5-1972

A Study of the Inheritance and Linkage Relationships of Three Glossy Characteristics in Barley

Jess R. Martineau
Utah State University

A STUDY OF THE INHERITANCE AND LINKAGE RELATIONSHIPS OF THREE GLOSSY CHARACTERISTICS IN BARLEY

by

Jess R. Martineau

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

of

MASTER OF SCIENCE

in

Plant Science

UTAH STATE UNIVERSITY
Logan, Utah

1972

ACKNOWLEDGMENTS

I express sincere gratitude to my major professor, Dr. W. G. Dewey, for his critical review of the thesis, and for his continued help and advice.

I would also like to express my thanks and appreciation to the members of my thesis committee, Dr. O. S. Cannon and Dr. D. R. McAllister, for devoting of their time and interest in my behalf.

To my wife, Shirley, I am especially indebted for all the long hours she helped me in the field and in the office.

Jess R. Martineau

Jess R. Martineau

TABLE OF CONTENTS

LIST OF TABLES

Table | Page

Table | Page

Table Page

ABSTRACT

A Study of the Inheritance and Linkage Relationships

of Three Glossy Characteristics in Barley

by

Jess R. Martineau, Master of Science

Utah State University, 1972

Major Professor: Dr. Wade G. Dewey
Department: Plant Science

Twenty-two barley crosses (Hordeum sp.) were studied in the F_2 generation to determine the inheritance of the following contrasting characters: (N, n), (E, e), (Tr, tr), (Li, li), (Gp, gp), (K, k), (Z, z), (Gl, gl), (Gs, gs), (B, b), (Trd, trd), (O, o), (R, r), (Rb, rb), and (Ge, ge).

The three factors for glossyness, (gl), (gs), and (ge), were studied in relation to the other factors and each other to determine possible linkage relationships.

(gl) was found to be linked with (k) with 16 percent recombination and to (z) with 13 percent recombination. (gs) appeared to be linked with (gp) in two crosses, with a third cross showing independence. No other linkage relationships were found.

(65 pages)

INTRODUCTION

Barley is one of the leading experimental organisms in the genetic studies of higher plants. The cultivated species are diploid, with seven chromosome pairs, each of which can be identified cytologically. Barley has a large number of contrasting characters, many of which have been assigned to relative positions on linkage maps. The mapping of chromosomes is of practical application in facilitating breeding operations, especially when certain genes are known to be associated with, or responsible for yield, quality, or disease resistance.

Among barley mutants, those with altered epidermal wax coating are among the most frequent. They range from a slight reduction to complete absence of wax and have been described as "bright green," "waxless" or "wachsfrei," "bloomless," "glaucous ear," "glaucous sheath," "waxless head," and "glossy" (Smith, 1951). The gene symbols ge, gs, wh, wh2, wl, and gl have been used to represent them (Smith, 1951). More recently (Lundqvist and Von Wettstein, 1962; Gustafsson et al., 1969) the symbol cer- from "eceriferum" (latin: cer = wax, and ferre = bear) has been proposed.

Close to 400 mutant characters have been recognized in barley (Nilan, 1964). This study involves 15 of these characters, with emphasis on the inheritance pattern of three glossy characteristics, their inter-relationships, and linkage relationships with the other 12 characters.

REVIEW OF LITERATURE

Comprehensive reviews of barley genetics studies have been published by Buckley (1930), Daane (1931), Robertson (1933, 1937, 1939), Robertson et al. (1941, 1947, 1955, 1965), Immer and Henderson (1943), Smith (1951), Woodward (1957a), Nilan (1964), and Haus et al. (1971).

This review will be confined to literature directly pertaining to material involved in this study. Assignment of genes to linkage groups is according to Nilan (1964) and Haus et al. (1971).

Inheritance of Individual Characters

Linkage group 1

Covered (N) versus naked (n) caryopsis. Woodward (1957b), Andersen (1958), Imam (1959), Doney (1961), Oldham (1962), and Tehrani (1966) all reported that covered is dominant over naked caryopsis and is conditioned by a single gene. Smith (1951) and Andersen (1958) reported the heterozygotes as being more or less intermediate.

Linkage group 2

Normal (E) versus elongated (awned) outer glume (e). A single gene difference was reported by Immer and Henderson (1943), Woodward (1957b), Heiner (1958), Andersen (1958), Imam (1959), Oldham (1962), and Tehrani

(1966). Gill (1951) and Doney (1961) reported two factors. LeBaron (1959) reported ratios of 3:1, 9:1, and 5:1 in the F_2 generation, indicating one or two factors.

Normal (Tr) versus triple-awned (tr) lemma. A number of workers including Andersen (1958), Heiner (1958), Imam (1959), LeBaron (1959), Doney (1961), and Tehrani (1966) reported triple-awned lemma to be recessive and due to one gene pair.

Liguled (Li) versus liguleless (li) plants. Ratios of three liguled to one liguleless plants were found in the F_2 by Heiner (1958), Imam (1959), LeBaron (1959), Doney (1961), Oldham (1962), and Tehrani (1966) all found rather poor fits to a 3:1 ratio. This they attributed to high seedling mortality and late maturity of grandpa plants.

Linkage group 4

Hooded (K) versus awned (k) spike. Smith (1951) lists 36 references supporting a 3:1 F_2 ratio, with hoods dominant to awns. Wheatley (1955) reported a one factor difference in some crosses and a two factor difference in other crosses. These latter crosses segregated 9 hooded to 7 awned spikes. Woodward (1955) and Woodward and Rasmusson (1957) also found a two factor difference. Many workers have noted a variety of awn and hood lengths. Albrechtsen (1957) studied crosses between hooded and short-awned, hooded and long-awned, and between long- and short-awned plants and concluded that two factor pairs were involved, (Kk) and (K_2k_2).

Nilan (1964) reported that Walker and co-workers found a recessive gene (kr) for hoods.

