.52	
Vv-Rr	61	15	16	2	94	.23	
Vv-Nn	65	11	13	5	94	.09	39.0 ± 6.5%
Vv-Ss	49	27	15	3	94	.07	36.0 ± 8.5%
Vv-Anan	31	45	4	14	94	.21	
Bb-Rr	58	11	19	6	94	.40	
Bb-Nn	58	11	20	5	94	.32	
Bb-Ss	46	23	18	7	94	.45	
Bb-Anan	23	46	12	13	94	.45	
Rr-Nn	64	13	14	3	94	.12	
Rr-Ss	50	27	14	3	94	.07	37.5 ± 8.7%
Rr-Anan	28	49	7	10	94	.40	
Nn-Ss	54	24	10	6	94	.14	
Nn-Anan	29	49	6	10	94	.28	
Ss-Anan	24	40	11	19	94	.40	
Cross B250**							
Vv-Bb	93	23	21	10	147	.31	
Vv-#3#2	66	50	16	15	147	.31	
Vv-Rr	87	29	25	6	147	.66	
Vv-Nn	93	23	25	6	147	.34	
Vv-Ss	95	21	20	11	147	.13	
Bb-#3#2	62	52	20	13	147	.48	
Bb-Rr	91	23	21	12	147	.28	
Bb-Nn	93	21	25	8	147	.48	
Bb-Ss	93	21	22	11	147	.24	
#2#3-Rr	49	16	63	19	147	.52	
#2#3-Nn	49	16	69	13	147	.12	
#2#3-Ss	54	11	61	21	147	.27	

* Only Family III was standard normal.
** Only Family I was standard normal.

Table 8. (continued)

Character Pairs	F2 Phenotypes a	b	c	d	Total n	P Value	C.O. ± S.E.
Cross B250 (cont.)							
Rr-Mn	95	17	23	12	147	.07	
Rr-Ss	87	25	28	7	147	.61	
Mn-Ss	92	26	23	6	147	.41	
Cross B259							
Prpr-Gege	165	69	106	62	404	.01-	
Prpr-V^tv	220	14	99	71	404	.01-	12.0 ± 2.6%
Prpr-Rr	164	50	143	27	404	.03	
Gege-V^tv	216	57	103	28	404	.01-	
Gege-Rr	217	86	110	21	404	.01-	
V^tv-Rr	255	64	72	13	404	.01	
Cross B266							
V^tv-Mn	63	29	36	12	140	.04	
V^tv-Bb	80	22	25	13	140	.42	
Mn-Bb	74	25	31	10	140	.72	
Cross B272							
V^tv-Mn	32	13	19	6	70	.21	
V^tv-Bb	34	11	23	2	70	.03	
Mn-Bb	43	8	14	5	70	.49	
Cross B279							
V^tv-Bb	117	32	36	15	200	.46	
V^tv-Mn	106	43	37	14	200	.51	
V^tv-Rr	122	27	42	9	200	.16	
Bb-Mn	110	43	33	14	200	.68	
Bb-Rr	128	25	36	11	200	.09	
Mn-Rr	116	27	48	9	200	.08	
Cross B283							
Vv-Mn	40	19	17	2	78	.29	
Vv-Rr	49	10	16	3	78	.40	
Vv-#2#3	45	14	10	9	78	.19	
Vv-Brbr	47	12	14	5	78	.86	
Mn-Rr	50	7	15	6	78	.19	
Mn-#2#3	41	16	14	7	78	.70	
Mn-Brbr	47	10	14	7	78	.60	
Rr-#2#3	43	22	12	1	78	.07	
Rr-Brbr	54	11	7	6	78	.06	31.0 ± 6.8%
#2#3-Brbr	36	17	23	0	78	.01+	26.6 ± 5.8%*

* This crossover and standard error was calculated by the maximum likelihood method.

inheritance. The only character not yet located in this cross was #3 vs. #2 glume hairs and as stated above showed independence with the other characters studied in this cross. The only discrepancy with other work in the literature observed in this cross was the fact that rough vs. smooth awns and long vs. short rachilla hairs showed independent inheritance. The reason for this is possibly due to the second factor pair for smooth awns which is not in linkage group 5.

Four character pairs segregated in cross B259. They are as follows: purple vs. white glumes (Prpr), glossy vs. non-glossy heads (Gegc), deficiens vs. six-row ($V^{t}v$), and rough vs. smooth awns (Rr). Purple vs. white glumes (Prpr) segregated in a 9:7 ratio in this cross as it did in cross B257 substantiating the fact that complementary factors must be involved with this character. Both parents in this cross were white as they were in cross B257; this would further indicate complementary factor inheritance for this purple factor in barley. Glossy vs. non-glossy heads (Gegc) did not fit as close to the 3:1 ratio as would normally be expected, the P value being less than .01. The classification for this character was done in the field and may not have been classified too accurately. The P value for rough vs. smooth awns (Rr) was also less than .01 in this cross, with the smooth awn phenotype being less than would be expected. It has been observed by others for the smooth awn class segregates to be consistently less than would be expected. The reason for this has not been established.

All of the dihybrids involving glossy vs. non-glossy heads (Gegc) had P values of less than .01 because of the poor fit of this character in the monohybrid ratio. The only indicated linkage was between purple

vs. white glumes (Prpr) and deficiens vs. six-row ($v^t v$). In this case the crossover value was 12.0 ± 2.6 percent.

In crosses B266, B272, and B279, only three or four already located independent characters were involved. In all three crosses both monohybrid and dihybrid segregations fit the expected independent ratios.

Cross B283 segregated for five character pairs as follows: two-row vs. six-row (Vv), hulled vs. naked caryopsis (Nn), rough vs. smooth awns (Rr), length of glume hairs (#2/#3), and normal vs. brachytic growth (Brbr). Length of glume hairs was the only one not yet definitely established as to location. No monohybrid ratios deviated significantly from the expected. There were two indicated linkages in this cross. The first was rough vs. smooth awns (Rr) in relation to normal vs. brachytic (Brbr); however, this suggested linkage is probably only a random misfit because both rough vs. smooth awns (Rr) and normal vs. brachytic (Brbr) have been established to be in different linkage groups when both parents are standard normal lines.

The second linkage in this cross shows #2 vs. #3 glume hairs to be linked with normal vs. brachytic growth (Brbr). In this case the double recessive class was missing so linkage could not be calculated by the products method; therefore, the maximum likelihood method was used for calculation of linkage. Evidently further study will have to be made to definitely locate the factor for length of glume hairs since it has showed possible linkage with several linkage groups in this study.

Tests for Interaction

A test for interaction was made for each character that appeared in two or more crosses. A summary of these data are presented in

Table 9. Of the ten characters included in this study, there were three which showed significant P values. In the case of rough vs. smooth awns (Rr), the total and pooled P values were significant. This would indicate that there was a consistent excess in one of the classes. An observation of the data shows that there was only one cross with a significant deviation from the expected ratio, but in every case the rough awned class was in excess. When the chi-squares were totaled and pooled, there was a significant deviation from the expected ratio; because the same class was in excess in every case. The interaction chi-square was not significant; this would indicate consistency from cross to cross.

In the case of glossy vs. non-glossy heads (Gegc), the total and interaction P values were significant. There were only two crosses segregating for this character. The chi-square value was 11.888 in cross B259 making the total chi-square deviate significantly. The interaction chi-square is also significant because the two classes deviated in opposite directions.

The P value for interaction is significant for normal vs. semi-sterility indicating inconsistency of deviations from expected in the different crosses involving semisterility. This was found to be the case upon inspection of the data.

Frequency Distribution of Chi-squares

A frequency distribution was made of the chi-squares in this study with degrees of freedom equaling 3. These include all the dihybrid chi-squares except those where linkage was involved or where one of the monohybrids did not fit the expected ratio. The total chi-square

Table 9. Tests of interaction for character pairs which appeared in two or more crosses.

Character	Source	D.F.	X^2	P Value
Two-row vs. six-row				
	Total	12	6.972	.85
	Pooled	2	.818	.65
	Interaction	10	6.154	.80
Deficiens vs. six-row				
	Total	14	20.625	.12
	Pooled	2	2.240	.32
	Interaction	12	18.385	.10
Hulled vs. hulless caryopsis				
	Total	10	9.684	.46
	Pooled	1	.557	.46
	Interaction	9	9.127	.42
Rough vs. smooth awns				
	Total	12	33.737	.01-
	Pooled	1	17.382	.01-
	Interaction	11	16.354	.15
Long vs. short rachilla hairs				
	Total	4	3.965	.42
	Pooled	1	.001	.99
	Interaction	3	3.964	.28
Hooded vs. awned				
	Total	3	2.210	.52
	Pooled	1	.755	.40
	Interaction	2	1.455	.48
Black vs. white caryopsis				
	Total	8	5.482	.71
	Pooled	1	.022	.89
	Interaction	7	5.461	.42
Glossy vs. non-glossy heads				
	Total	2	12.013	.01-
	Pooled	1	4.934	.03
	Interaction	1	7.079	.01-
Purple vs. white glumes				
	Total	2	1.183	.56
	Pooled	1	1.130	.28
	Interaction	1	.054	.82
Normal vs. semisterility				
	Total	6	15.036	.02
	Pooled	1	.627	.47
	Interaction	5	14.409	.01-

of this data was calculated and found to be 17.986. With this total chi-square the degrees of freedom equaled 13 and the P value was .15. The summary of this data is presented in Table 10. From an inspection of the above table it can be seen that the observed and theoretical distribution do not differ greatly. It can be concluded that the chi-squares with degrees of freedom equaling 3 in this study fit the theoretical distribution.

Table 10. Frequency distribution of chi-squares with three degrees of freedom.

Probability Interval	Class Interval	Theoretical Percentage Distribution	Distribution of 120 Samples (O)	Theoretical Distribution (C)
1.00-.99	.000- .115	1	1	1.2
.99-.96	.155- .185	1	0	1.2
.98-.95	.185- .352	3	3	3.6
.95-.90	.352- .584	5	1	6.0
.90-.80	.584- 1.005	10	8	12.0
.80-.70	1.005- 1.424	10	6	12.0
.70-.50	1.424- 2.366	20	21	24.0
.50-.30	2.366- 3.665	20	36	24.0
.30-.20	3.665- 4.642	10	13	12.0
.20-.10	4.642- 6.251	10	13	12.0
.10-.05	6.251- 7.815	5	6	6.0
.05-.02	7.815- 9.837	3	4	3.6
.02-.01	9.837-11.341	1	2	1.2
.01-	11.341-	1	2	1.2

$$\text{Total } X^2 = \Sigma\frac{(O-C)^2}{C} = 17.986$$

Degrees of freedom = 13

Probability = .15

DISCUSSION

Translocation studies in barley is a new project having its origin only 4 or 5 years ago at Minnesota. As the study progresses new angles appear which should be considered in the future.

The evidence for a reciprocal translocation in line cl483-6 for example was presented in the analysis of data. However, there were discrepancies in some crosses involving the same line. The reason why two crosses should give evidence of an interchange and three other crosses involving the same translocation fail to do so cannot be fully explained. There is a possibility that the translocation line used as one parent in these crosses was not homozygous for the same chromosomal aberration.

Evidence was presented for complementary factor inheritance for purple vs. white glumes in barley. Further study will need to be made, especially in isolating the lines for each factor and locating them in relation to the seven linkage groups. Even chemical tests of the genes may be made before deciding which is the P and C factors.