Normal (Z) versus zoned (z) leaf. Two gene pairs which behave in the same manner, but are not linked, have been reported. Both are recessive for zoned leaf. Wheatley (1955), Heiner (1958), Andersen (1958), LeBaron (1959), Doney (1961), and Oldham (1962) all reported a poor fit to a 3:1 F_2 ratio and attributed this to mortality of some of the immature, zoned leaf plants.

Normal (Gl) versus glossy (gl) leaf. Glossy leaf (sometimes called glossy seedling) is characterized by the absence of epidermal wax on the leaf blade surface, while the stems, sheaths and heads have a normal, bluish, wax coating. Robertson and Coleman (1942), Immer and Henderson (1943), Jenkins (1950), Woodward (1950), Smith (1951), Al-Jibouri (1953), Smith (1953), Wheatley (1955), Heiner (1958), Imam (1959), Doney (1961), Oldham (1962), Nilan (1964), Tehrani (1966), and Haus et al. (1971) all reported glossy leaf to be recessive and monofactorially inherited. Several of these authors (Wheatley, 1955; Heiner, 1958; Imam, 1959; Doney, 1961; Oldham, 1962; and Tehrani, 1966) reported low probability values for a 3:1 ratio. This they attribute to poor germination and a differential mortality of glossy-leaved plants. Several of these authors also reported that seeds grown on glossy-leaved plants have a scalded appearance.

A second gene (Gl_2gl_2) was reported by Robertson, Weibe, and Immer (1941), Kasha and Walker (1960), Kasha (Nilan, 1964), and Livers (Nilan, 1964). Robertson and Coleman (1942) also reported a (Gl_2gl_2) gene pair, but the entire plant was glossy. Takahashi (Robertson et al., 1965) reported a (Gl_3gl_3) and Walker et al. (1963) reported a (Gl_4gl_4).

Normal (Gs) versus glossy (gs) sheath and spike. The (Gsgs) and (Gege) factors (ge for glossy spike alone) are rather difficult to review, due in part to the confusion caused by the symbols and terminology employed in the literature. According to Rasmusson and Lambert, who studied 14 different glossy-sheath lines:

> Glossy-sheath mutants in barley are characterized by the absence of a waxy coating on the sheaths and stems. The absence of wax results in a striking glossy or shiny appearance. (Rasmusson and Lambert, 1965, p. 252)

Albrechtsen (1957), Doney (1961), and Tehrani (1966) used (Gsgs) to refer to normal versus glossy stem, without reference to the condition of the sheath or ear. Andersen (1958), and Oldham (1962) used (Gsgs) to refer to normal versus glossy stems and spikes. Sorensen (1952), Heiner (1958), Woodward (1957b), and LeBaron (1959) used (Gsgs) to refer to normal versus glossy sheath and spike. Smith (1953) referred to glossy culm and spike, but described it as "waxy, and without bloom." (It appears reasonable to assume the last seven authors were referring to the same factor.)

Other authors have employed the term "glaucous," some using it as a synonym for glossy, others as an antonym. Immer and Henderson (1943) used (Gsgs) to refer to "non-glaucous versus glaucous sheath." Several authors appear to mis-use the term. Wheatley (1955) used (Gsgs) in connection with glaucous sheath and spike, but described glaucous as "waxy, and without bloom." According to Isom:

> The glaucous characteristic (Ge) is dominant to the normal (ge) which possess the characteristic "bloom" effect on cereals. The (Ge) factor is expressed only on the spike. The absence of "bloom" on the spike gives it a greenish, oily or waxy characteristic termed "glaucous." (Isom, 1951, p. 14)

Imam (1959) uses (Gsgs) in reference to normal versus glossy stem and spike, and (Gege) to refer to normal versus glaucous stem and spike. Just what glaucous refers to here is not understood by the author, since the presence and the absence of wax has already been represented by (Gsgs).

The confusion may be due to the fact that waxy surfaces are usually considered to be shiny, or "glossy," but the wax on barley plants gives them a dull, frosted appearance, such as that found on some plums, grapes, and cabbage leaves. Regardless of the symbols and terms used, there appears to be at least one factor for glossy sheaths and spikes, another for glossy spikes (ear) alone, and several for glossy sheaths and stems.

Assuming, perhaps erroneously, that the terms sheath, stem, and culm have been used by the above authors to refer to the same thing, all glossy-sheath or glossy-sheath-and-spike mutants reviewed here were reported to be recessive, and conditioned by a single gene. Kasha and Walker (1960) and Robertson (Nilan, 1964) reported a second factor for glossy sheath and stem, (gs_2). Walker and co-workers (Nilan, 1964) reported a (gs_3), Smith (1951) reported that Ivanov found (gs_4) which Walker et al. (1963) confirmed, and Rasmusson and Lambert (1965) reported (gs_5) and (gs_6).

Linkage group 5

Black (B) versus white (b) lemma and pericarp. Smith (1951) listed 30 articles reporting black chaff dominant to white, and due to one factor. Woodward (1941, 1942) proposed an allelomorphic series of three genes for the degree of pigmentation; black (BB), grey (B^gB^g), and white (bb). The darker color, in each combination, was dominant over the lighter, and segregated monofactorially. Das (1957) reported control by two genes and a 9:7 ratio in the F_2 generation.

Normal (Trd) versus third (trd) outer glume. The third outer glume is recessive and has been reported by Konzak (1953), Heiner (1958), Andersen (1958), and Nilan (1964), to be monofactorially inherited.

Linkage group 6

Normal (O) versus orange (o) lemma. Buckley (1930), Myler and Stanford (1942), Heiner (1958), Oldham (1962), and Robertson et al. (1965) reported orange lemma as being recessive and due to one factor.