The F_3 progenies being grown this year should assist in clearing up the discrepancies found in the various F_2 segregations including the inheritance of purple vs. white glumes.

No cytological work was done as a part of this study. Work of this kind should be carried on in connection with the genetical work to definitely establish the ring formation of the interchanges and the relation between semisterility and genes on the seven linkage groups.

SUMMARY

Thirteen crosses were analyzed in the F_2 generation, seven of which segregated for semisterility.

In this study translocations showed the following characteristic behavior: (1) All F_1 plants were semisterile when a translocation normal was crossed to a standard normal. (2) Semisterile plants when selfed segregated in a special ratio of one normal to one semisterile. (3) Semisterility due to a translocation may be used in linkage tests as a dominant gene located at the point of interchange. This agrees with the findings of other workers.

Three different translocation lines were involved in this study in addition to six crosses in which both parents were standard normal lines.

In translocation line cl483-6, linkage groups 3 and 5 seem to be involved in the interchange. This is indicated by both hulled vs. naked caryopsis (Mn) in linkage group 3, and rough vs. smooth awns (Rr) in linkage group 5 being linked with semisterility in addition to being linked with each other. However, there were discrepancies in some crosses.

Translocation line cl483-4 shows independence with all the character pairs studied as follows: deficiens vs. six-row ($v^t v$), glossy vs. non-glossy heads (Gegs), rough vs. smooth awns (Rr), and purple vs. white glumes (Prpr).

Linkage group 4 is evidently one of the linkage groups involved in translocation line cl462-2. The crossover value between normal vs. semisterility and hooded vs. awned (Kk) was 20.0 ± 7.3 percent. Normal vs. semisterility showed independence with two-row vs. six-row (Vv) and

normal vs. male sterility (Msms) in this line.

In two crosses purple glumes showed complementary factor inheritance. In each case both parents were white, but the F_2 progeny segregated in a 9:7 ratio for purple vs. white glumes (Prpr).

The factors for length of glume hairs showed possible association with several linkage groups.

A summary for the tests of interaction for each character pair was made. Rough vs. smooth awns (Rr) showed significant total and pooled chi-squares; glossy vs. non-glossy heads showed significant total and interaction chi-squares; and normal vs. semisterility showed a significant interaction chi-square. All other probability values were greater than .01.

A frequency distribution of the chi-squares was calculated in the dihybrid segregations with the exception of those cases where linkage or a poor fit of a monohybrid was involved. This data were summarized in Table 10. It was concluded that the chi-squares in this study fit the theoretical distribution.

APPENDIX

A summary of all dihybrid character pairs included in this study. Observed and calculated values, ratios, chi-squares, and probability values are included.

Character	Obs.	Cal.	Ratio	X^2	Probability
Cross B243					
Ss in relation to Kk*					
S K	90	83.25	9		
S k	25	27.75	3		
s K	28	27.75	3		
s k	5	9.25	1	2.775	.45
Ss in relation to #2+3#1					
S #2+3	79	83.25	9		
S #1	36	27.75	3		
s #2+3	26	27.75	3		
s #1	7	9.25	1	3.327	.35
Ss in relation to Rr					
S R	21	16.88	9		
S r	4	5.63	3		
s R	5	5.63	3		
s r	0	1.875	1	3.376	.32
Ss in relation to Xcxc					
S XcXc	43	37	3		
S Xcxc	72	74	6		
s XcXc	8	12.33	1		
s Xcxc	25	24.67	2	2.552	.47
Kk in relation to #2+3#1					
K #2+3	87	83.25	9		
K #1	31	27.75	3		
k #2+3	18	27.75	3		
k #1	12	9.25	1	4.792	.19
Kk in relation to Rr					
K R	--	----			
K r	--	----			
k R	26	22.5	3		
k r	4	7.5	1	2.178	.15

* A description of each of the character pairs is listed in Table 2.

Appendix (continued)

Character	Obs.	Cal.	Ratio	X^2	Probability
Cross B243 (cont.)					
Kk in relation to Xexc					
K XcXc	39	37	3		
K Xexc	79	74	6		
k XcXc	12	12.33	1		
k Xexc	18	24.67	2	2.288	.52
#2+3#1 in relation to Rr					
#2+3 R	16	16.875	9		
#2+3 r	2	5.625	3		
#1 R	10	5.625	3		
#1 r	2	1.875	1	5.793	.14
#2+3#1 in relation to Xexc					
#2+3 XcXc	36	37	3		
#2+3 Xexc	69	74	6		
#1 XcXc	15	12.33	1		
#1 Xexc	28	24.67	2	1.393	.72
Rr in relation to Xexc					
R XcXc	10	7.5	3		
R Xexc	16	15	6		
r XcXc	2	2.5	1		
r Xexc	2	5	2	2.710	.45
Ss in relation to Nor.SS					
S Nor.	57	55.5	3		
S SS	56	55.5	3		
s Nor.	12	18.5	1		
s SS	21	18.5	1	2.775	.45
Kk in relation to Nor.SS					
K Nor.	52	55.5	3		
K SS	66	55.5	3		
k Nor.	17	18.5	1		
k SS	15	18.5	1	3.964	.27
#2+3#1 in relation to Nor.SS					
#2+3 Nor.	42	55.5	3		
#2+3 SS	63	55.5	3		
#1 Nor.	27	18.5	1		
#1 SS	16	18.5	1	8.543	.03
Rr in relation to Nor.SS					
R Nor.	15	11.25	3		
R SS	11	11.25	3		
r Nor.	2	3.75	1		
r SS	2	3.75	1	2.889	.22

Appendix (continued)

Character	Obs.	Cal.	Ratio	X^2	Probability
Cross B243 (cont.)					
Xexe in relation to Ner.SS					
XeXe Ner.	26	24.67	1		
XeXe SS	25	24.67	1		
Xexe Ner.	45	49.33	2		
Xexe SS	54	49.33	2	1.331	.72
Cross B245					
Nn in relation to Rr					
N R	37	36.56	9		
N r	7	12.19	3		
n R	19	12.19	3		
n r	2	4.06	1	7.065	.08
Nn in relation to lL					
N l	147	154.8	9		
N L	57	51.5	3		
n l	42	51.5	3		
n L	29	17.2	1	10.843	.01
Nn in relation to eE					
N e	139	154.8	9		
N E	65	51.5	3		
n e	49	51.5	3		
n E	22	17.2	1	6.612	.09
Nn in relation to Kk					
N K	160	154.8	9		
N k	44	51.5	3		
n K	50	51.5	3		
n k	21	17.2	1	2.150	.54
Nn in relation to Prpr					
N Pr	153	154.8	9		
N pr	51	51.5	3		
n Pr	57	51.5	3		
n pr	14	17.2	1	1.210	.75
Rr in relation to lL					
R l	34	36.56	9		
R L	22	12.19	3		
r l	8	12.19	3		
r L	1	4.06	1	11.821	.01*
Rr in relation to eE					
R e	26	36.56	9		
R E	30	12.19	3		
r e	2	12.19	3		
r E	7	4.06	1	39.718	.01*

Appendix (continued)

Character	Obs.	Cal.	Ratio	X^2	Probability
Cross B245 (cont.)					
Rr in relation to Kk					
R K	--	----			
R k	56	48.75	3		
r K	--	----			
r k	9	16.25	1	4.311	.04
Rr in relation to Prpr					
R Pr	45	36.56	9		
R pr	11	12.19	3		
r Pr	7	12.19	3		
r pr	2	4.06	1	5.320	.06
lL in relation to eE					
l e	104	154.8	9		
l E	85	51.5	3		
L e	84	51.5	3		
L E	2	17.2	1	72.404	.01-
lL in relation to Kk					
l K	147	154.8	9		
l k	42	51.5	3		
L K	63	51.5	3		
L k	23	17.2	1	6.671	.08
lL in relation to Prpr					
l Pr	135	154.8	9		
l pr	54	51.5	3		
L Pr	75	51.5	3		
L pr	11	17.2	1	15.630	.01-
eE in relation to Kk					
e K	160	154.8	9		
e k	28	51.5	3		
E K	50	51.5	3		
E k	37	17.2	1	33.735	.01-
eE in relation to Prpr					
e Pr	153	154.8	9		
e pr	35	51.5	3		
E Pr	57	51.5	3		
E pr	30	17.2	1	15.420	.01-
Kk in relation to Prpr					
K Pr	156	154.8	9		
K pr	52	51.5	3		
k Pr	52	51.5	3		
k pr	13	17.2	1	1.102	.76

Appendix (continued)

Character	Obs.	Cal.	Ratio	X^2	Probability
Cross B245 (cont.)					
Nn in relation to Nor.SS					
N Nor.	74	103.125	3		
N SS	130	103.125	3		
n Nor.	43	34.375	1		
n SS	28	34.375	1	16.870	.01"
Rr in relation to Nor.SS					
R Nor.	32	24.375	3		
R SS	24	24.375	3		
r Nor.	2	8.125	1		
r SS	7	8.125	1	7.164	.07
lL in relation to Nor.SS					
l Nor.	73	103.125	3		
l SS	116	103.125	3		
L Nor.	44	34.375	1		
L SS	42	34.375	1	14.844	.01"
eE in relation to Nor.SS					
e Nor.	74	103.125	3		
e SS	114	103.125	3		
E Nor.	43	34.375	1		
E SS	44	34.375	1	14.285	.01"
Kk in relation to Nor.SS					
K Nor.	83	103.125	3		
K SS	127	103.125	3		
k Nor.	34	34.375	1		
k SS	31	34.375	1	9.790	.02
Prpr in relation to Nor.SS					
Pr Nor.	85	103.125	3		
Pr SS	125	103.125	3		
pr Nor.	32	34.375	1		
pr SS	33	34.375	1	8.037	.02"
Cross B248, Family I + II					
Y^tv in relation to Bb					
Y^t B	78	80.5	9		
Y^t b	24	26.8	3		
v B	31	26.8	3		
v b	10	8.9	1	1.863	.62
Y^tv in relation to #3#2					
Y^t #3	47	53.6	3		
Y^t #2	55	53.6	3		
v #3	27	17.9	1		
v #2	14	17.9	1	6.325	.09

Appendix (continued)

Character	Obs.	Cal.	Ratio	X^2	Probability
Cross B 246 (cont.)					
$V^t v$ in relation to Rr					
V^t R	85	80.5	9		
V^t r	17	26.8	3		
v R	30	26.8	3		
v r	11	8.9	1	4.713	.19
$V^t v$ in relation to Nn					
V^t N	73	80.5	9		
V^t n	29	26.8	3		
v N	30	26.8	3		
v n	11	8.9	1	1.757	.66
Bb in relation to #3#2					
B #3	56	53.6	3		
B #2	51	53.6	3		
b #3	16	17.9	1		
b #2	18	17.9	1	.890	.88
Bb in relation to Rr					
B R	88	80.5	9		
B r	21	26.8	3		
b R	27	26.8	3		
b r	7	8.9	1	2.361	.50
Bb in relation to Nn					
B N	82	80.5	9		
B n	27	26.8	3		
b N	21	26.8	3		
b n	15	8.9	1	3.174	.32
#3#2 in relation to Rr					
#3 R	57	53.6	3		
#3 r	17	17.9	1		
#2 R	58	53.6	3		
#2 r	11	17.9	1	3.279	.36
#3#2 in relation to Nn					
#3 N	59	53.6	3		
#3 n	15	17.9	1		
#2 N	44	53.6	3		
#2 n	25	17.9	1	3.015	.39
Rr in relation to Nn					
R N	78	80.5	9		
R n	37	26.8	3		
r N	25	26.8	3		
r n	3	8.9	1	7.932	.05*