Linkage group 7

Rough (R) versus smooth (r) awns. Several investigators--Daane (1931), Byington (1940), Jenkins (1950), Woodward (1950), Gill (1951), Andersen (1958), and Doney (1961)--have reported a single factor inheritance with rough awns being dominant. Al-Jibouri (1953), Heiner (1958), Imam (1959), and Oldham (1962), reported single factor ratios in some crosses and two or more factors in other crosses. Nilan (1964) and Tehrani (1966) reported two factor inheritance. Hayes and co-workers (Smith, 1951) reported one main dominant factor for rough awns, with modifying factors affecting the degree of roughness.

Unassigned factor pairs

Normal (Rb) versus ribbon-grass (rb). Robertson et al (1947), Gill (1951), Wheatley (1955), Andersen (1958), Heiner (1958), Doney (1961), and Tehrani (1966) reported ribbon-grass to be recessive with a single factor mode of inheritance. Oldham is of the opinion that some plants carrying the gene for ribbon-grass do not show it. Tehrani reported that weather conditions affect the expression of this trait, with more plants showing (rb) when under stress. She also contributes poor fit to 3:1 F_2 ratios to a "relatively high seedling mortality."

Normal (Ge) versus glossy (ge) ear. Immer and Henderson (1943), Waddoups (1949), Smith (1951), Isom (1951), and Nilan (1964) reported one factor, with glossy ear as recessive. Woodward (1957b) reported one factor, but glossy ear as dominant. Tehrani (1966) found glossy ear dominant in one cross, and recessive in another, segregating 9:7 and 7:9, respectively. Imam (1959) reported "glaucous" ear as being dominant, but failed to say whether glaucous was with or without the wax. Isom (1951) reported glaucous (ge) was dominant, and defined "glaucous" as being glossy.

Reported Linkages Involving Glossys

Normal (Gl) versus glossy (gl) leaf in relation to other factor pairs

Recombination %	Phase	Authority
	(Glgl) in relation to (Kk)	
10.0		Immer and Henderson (1943)
12.5	Repulsion	Tehrani (1966)
15.5		Woodward (1955)
16.0	Coupling	Heiner (1958)
16.4	Repulsion	Woodward (1955)
17.5	Coupling	Woodward (1957b)
18.5	Repulsion	Albrechtsen (1957)
19.3		Isom (1951)
19.3	Coupling	Woodward (1955)
22.0	Repulsion	Oldham (1962)
22.2	Coupling	Woodward (1957a)
23.0	Repulsion	Woodward (1957b)
23.5		Woodward (1950)
24.0	Coupling	Heiner (1958)
25.0	Repulsion	Oldham (1962)
25.5		Wheatley (1955)
26.3	Coupling	Albrechtsen (1957)
28.0	Repulsion	Heiner (1958)
28.2		Imam (1959)
29.0	Repulsion	Oldham (1962)
33.5		Al-Jibouri (1953)
34.5	Repulsion	Woodward (1957a)
	(Glgl) in relation to (Zz)	
3.0	Repulsion	Immer and Henderson (1943)
7.0	Coupling	Immer and Henderson (1943)
8.5	Repulsion	Albrechtsen (1957)
8.5	Coupling	Doney (1961)
9.3	Coupling	Woodward (1957a)
12.5	Coupling	Doney (1961)
14.0	Repulsion	Smith (1953)
14.0	Repulsion	Woodward (1957a)
30.0	Coupling	Albrechtsen (1957)

Recombination %	Phase	Authority
30.0	Repulsion	Doney (1961)
33.0		Immer and Henderson (1943)
35.5	Repulsion	Woodward (1957b)
	(Glgl) in relation to (Rbrb)	
34.5	Repulsion	Woodward (1955)
	(Gl_2gl_2) in relation to (Kk)	
25.0		Robertson and Coleman (1942)
	(Gl_2gl_2) in relation to (Lili)	
28.0		Robertson and Coleman (1942)
	(Gl_3gl_3) in relation to (Kk)	
31.9	Coupling	Robertson et al. (1965)
	(Gl_4gl_4) in relation to (Oo)	
30.4	Repulsion	Walker et al. (1963)
	(Gl_4gl_4) in relation to (Gs_4gs_4)	
29.4	Coupling	Walker et al. (1963)
30.4	Repulsion	Walker et al. (1963)

Normal (Gs) versus glossy (gs) sheath and spike in relation to other factor pairs

	(Gsgs) in relation to (Glgl)	
14.0	Repulsion	Woodward (1955)
21.7	Coupling	Imam (1959)
35.0	Coupling	Woodward (1957b)
38.5	Coupling	Heiner (1958)
	(Gsgs) in relation to (Kk)	
29.0	Repulsion	Woodward (1955)
39.0		Woodward (1957a)
40.0		Woodward (1957a)

Recombination %	Phase	Authority
	(Gsgs) in relation to (Lili)	
36.3	Repulsion	Imam (1959)
	(Gsgs) in relation to (Rr)	
34.5	Repulsion	Tehrani (1966)
	(Gsgs) in relation to (Nn)	
15.1	Repulsion	Woodward (1955)
	(Gsgs) in relation to (Zz)	
18.0	Repulsion	Woodward (1955)
23.9	Repulsion	Albrechtsen (1957)
24.5	Repulsion	Woodward (1957b)
33.5	Repulsion	Tehrani (1966)

Normal (Ge) versus glossy (ge) ear in relation to other factor pairs

	(Gege) in relation to (Kk)	
19.3		Isom (1951)
24.5		Woodward (1957a)
28.0	Coupling	Heiner (1958)
29.0	Repulsion	Tehrani (1966)
30.5		Al-Jibouri (1953)
	(Gege) in relation to (Bb)	
29.0	Repulsion	Tehrani (1966)

(Glgl) appears to belong in linkage group four, due to its linkage to (Kk) and (Zz). Woodward (1957a) also reported a weak association between glossy leaf and ribbon-grass. Since (Rb) has not yet been located, this would indicate it might also belong in group four.