Appendix (continued)

Character	Obs.	Cal.	Ratio	x^2	Probability
Cross B248 (cont.)					
$V^t v$ in relation to Nor.SS					
V^t Nor.	59	53.6	3		
V^t SS	43	53.6	3		
v Nor.	29	17.9	1		
v SS	12	17.9	1	11.468	.01*
Bb in relation to Nor.SS					
B Nor.	66	53.6	3		
B SS	43	53.6	3		
b Nor.	22	17.9	1		
b SS	12	17.9	1	7.849	.05
#3#2 in relation to Nor.SS					
#3 Nor.	40	35.75	1		
#3 SS	34	35.75	1		
#2 Nor.	48	35.75	1		
#2 SS	21	35.75	1	10.874	.01
Rr in relation to Nor.SS					
R Nor.	79	53.6	3		
R SS	36	53.6	3		
r Nor.	9	17.9	1		
r SS	19	17.9	1	22.308	.01*
Nn in relation to Nor.SS					
N Nor.	54	53.6	3		
N SS	49	53.6	3		
n Nor.	34	17.9	1		
n SS	6	17.9	1	22.790	.01*
Cross B248, Family III					
$V^t v$ in relation to Bb					
V^t B	28	34.9	9		
V^t b	13	11.6	3		
v B	13	11.6	3		
v b	8	3.9	1	6.013	.11
$V^t v$ in relation to #3#2					
V^t #3	24	34.9	9		
V^t #2	17	11.6	3		
v #3	18	11.6	3		
v #2	3	3.9	1	9.657	.03
$V^t v$ in relation to Rr					
V^t R	36	34.9	9		
V^t r	5	11.6	3		
v R	17	11.6	3		
v r	4	3.9	1	6.306	.09

Appendix (continued)

Character	Obs.	Cal.	Ratio	X^2	Probability
Cross B248 (cont.)					
$V^t v$ in relation to Nn					
V^t N	34	34.9	9		
V^t n	7	11.6	3		
v N	15	11.6	3		
v n	6	3.9	1	3.975	.28
Bb in relation to #3#2					
B #3	27	34.9	9		
B #2	14	11.6	3		
b #3	15	11.6	3		
b #2	6	3.9	1	4.412	.22
Bb in relation to Rr					
B R	36	34.9	9		
B r	5	11.6	3		
b R	17	11.6	3		
b r	4	3.9	1	6.306	.09
Bb in relation to Nn					
B N	32	34.9	9		
B n	9	11.6	3		
b N	17	11.6	3		
b n	4	3.9	1	3.340	.32
#3#2 in relation to Rr					
#3 R	34	34.9	9		
#3 r	8	11.6	3		
#2 R	19	11.6	3		
#2 r	1	3.9	1	8.018	.04
#3#2 in relation to Nn					
#3 N	36	34.9	9		
#3 n	6	11.6	3		
#2 N	13	11.6	3		
#2 n	7	3.9	1	5.371	.15
Rr in relation to Nn					
R N	42	34.9	9		
R n	11	11.6	3		
r N	7	11.6	3		
r n	2	3.9	1	4.110	.24
Cross B249					
Vv in relation to Bb					
V B	57	52.875	9		
V b	19	17.625	3		
v B	12	17.625	3		
v b	6	5.875	1	2.227	.52

Appendix (continued)

Character	Obs.	Cal.	Ratio	X^2	Probability
Cross B249 (cont.)					
Vv in relation to Rr					
V R	61	52.875	9		
V r	15	17.625	3		
v R	16	17.625	3		
v r	2	5.875	1	4.345	.23
Vv in relation to Nn					
V N	65	52.875	9		
V n	11	17.625	3		
v N	13	17.625	3		
v n	5	5.875	1	6.615	.09
Vv in relation to Ss					
V S	49	52.875	9		
V s	27	17.625	3		
v S	15	17.625	3		
v s	3	5.875	1	7.059	.07
Vv in relation to Anan					
V AnAn	31	23.5	3		
V Anan	45	47	6		
v AnAn	4	7.83	1		
v Anan	14	15.67	2	4.537	.21
Bb in relation to Rr					
B R	58	52.875	9		
B r	11	17.625	3		
b R	19	17.625	3		
b r	6	5.875	1	3.097	.40
Bb in relation to Nn					
B N	58	52.875	9		
B n	11	17.625	3		
b N	20	17.625	3		
b n	5	5.875	1	3.437	.32
Bb in relation to Ss					
B S	46	52.875	9		
B s	23	17.625	3		
b S	18	17.625	3		
b s	7	5.875	1	2.757	.45
Bb in relation to Anan					
B AnAn	25	23.5	3		
B Anan	46	47	6		
b AnAn	12	7.83	1		
b Anan	13	15.67	2	2.708	.45

Appendix (continued)