(Gsgs) has been associated with (Glgl), (Kk), and (Zz) in group four, but also with (Nn) in group one, with (Lili) in two, and with (Rr) in linkage group seven.

Walker et al. (1963) reported that (Gs_3gs_3) was linked to a gene (Brbr) in linkage group one, with 24.1 percent recombination in the repulsion phase. The same workers also reported (Gs_4gs_4) to be linked with (Gl_4gl_4) which in turn appeared to be linked with (Oo), placing (Gs_4gs_4) and (Gl_4gl_4) in linkage group six. In the same study, (Gs_5gs_5) showed association with (Ee) and (Vv) in group two.

Several authors place (Gege) in linkage group four, but one reported an association with (Bb), which would place it in group five.

Reports of more than 40% recombination are not included in this review, as they are interpreted by the author to indicate independence.

MATERIALS AND METHODS

The crosses used in this study were made by Dr. W. G. Dewey in 1970, using material from the late R. W. Woodward's barley genetic tester stocks. The F_o seed was planted in the greenhouse during the winter of 1970-1971, the smaller, weaker seeds having first been germinated on blotter paper in petri dishes. As soon as the heads began to emerge from the boot, they were covered with glassine bags to prevent out-crossing. The F_1 plants were classified individually as to phenotype, and each plant was checked to be sure it was the result of a cross and was not due to selfing. The F_1 plants were harvested and kept separate, so that seed from each F_1 plant constituted a family. There were 22 crosses, designated J-1 through J-22, with from one to ten families within a cross, designated "a" through "j." The crosses, their parents, and the characters segregating in each cross are presented in Table 1.

The F_2 generation was grown during the summer of 1971 at the Evans Experimental Farm, in rows two feet apart. The seed was hand-spaced 3-5 inches apart to promote tillering, and to facilitate classification. A few plants of each parental type were grown to use as a reference in classification. Counts were taken in the field of characters which were visible only before maturity, e.g., glossy leaf, glossy stem and sheath, glossy ear, zoned leaf, and ribbon-grass. Plants showing these characters were tagged,

Table 1. Crosses, parents, and segregating characters

Cross	Parentage	Segregating characters
J-1	Bt-62	Ge Gl Gs N r rb Tr
	Bt-176	ge gl gs n R Rb tr
J-2	Bt-126	ge gl gs Gp n R Tr
	Bt-123	Ge Gl Gs gp N r tr
J-3	Bt-61	ge* gs*
	Bt-35	ge* ge*
J-4	Bt-126	ge gl gs k
	T-360	Ge Gl Gs K
J-5	T-841	ge Gl gs N r o
	Bt-210	Ge gl Gs n R O
J-6	T-841	ge Gl gs Li r Rb o
	Bt-105	Ge gl Gs li R rb O
J-7	Bt-76	Ge Gl Gs N r rb e
	Bt-126	ge gl gs n R Rb E
J-8	Bt-61	ge Gl gs Li r Rb
	Bt-105	Ge gl Gs li R rb
J-9	T-841	k r o
	Bt-194	K R O
J-10	T-399	ge gl* gs Li n Rb z
	Bt-105	Ge gl* Gs li N rb Z
J-11	T-399	ge* gl gs n R z
	Woodvale	ge* Gl Gs N r Z
J-12	Bt-127	ge gl gs N Trd b
	Bt-118	Ge Gl Gs n trd B
J-13	Bt-70	Ge gl Gs k n
	Bt-194	ge Gl gs K N

Table 1 Continued

Cross	Parentage	Segregating characters
J-14	Bt-106	Ge Gl Gs li R rb E
	Bt-162	ge gl gs Li r Rb e
J-15	Bt-127	ge gl gs k N
	T-360	Ge Gl Gs K n
J-16	Bt-142	Ge Gl Gs gp N r tr
	Bt-126	ge gl gs Gp n R Tr
J-17	Bt-176	ge gs tr
	Bt-210	Ge Gs Tr
J-18	Bt-62	Ge Gl Gs N r rb
	Bt-126	ge gl gs n R Rb
J-19	Bt-115	ge* gl Gs n R
	Bt-61	ge* Gl gs N r
J-20	Bt-105	Ge gl Gs li rb b
	Bt-57	ge Gl gs Li Rb B
J-21	Bt-126	ge gl gs Li n Rb
	Bt-106	Ge Gl Gs li N rb
J-22	Bt-123	Ge Gl Gs gp r tr
	Bt-127	ge gl gs Gp R Tr

* Parents showed the same phenotypes, but segregated for these characters in the F_2.

with the appropriate phenotype written on each tag. At maturity, two heads and the tag were taken from each plant, and placed in individual envelopes which were bundled and labeled according to family and cross. These heads were later classified individually for such characteristics as chaff color, awn type, hulled versus hulless kernels, etc.

The data were tabulated and each family analyzed for inheritance of the individual characters. Families were grouped and the characters analyzed as a complete cross, and checked for homogeneity. Data from crosses were then pooled and analyzed as a group, again checking for homogeneity. The data are presented by crosses, except for a few cases where a break-down by family aids in the interpretation.

Chi-square values were calculated to test observed inheritance patterns against hypothesized ratios. The probability values were taken from Snedecor and Cochran (1967). Each of the glossy characters was studied in conjunction with the other characters and with each other in an attempt to identify possible linkages. The partitioned chi-square method (Mather, 1943) was used to detect the presence of linkage, and the product-moment method (Fisher and Balmukand, 1928) was used to estimate the linkage intensities.

Characters Used in This Study and Their Gene Symbols

A total of 15 pairs of contrasting characteristics were used in this study. The gene symbols and their linkage groups are those suggested by Nilan (1964) and by Haus et al. (1971).

Linkage group 1

Covered versus naked caryopsis	N, n

Linkage group 2

Normal versus elongated (awned) outer glume	E, e
Normal versus triple awned lemma	Tr, tr
Liguled versus liguleless plants	Li, li
Normal versus grandpa plants	Gp, gp

Linkage group 4

Hooded versus awned spike	K, k
Normal versus zoned leaf	Z, z
Normal versus glossy leaf	Gl, gl
Normal versus glossy sheath and spike	Gs, gs

Linkage group 5

Black versus white lemma and pericarp	B, b
Normal versus third outer glume	Trd, trd

Linkage group 6

Normal versus orange lemma	O, o

Linkage group 7

Rough versus smooth awns	R, r

Unassigned factor pairs

Normal versus ribbon-grass	Rb, rb
Normal versus glossy ear	Ge, ge

EXPERIMENTAL RESULTS AND DISCUSSION

The results of this study will be presented in the following order:

1. The inheritance of individual characters.
2. (Glgl) in relation to other characters studied.
3. (Gsgs) in relation to other characters studied.
4. (Gege) in relation to other characters studied.

Inheritance of Individual Characters

Linkage group 1

Covered (N) versus naked (n) caryopsis. Table 2 suggests that naked caryopsis is recessive and conditioned by one gene pair, which agrees with former reports (Smith, 1951). However, a low probability value was obtained for cross J-16.

Linkage group 2

Normal (E) versus elongated (e) awned, outer glume. Only two crosses were segregating for (E, e) but they both indicate a simple Mendelian mode of inheritance, with normal being dominant. Taken by family, only one P value dropped below the .05 level, but all families are consistently low in plants showing (e). Even though one of the two crosses does not fit a 3:1 ratio too well, all but one of the total number of families do, which supports single

Table 2. Segregation of covered (N) versus naked (n) caryopsis in the F_2 generation. Chi-square and P values based on a 3:1 ratio.

Cross	N	n	Total	X^2	D.F.	P
J-1	29	9	38	.04	1	.75-.90
J-2	82	36	118	1.48	1	.10-.25
J-5	167	56	223	.00	1	> .95
J-7	209	56	265	2.12	1	.10-.25
J-10	258	82	340	.15	1	.50-.75
J-11	227	67	294	.76	1	.25-.50
J-12	229	88	317	1.29	1	.25-.50
J-13	235	87	322	.69	1	.25-.50
J-15	69	20	89	.31	1	.50-.75
J-16	271	58	329	9.53	1	< .01*
J-18	225	68	293	.51	1	.25-.50
J-19	67	21	88	.07	1	.75-.90
J-21	247	91	338	.67	1	.25-.50
Sum of 13 chi-squares				17.62	13	.10-.25
Totals	2315	739	3054	1.06	1	.25-.50
Interaction chi-square				16.56	12	.10-.25

*Significant at the 5 percent level.

factor inheritance. Both one (LeBaron, 1959) and two (Oldham, 1962) factor pairs have been reported. Table 3 gives the data for (E, e).

Normal (Tr) versus triple-awned (tr) lemma. All four crosses shown in Table 4 indicate that the triple-awned factor is recessive and simply inherited, which is in accordance with the literature (Tehrani, 1966).

Liguled (Li) versus liguleless (li) plants. A single gene difference for liguled versus liguleless plants is suggested by data in Table 5. The liguleless condition appears recessive as reported in the literature (Nilan, 1964).

Normal (Gp) versus grandpa (gp) plants. Low P values based on a 3:1 ratio have been reported for this character (Doney, 1961; Oldham, 1962; Tehrani, 1966), but Table 6 shows good P values, suggesting that the grandpa character is recessive and monofactorially inherited.

Linkage group 4

Hooded (K) versus awned (k) spikes. The majority of authors reporting on this character found it to be due to one gene pair, but several indicated that two factors might be involved (Woodward, 1955; Woodward and Rasmusson, 1957). All authors reviewed here reported hoods to be dominant over awns. Table 7 indicates hoods to be dominant, and due to one gene pair.

Normal (Z) versus zoned (z) leaf. Previous authors have reported poor ratios for zoned leaf (LeBaron, 1959; Oldham, 1962), but Table 8 shows good P values based on a 3:1 ratio. Zoned leaf appears to be recessive, as the literature indicates (Andersen, 1958; Doney, 1961).

Table 3. Segregation of normal (E) versus elongated awned (e) outer glume, in the F_2 generation. Chi-square and P values based on a 3:1 ratio.

Cross and family		E	e	Total	X^2	D. F.	P
J-7	a	45	10	55	1.36	1	.10-.25
	b	27	5	32	1.51	1	.10-.25
	c	33	14	47	.57	1	.25-.50
	d	37	10	47	.35	1	.50-.75
	e	37	3	40	6.53	1	.01-.03*
	f	36	8	44	1.09	1	.25-.50
Sum of six chi-squares					11.41	6	.05-.10
Totals		215	50	265	5.32	1	.01-.03*
Interaction chi-square					6.09	5	.25-.50
J-14	a	18	5	23	.13	1	.50-.75
	b	32	5	37	2.00	1	.10-.25
	c	1	2	3	2.77	1	.05-.10
	d	30	12	42	.28	1	.50-.75
	e	19	7	26	.05	1	.75-.90
Sum of five chi-squares					5.23	5	.50-.75
Totals		100	31	131	.12	1	.50-.75
Interaction chi-square					5.11	4	.25-.50

*Significant at the 5 percent level.

Table 4. Segregation of normal (Tr) versus triple-awned (tr) lemma in F_2 generation. Chi-square and P values based on a 3:1 ratio.

Cross	Tr	tr	Total	X^2	D.F.	P
J-2	88	28	116	.04	1	.75-.90
J-16	240	89	329	.73	1	.25-.50
J-17	115	51	166	2.89	1	.05-.10
J-22	201	72	273	.28	1	.50-.75
Sum of four chi-squares				3.94	4	.25-.50
Totals	644	240	884	2.17	1	.10-.25
Interaction chi-square				1.77	3	.50-.75

Table 5. Segregation of liguled (Li) versus liguleless (li) plants in the F_2 generation. Chi-square and P values based on a 3:1 ratio.