Character	Obs.	Cal.	Ratio	X^2	Probability
Cross B249 (cont.)					
Rr in relation to Nn					
R N	64	52.875	9		
R n	13	17.625	3		
r N	14	17.625	3		
r n	3	5.875	1	5.707	.12
Rr in relation to Ss					
R S	50	52.875	9		
R s	27	17.625	3		
r S	14	17.625	3		
r s	3	5.875	1	7.296	.07
Rr in relation to Anan					
R AnAn	28	23.5	3		
R Anan	49	47	6		
r AnAn	7	7.83	1		
r Anan	10	15.67	2	3.086	.40
Nn in relation to Ss					
N S	54	52.875	9		
N s	24	17.625	3		
n S	10	17.625	3		
n s	6	5.875	1	5.631	.14
Nn in relation to Anan					
N AnAn	29	23.5	3		
N Anan	49	47	6		
n AnAn	6	7.83	1		
n Anan	10	15.67	2	3.852	.28
Ss in relation to Anan					
S AnAn	24	23.5	3		
S Anan	40	47	6		
s AnAn	11	7.83	1		
s Anan	19	15.67	2	3.044	.40
Cross B250, Family I					
Vv in relation to Bb					
V B	93	82.8	9		
V b	23	27.6	3		
v B	21	27.6	3		
v b	10	9.2	1	3.599	.31
Vv in relation to #3#2					
V #3	66	55.1	3		
V #2	50	55.1	3		
v #3	16	18.4	1		
v #2	15	18.4	1	3.570	.31

Appendix (continued)

Character	Obs.	Cal.	Ratio	X^2	Probability
Cross B250 (cont.)					
Vv in relation to Rr					
V R	87	82.8	9		
V r	29	27.5	3		
v R	25	27.5	3		
v r	6	9.2	1	1.635	.66
Vv in relation to Nn					
V N	93	82.8	9		
V n	23	27.5	3		
v N	25	27.5	3		
v n	6	9.2	1	3.333	.34
Vv in relation to Ss					
V S	95	82.8	9		
V s	21	27.5	3		
v S	20	27.5	3		
v s	11	9.2	1	5.732	.13
Bb in relation to #3#2					
B #3	62	55.1	3		
B #2	52	55.1	3		
b #3	20	18.4	1		
b #2	13	18.4	1	2.762	.48
Bb in relation to Rr					
B R	91	82.8	9		
B r	23	27.5	3		
b R	21	27.5	3		
b r	12	9.2	1	3.937	.28
Bb in relation to Nn					
B N	93	82.8	9		
B n	21	27.5	3		
b N	25	27.5	3		
b n	8	9.2	1	3.177	.48
Bb in relation to Ss					
B S	93	82.8	9		
B s	21	27.5	3		
b S	22	27.5	3		
b s	11	9.2	1	4.245	.24
#3#2 in relation to Rr					
#3 R	63	55.1	3		
#3 r	19	18.4	1		
#2 R	49	55.1	3		
#2 r	16	18.4	1	2.141	.52

Appendix (continued)

Character	Obs.	Cal.	Ratio	χ^2	Probability
Cross B250 (cont.)					
#3#2 in relation to Nn					
#3 N	69	55.1	3		
#3 n	13	18.4	1		
#2 N	49	55.1	3		
#2 n	16	18.4	1	6.080	.12
#3#2 in relation to Ss					
#3 S	61	55.1	3		
#3 s	21	18.4	1		
#2 S	54	55.1	3		
#2 s	11	18.4	1	3.936	.27
Rr in relation to Nn					
R N	95	82.8	9		
R n	17	27.5	3		
r N	23	27.5	3		
r n	12	9.2	1	7.396	.07
Rr in relation to Ss					
R S	87	82.8	9		
R s	25	27.5	3		
r S	28	27.5	3		
r s	7	9.2	1	.976	.81
Nn in relation to Ss					
N S	92	82.8	9		
N s	26	27.5	3		
n S	23	27.5	3		
n s	6	9.2	1	2.953	.41
Cross B250, Family II					
Bb in relation to Rr					
B R	68	69.75	9		
B r	21	23.25	3		
b R	27	23.25	3		
b r	8	7.75	1	.881	.82
Bb in relation to Vv					
B V	64	69.75	9		
B v	25	23.25	3		
b V	29	23.25	3		
b v	6	7.75	1	2.526	.48
Bb in relation to Nn					
B N	60	69.75	9		
B n	29	23.25	3		
b N	28	23.25	3		
b n	9	7.75	1	3.303	.35

Appendix (continued)

Character	Obs.	Cal.	Ratio	x^2	Probability
Cross B250 (cont.)					
Bb in relation to Ss					
B S	69	69.75	9		
B s	20	23.25	3		
b S	22	23.25	3		
b s	13	7.75	1	4.096	.26
Bb in relation to #3#2					
B #3	67	69.75	9		
B #2	22	23.25	3		
b #3	25	23.25	3		
b #2	10	7.75	1	.986	.82
Rr in relation to Vv					
R V	69	69.75	9		
R v	26	23.25	3		
r V	24	23.25	3		
r v	5	7.75	1	1.333	.72
Rr in relation to Nn					
R N	67	69.75	9		
R n	28	23.25	3		
r N	19	23.25	3		
r n	10	7.75	1	2.509	.46
Rr in relation to Ss					
R S	64	69.75	9		
R s	31	23.25	3		
r S	27	23.25	3		
r s	2	7.75	1	7.928	.05
Rr in relation to #3#2					
R #3	70	69.75	9		
R #2	25	23.25	3		
r #3	22	23.25	3		
r #2	7	7.75	1	.296	.96
Vv in relation to Nn					
V N	65	69.75	9		
V n	28	23.25	3		
v N	21	23.25	3		
v n	10	7.75	1	2.165	.53
Vv in relation to Ss					
V S	70	69.75	9		
V s	23	23.25	3		
v S	21	23.25	3		
v s	10	7.75	1	.874	.83

Appendix (continued)

Character	Obs.	Cal.	Ratio	χ^2	Probability
Cross B250 (cont.)					
Vv in relation to #3#2					
V #3	73	69.75	9		
V #2	20	23.25	3		
v #3	20	23.75	3		
v #2	11	7.75	1	2.423	.50
Nn in relation to Ss					
N S	62	69.75	9		
N s	24	23.25	3		
n S	29	23.25	3		
n s	9	7.75	1	2.509	.47
Nn in relation to #3#2					
N #3	70	69.75	9		
N #2	16	23.25	3		
n #3	22	23.25	3		
n #2	16	7.75	1	11.106	.01+
Ss in relation to #3#2					
S #3	66	69.75	9		
S #2	23	23.25	3		
s #3	24	23.25	3		
s #2	9	7.75	1	.281	.96
Bb in relation to Nor.SS					
B Nor.	41	46.5	3		
B SS	46	46.5	3		
b Nor.	21	15.5	1		
b SS	14	15.5	1	2.796	.42
Rr in relation to Nor.SS					
R Nor.	52	46.5	3		
R SS	45	46.5	3		
r Nor.	16	15.5	1		
r SS	11	15.5	1	2.022	.56
Vv in relation to Nor.SS					
V Nor.	48	46.5	3		
V SS	45	46.5	3		
v Nor.	14	15.5	1		
v SS	17	15.5	1	.386	.94
Nn in relation to Nor.SS					
N Nor.	31	46.5	3		
N SS	55	46.5	3		
n Nor.	31	15.5	1		
n SS	7	15.5	1	26.905	.01-

Appendix (continued)

Character	Obs.	Cal.	Ratio	X^2	Probability
Cross B250 (cont.)					
Ss in relation to Nor.SS					
S Nor.	46	46.5	3		
S SS	45	46.5	3		
s Nor.	16	15.5	1		
s SS	17	15.5	1	.215	.97
#3#2 in relation to Nor.SS					
#3 Nor.	44	46.5	3		
#3 SS	48	46.5	3		
#2 Nor.	18	15.5	1		
#2 SS	14	15.5	1	.731	.87
Cross B252					
Vv in relation to Rr					
V R	154	153	9		
V r	47	51	3		
v R	41	51	3		
v r	30	17	1	12.222	.01
Vv in relation to Gsgs					
V Gs	146	153	9		
V gs	53	51	3		
v Gs	59	51	3		
v gs	12	17	1	2.967	.40
Rr in relation to Gsgs					
R Gs	145	153	9		
R gs	50	51	3		
r Gs	62	51	3		
r gs	15	17	1	3.046	.40
Vv in relation to Nor.SS					
V Nor.	150	153	9		
V SS	51	51	3		
v Nor.	48	51	3		
v SS	23	17	1	2.353	.50
Rr in relation to Nor.SS					
R Nor.	142	153	9		
R SS	53	51	3		
r Nor.	56	51	3		
r SS	21	17	1	2.301	.51
Gsgs in relation to Nor.SS					
Gs Nor.	144	153	9		
Gs SS	63	51	3		
gs Nor.	54	51	3		
gs SS	11	17	1	5.647	.14

Appendix (continued)

Character	Obs.	Cal.	Ratio	X^2	Probability
Cross B257					
$V^t v$ in relation to Gege					
V^t Ge	228	216	9		
V^t ge	69	72	3		
v Ge	62	72	3		
v ge	25	24	1	2.223	.51
$V^t v$ in relation to Rr					
V^t R	234	216	9		
V^t r	63	72	3		
v R	64	72	3		
v r	23	24	1	3.556	.32
$V^t v$ in relation to Prpr					
V^t Pr	202	162	27		
V^t pr	95	126	21		
v Pr	22	54	9		
v pr	65	42	7	49.062	.01*
Gege in relation to Rr					
Ge R	230	216	9		
Ge r	61	72	3		
ge R	68	72	3		
ge r	25	24	1	2.797	.45
Gege in relation to Prpr					
Ge Pr	175	162	27		
Ge pr	116	126	21		
ge Pr	49	54	9		
ge pr	44	42	7	2.395	.32
Rr in relation to Prpr					
R Pr	163	162	27		
R pr	135	126	21		
r Pr	61	54	9		
r pr	25	42	7	8.437	.04
$V^t v$ in relation to Nor.SS					
V^t Nor.	146	144	3		
V^t SS	151	144	3		
v Nor.	48	48	1		
v SS	39	48	1	2.056	.55
Gege in relation to Nor.SS					
Ge Nor.	145	144	3		
Ge SS	146	144	3		
ge Nor.	49	48	1		
ge SS	44	48	1	.389	.94

Appendix (continued)

Character	Obs.	Cal.	Ratio	X^2	Probability
Cross B257 (cont.)					
Rr in relation to Nor.SS					
R Nor.	151	144	3		
R SS	147	144	3		
r Nor.	43	48	1		
r SS	43	48	1	1.445	.68
Prpr in relation to Nor.SS					
Pr Nor.	114	108	9		
Pr SS	110	108	9		
pr Nor.	80	84	7		
pr SS	80	84	7	.750	.84
Cross B259					
Prpr in relation to Gege					
Pr Ge	165	169.69	27		
Pr ge	69	56.56	9		
pr Ge	108	132.46	21		
pr ge	62	44.19	7	14.561	.01"
Prpr in relation to $V^t v$					
Pr V^t	220	169.69	27		
Pr v	14	56.56	9		
pr V^t	99	132.46	21		
pr v	71	44.19	7	71.659	.01"
Prpr in relation to Rr					
Pr R	184	169.69	27		
Pr r	50	56.56	9		
pr R	143	132.46	21		
pr r	27	44.19	7	9.493	.05
Gege in relation to $V^t v$					
Ge V^t	216	227.25	9		
Ge v	57	75.75	3		
ge V^t	103	75.75	3		
ge v	25	25.25	1	15.300	.01"
Gege in relation to Rr					
Ge R	217	227.25	9		
Ge r	56	75.75	3		
ge R	110	75.75	3		
ge r	21	25.25	1	21.813	.01"
$V^t v$ in relation to Rr					
V^t R	255	227.25	9		
V^t r	64	75.75	3		
v R	72	75.75	3		
v r	13	25.25	1	11.340	.01