Cross	Li	li	Total	X^2	D.F.	P
J-6	197	80	277	2.23	1	.10-.25
J-8	293	106	399	.52	1	.25-.50
J-10	281	73	354	3.61	1	.05-.10
J-14	96	36	132	.36	1	.50-.75
J-20	291	79	370	2.63	1	.10-.25
J-21	258	80	338	.32	1	.50-.75
Sum of six chi-squares				9.67	6	.10-.25
Totals	549	159	708	2.44	1	.10-.25
Interaction chi-square				7.23	5	.10-.25

Table 6. Segregation of normal (Gp) versus grandpa (gp) plants in the F_2 generation. Chi-square and P values based on a 3:1 ratio.

Cross	Gp	gp	Total	X^2	D.F.	P
J-2	90	27	117	.23	1	.50-.75
J-16	244	86	330	.20	1	.50-.75
J-22	227	79	306	.11	1	.50-.75
Sum of three chi-squares				.54	3	.90-.95
Totals	561	192	753	.09	1	.75-.90
Interaction chi-square				.45	2	.75-.90

Table 7. Segregation of hooded (K) versus awned (k) spike in the F_2 generation. Chi-square and P values based on a 3:1 ratio.

Cross	K	k	Total	X^2	D.F.	P
J-4	105	22	127	3.99	1	.03-.05*
J-9	258	77	335	.72	1	.25-.50
J-13	240	82	322	.04	1	.75-.90
J-15	68	22	90	.01	1	.90-.95
Sum of four chi-squares				4.76	4	.25-.50
Totals	671	203	874	1.45	1	.10-.25
Interaction chi-square				3.31	3	.25-.50

*Significant at the 5 percent level.

Table 8. Segregation of normal (Z) versus zoned (z) leaf in the F_2 generation. Chi-square and P values are based on a 3:1 ratio.

Cross	Z	z	Total	X^2	D.F.	P
J-10	375	132	507	.29	1	.50-.75
J-11	314	95	409	.68	1	.25-.50
Sum of two chi-squares				.97	2	.50-.75
Totals	689	227	916	.03	1	.75-.90
Interaction chi-square				.94	1	.25-.50

Normal (Gl) versus glossy (gl) leaf. Table 9 gives the data for the segregation of normal versus glossy leaf by families. Several low P values based on a 3:1 ratio were obtained, due to consistently low numbers of glossy-leaf plants. While most families fit a 3:1 ratio, the accumulation of low numbers gives a low P value for most of the crosses taken as a whole. Most authors report low P values for a 3:1 ratio, due to low numbers of glossy-leaf plants, and attribute it to a differential mortality of glossy-leaf plants (Imam, 1959; Doney, 1961; Oldham, 1962; Tehrani, 1966). Glossy leaf is recessive and appears to be conditioned by a single gene.

Cross J-10 was a cross between two (gl) plants, yet it segregated in a 3:1 ratio, but with low P values. Cross J-11 was a cross between (Gl) and (gl), yet showed no segregation. Data from these two crosses may possibly have been interchanged. These two crosses are also the only two showing zoned leaf. Since zoned leaf plants are a bright yellow, and glossy

Table 9. Segregation of normal (Gl) versus glossy (gl) leaf in the F_2 generation. Chi-square and P values based on a 3:1 ratio.

Cross	Gl	gl	Total	X^2	D.F.	P
J-1 a	40	3	43	.45	1	< .01*
J-2 a	54	11	65	2.27	1	.10-.25
b	48	10	58	1.87	1	.10-.25
Sum of two chi-squares				4.14	2	.10-.25
Totals	102	21	123	4.12	1	.03-.05*
Interaction chi-square				.02	1	.90
J-4 a	37	11	48	.11	1	.50-.75
b	70	8	78	9.04	1	< .01*
Sum of two chi-squares				9.15	2	.01-.03*
Totals	107	19	126	6.52	1	.01-.03*
Interaction chi-square				2.63	1	.10-.25
J-5 a	59	12	71	2.48	1	.10-.25
b	49	11	60	1.43	1	.10-.25
c	41	7	48	2.77	1	.05-.10
d	55	10	65	3.20	1	.05-.10
e	63	11	74	4.05	1	.03-.05*
Sum of five chi-squares				13.93	5	.01-.03*
Totals	267	51	318	13.63	1	< .01*
Interaction chi-square				.30	4	.99

Table 9. Continued

Cross	Gl	gl	Total	X^2	D.F.	P
J-6 a	35	9	44	.48	1	.25-.50
b	39	10	49	.55	1	.25-.50
c	34	8	42	.80	1	.25-.50
d	33	14	47	.57	1	.25-.50
e	37	10	47	.38	1	.50-.75
f	40	8	48	1.77	1	.10-.25
g	34	16	50	1.31	1	.25-.50
h	37	10	47	.35	1	.50-.75
i	26	7	33	.25	1	.50-.75
j	41	8	49	1.96	1	.10-.25
Sum of 10 chi-squares				8.42	10	.50-.75
Totals	356	100	456	2.29	1	.10-.25
Interaction chi-square				6.13	9	.50-.75
J-7 a	39	17	56	.85	1	.25-.50
b	23	9	32	.17	1	.50-.75
c	41	6	47	1.43	1	.10-.25
d	36	10	46	.27	1	.50-.75
e	35	8	43	.93	1	.25-.50
f	35	9	44	.48	1	.25-.50
Sum of six chi-squares				4.13	6	.50-.75
Totals	209	59	268	1.18	1	.25-.50
Interaction chi-square				2.95	5	.50-.75

Table 9. Continued

Cross	Gl	gl	Total	X^2	D.F.	P
J-8 a	30	6	36	2.00	1	.10-.25
b	53	14	67	.60	1	.25-.50
c	55	14	69	.63	1	.25-.50
d	45	8	53	2.77	1	.05-.10
e	45	9	54	2.00	1	.10-.25
f	41	8	49	1.96	1	.10-.25
g	99	17	116	6.63	1	.01
Sum of seven chi-squares				16.59	7	.01-.03
Totals	368	76	444	14.72	1	< .01*
Interaction chi-square				1.87	6	.90-.95
J-10a	32	4	36	3.71	1	.05-.10
b	41	6	47	3.75	1	.05-.10
c	39	4	43	2.53	1	.10-.25
d	40	9	49	1.15	1	.25-.50
e	28	15	43	2.24	1	.10-.25
f	40	4	44	5.93	1	.01-.03*
g	38	10	48	.44	1	.50-.75
h	32	10	42	.03	1	.75-.90
i	37	8	45	1.25	1	.25-.50
Sum of nine chi-squares				21.03	7	.01-.03*
Totals	327	70	397	11.49	1	< .01*
Interaction chi-square				9.54	6	.25-.50
J-12a	38	10	48	.44	1	.50-.75
b	41	7	48	2.67	1	.10-.25
c	43	8	51	2.38	1	.10-.25
d	36	9	45	.60	1	.25-.50
e	45	6	51	4.76	1	.03-.05*
f	44	8	52	2.56	1	.10-.25
g	42	6	48	4.00	1	.03-.05*
h	46	6	52	5.03	1	.01-.03*
Sum of eight chi-squares				22.44	8	< .01*
Totals	335	60	395	20.28	1	< .01*
Interaction chi-square				2.16	7	.95-.98

Table 9. Continued

Cross		Gl	gl	Total	X^2	D. F.	P
J-13	a	38	9	47	.85	1	.25-.50
	b	31	6	37	1.52	1	.10-.25
	c	27	9	36	.00	1	> .90
	d	27	9	36	.00	1	> .90
	e	36	11	47	.08	1	.75-.90
	f	31	9	40	.13	1	.50-.75
	g	36	10	46	.27	1	.50-.75
	h	30	9	39	.08	1	.75-.90
Sum of eight chi-squares					2.43	8	.95-.98
Totals		256	72	328	1.63	1	.10-.25
Interaction chi-square					.80	7	> .99
J-14	a	21	5	26	.47	1	.25-.50
	b	34	8	42	.80	1	.25-.50
	c	2	1	3	.11	1	.50-.75
	d	35	6	41	2.35	1	.10-.25
	e	13	2	15	1.09	1	.25-.50
Sum of five chi-squares					4.82	5	.25-.50
Totals		105	22	127	3.99	1	.03-.05
Interaction chi-square					.83	4	.90-.95
J-15	a	30	15	45	1.67	1	.10-.25
	b	34	10	44	.11	1	.50-.75
	c	31	6	37	1.52	1	.10-.25
	d	39	9	48	1.00	1	.25-.50
	e	28	11	39	.21	1	.50-.75
	f	31	11	42	.03	1	.75-.90
	g	31	8	39	.41	1	.50-.75
	h	30	11	41	.07	1	.75-.90
	i	39	12	51	.05	1	.75-.90
Sum of nine chi-squares					5.07	9	.75-.90
Totals		293	93	386	.17	1	.50-.75
Interaction chi-square					4.90	8	.75-.90

Table 9. Continued

Cross		Gl	gl	Total	X^2	D.F.	P
J-16	a	42	7	49	3.00	1	.05-.10
	b	44	4	48	7.11	1	< .01*
	c	43	5	48	5.44	1	.01-.03*
	d	48	2	50	11.76	1	< .01*
	e	41	5	46	4.89	1	.03-.05*
	f	41	6	47	3.75	1	.05-.10
	g	42	6	48	4.00	1	.03-.05*
	h	45	5	50	6.00	1	.01-.03*
	i	34	4	38	4.24	1	.03-.05*
Sum of nine chi-squares					50.19	9	< .01*
Totals		380	44	424	48.35	1	< .01*
Interaction chi-square					1.84	8	.98-.99
J-18	a	40	6	46	3.51	1	.05-.10
	b	37	8	45	1.25	1	.25-.50
	c	39	8	47	1.60	1	.10-.25
	d	39	6	45	3.27	1	.05-.10
	e	40	7	47	2.58	1	.10-.25
	f	39	6	45	2.83	1	.05-.10
	g	35	10	45	.19	1	.50-.75
	h	42	7	49	3.00	1	.05-.10
Sum of eight chi-squares					18.23	8	.01-.03*
Totals		311	58	369	16.96	1	< .01*
Interaction chi-square					1.27	7	.98-.99

Table 9. Continued

Cross		Gl	gl	Total	X^2	D.F.	P
J-19	a	38	9	47	.85	1	.25-.50
	b	43	6	49	4.25	1	.03-.05*
	c	36	8	44	1.09	1	.25-.50
	d	35	8	43	.93	1	.25-.50
	e	42	7	49	3.00	1	.05-.10
	f	31	7	38	.88	1	.25-.50
	g	32	9	41	.20	1	.50-.75
	h	30	9	39	.08	1	.75-.90
	i	32	12	44	.12	1	.50-.75
Sum of nine chi-squares					11.40	9	.10-.25
Totals		319	75	394	7.48	1	< .01*
Interaction chi-square					3.92	8	.75-.90
J-20	a	34	13	47	.17	1	.50-.75
	b	38	11	49	.17	1	.50-.75
	c	36	8	44	1.09	1	.25-.50
	d	34	9	43	.37	1	.50-.75
	e	39	9	48	1.00	1	.25-.50
	f	32	10	42	.03	1	.75-.90
	g	32	16	48	1.77	1	.10-.25
	h	33	15	48	1.00	1	.25-.50
	i	25	9	34	.04	1	.75-.90
Sum of nine chi-squares					5.64	9	.75-.90
Totals		303	100	403	.01	1	> .90
Interaction chi-square					5.63	8	.50-.75