Appendix (continued)

Character	Obs.	Cal.	Ratio	X^2	Probability
Cross B266					
$V^t v$ in relation to Nn					
V^t N	63	78.75	9		
V^t n	29	26.25	3		
v N	36	26.25	3		
v n	12	8.75	1	8.267	.04
$V^t v$ in relation to Bb					
V^t B	80	78.75	9		
V^t b	22	26.25	3		
v B	25	26.25	3		
v b	13	8.75	1	2.832	.42
Nn in relation to Bb					
N B	74	78.75	9		
N b	25	26.25	3		
n B	31	26.25	3		
n b	10	8.75	1	1.384	.72
Cross B272					
$V^t v$ in relation to Nn					
V^t N	32	39.375	9		
V^t n	13	13.125	3		
v N	19	13.125	3		
v n	6	4.375	1	4.616	.21
$V^t v$ in relation to Bb					
V^t B	34	39.375	9		
V^t b	11	13.125	3		
v B	23	13.125	3		
v b	2	4.375	1	9.797	.03
Nn in relation to Bb					
N B	43	39.375	9		
N b	8	13.125	3		
n B	14	13.125	3		
n b	5	4.375	1	2.463	.49
Cross B279					
$V^t v$ in relation to Bb					
V^t B	117	112.5	9		
V^t b	32	37.5	3		
v B	36	37.5	3		
v b	15	12.5	1	1.547	.48

Appendix (continued)

Character	Obs.	Cal.	Ratio	X^2	Probability
Cross B279 (cont.)					
$V^t v$ in relation to Nn					
V^t N	106	112.5	9		
V^t n	43	37.5	3		
v N	37	37.5	3		
v n	14	12.5	1	1.369	.51
$V^t v$ in relation to Rr					
V^t R	122	112.5	9		
V^t r	27	37.5	3		
v R	42	37.5	3		
v r	9	12.5	1	5.262	.16
Bb in relation to Nn					
B N	110	112.5	9		
B n	43	37.5	3		
b N	33	37.5	3		
b n	14	12.5	1	1.532	.68
Bb in relation to Rr					
B R	128	112.5	9		
B r	25	37.5	3		
b R	36	37.5	3		
b r	11	12.5	1	6.542	.09
Nn in relation to Rr					
N R	116	112.5	9		
N r	27	37.5	3		
n R	48	37.5	3		
n r	9	12.5	1	6.969	.08
Cross B281					
Vv in relation to Kk					
V K	67	69.75	9		
V k	22	23.25	3		
v K	24	23.25	3		
v k	11	7.75	1	1.563	.68
Vv in relation to Mms					
V Ms	66	69.75	9		
V ms	23	23.25	3		
v Ms	23	23.25	3		
v ms	12	7.75	1	2.530	.48

Appendix (continued)

Character	Obs.	Cal.	Ratio	X^2	Probability
Cross B281 (cont.)					
Kk in relation to Msms					
K Ms	62	69.75	9		
K ms	29	23.25	3		
k Ms	27	23.25	3		
k ms	6	7.75	1	2.283	.52
Vv in relation to Nor.SS					
V Nor.	28	33.375	3		
V SS	38	33.375	3		
v Nor.	10	11.125	1		
v SS	13	11.125	1	1.936	.58
Kk in relation to Nor.SS					
K Nor.	22	33.375	3		
K SS	40	33.375	3		
k Nor.	16	11.125	1		
k SS	11	11.125	1	7.339	.03
Msms in relation to Nor.SS					
Ms Nor.	38	44.5	1		
Ms SS	51	44.5	1		
ms Nor.	--	----			
ms SS	--	----		1.899	.19
Cross B283					
Vv in relation to Nn					
V N	40	43.875	9		
V n	19	14.625	3		
v N	17	14.625	3		
v n	2	4.875	1	3.732	.29
Vv in relation to Rr					
V R	49	43.875	9		
V r	10	14.625	3		
v R	16	14.625	3		
v r	3	4.875	1	2.912	.40
Vv in relation to #2#3					
V #2	45	43.875	9		
V #3	14	14.625	3		
v #2	10	14.625	3		
v #3	9	4.875	1	5.009	.19
Vv in relation to Brbr					
V Br	47	43.875	9		
V br	12	14.625	3		
v Br	14	14.625	3		
v br	5	4.875	1	.724	.86

Appendix (continued)

Character	Obs.	Cal.	Ratio	X^2	Probability
Cross B283 (cont.)					
Nn in relation to Rr					
N R	50	43.875	9		
N r	7	14.625	3		
n R	15	14.625	3		
n r	6	4.875	1	5.098	.19
Nn in relation to #2#3					
N #2	41	43.875	9		
N #3	16	14.625	3		
n #2	14	14.625	3		
n #3	7	4.875	1	1.425	.70
Nn in relation to Brbr					
N Br	47	43.875	9		
N br	10	14.625	3		
n Br	14	14.625	3		
n br	7	4.875	1	2.803	.60
Rr in relation to #2#3					
R #2	43	43.875	9		
R #3	22	14.625	3		
r #2	12	14.625	3		
r #3	1	4.875	1	7.288	.07
Rr in relation to Brbr					
R Br	54	43.875	9		
R br	11	14.625	3		
r Br	7	14.625	3		
r br	6	4.875	1	7.468	.06
#2#3 in relation to Brbr					
#2 Br	38	43.875	9		
#2 br	17	14.625	3		
#3 Br	23	14.625	3		
#3 br	0	4.875	1	10.943	.01+

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