Table 9. Continued

Cross		Gl	gl	Total	X^2	D.F.	P
J-21	a	40	10	50	.67	1	.25-.50
	b	38	7	45	2.15	1	.10-.25
	c	39	9	48	1.00	1	.25-.50
	d	28	9	37	.01	1	> .90
	e	42	8	50	2.16	1	.10-.25
	f	39	9	48	1.00	1	.25-.50
	g	43	5	48	5.44	1	.01-.03*
	h	32	3	35	5.04	1	.01-.03*
	i	39	5	44	4.36	1	.03-.05*
Sum of nine chi-squares					21.83	9	< .01*
Totals		340	65	405	17.31	1	< .01*
Interaction chi-square					4.52	8	.75-.90
J-22	a	27	4	31	2.19	1	.10-.25
	b	29	7	36	.59	1	.25-.50
	c	36	3	37	6.67	1	< .01*
	d	26	5	31	1.31	1	.25-.50
	e	43	12	55	.29	1	.50-.75
	f	31	8	39	.41	1	.50-.75
	g	28	4	32	2.67	1	.10-.25
	h	34	5	39	3.08	1	.05-.10
	i	31	4	35	3.44	1	.05-.10
	j	20	9	29	.56	1	.25-.50
Sum of 10 chi-squares					21.21	10	.01-.03*
Totals		303	61	364	13.14	1	< .01*
Interaction chi-square					8.08	9	.50-.75

*Significant at the 5 percent level.

leaves are a bright green, perhaps the zoned leaf masked the expression of glossy leaf, or at least confused the classification.

Normal (Gs) versus glossy (gs) sheath and spike. All the crosses presented in Table 10, with the exception of J-3, show acceptable P values for 3 normal to 1 (gs) plant. The P value in J-3 falls below the .05 level due to the low number of (gs) plants in that cross. One in 20 crosses would be expected to show a poor fit due to chance alone, so the author concludes that glossy sheath and spike is indeed recessive and conditioned by one gene, as suggested in the literature (Nilan, 1964; Robertson et al., 1965).

Linkage group 5

Black (B) versus white (b) lemma and pericarp. Only two crosses segregated for (B, b) as shown in Table 11; but they both show a good fit to a 3:1 ratio, with black as the dominant character. A variation in the intensity of the color was noted, which may indicate an allelomorphic series such as has previously been reported (Woodward, 1941, 1942).

Normal (Trd) versus third (trd) outer glume. Although only one cross (Table 12) was segregating for this character, data from it support reports in the literature of a single factor pair inheritance, with the third outer glume being recessive (Nilan, 1964).

Linkage group 6

Normal (O) versus orange (o) lemma. This mutant has been investigated less than most of those in this study, but the authors reporting on it

Table 10. Segregation of normal (Gs) versus glossy (gs) sheath and spike in the F_2 generation. Chi-square and P values based on a 3:1 ratio.

Cross	Gs	gs	Total	X^2	D.F.	P
J-1	31	7	38	.88	1	.25-.50
J-2	87	31	118	.11	1	.50-.75
J-3	194	40	234	7.80	1	< .01*
J-4	96	31	127	.03	1	.75-.90
J-5	170	57	227	.00	1	> .95
J-6	205	72	277	.15	1	.50-.75
J-7	186	80	266	3.65	1	.05-.10
J-8	301	98	399	.04	1	.75-.90
J-10	267	74	341	1.97	1	.10-.25
J-11	216	81	297	.81	1	.25-.50
J-12	243	79	322	.04	1	.75-.90
J-13	243	79	322	.04	1	.75-.90
J-14	98	33	131	.00	1	> .95
J-15	73	17	90	1.79	1	.10-.25
J-16	245	85	330	.11	1	.50-.75
J-17	115	52	167	3.36	1	.05-.10
J-18	234	90	324	1.33	1	.10-.25
J-19	67	21	88	.07	1	.75-.90
J-20	286	83	369	1.24	1	.25-.50
J-21	248	90	338	.48	1	.25-.50
J-22	239	67	306	1.57	1	.10-.25
Sum of 21 chi-squares				25.47	21	.10-.25
Total	3844	1267	5111	.12	1	.50-.75
Interaction				25.35	20	.10-.25

*Significant at the 5 percent level.

Table 11. Segregation of black (B) versus white (b) lemma and pericarp in the F_2 generation. Chi-square and P values based on a 3:1 ratio.

Cross	B	b	Total	X^2	D.F.	P
J-12	245	77	322	.20	1	.50-.75
J-20	272	98	370	.44	1	.50-.75
Sum of two chi-squares				.64	2	.50-.75
Total	517	175	692	.03	1	.75-.90
Interaction				.61	1	.25-.50

Table 12. Segregation of normal (Trd) versus third (trd) outer glume in the F_2 generation. Chi-square and P values based on a 3:1 ratio.

Cross	O	o	Total	X^2	D.F.	P
J-12	249	73	322	.33	1	.50-.75

(Robertson et al., 1965) suggested that it is recessive and simply inherited. The data from three crosses in Table 13 support these reports.

Table 13. Segregation of normal (O) versus orange (o) lemma in the F_2 generation. Chi-square and P values based on a 3:1 ratio.

Cross	O	o	Total	X^2	D. F.	P
J-5	173	51	224	.60	1	.25-.50
J-6	208	69	277	.00	1	> .95
J-9	240	95	335	2.01	1	.10-.25
Sum of three chi-squares				2.61	3	.25-.50
Total	621	215	836	.23	1	.50-.75
Interaction				2.38	2	.25-.50

Linkage group 7

Rough (R) versus smooth (r) awns. Table 14 shows rough awns to be dominant over smooth, and due to one factor. Both one (Smith, 1951) and two (Nilan, 1964) factors have been reported.

Unassigned factor pairs

Normal (Rb) versus ribbon-grass (rb). Table 15 shows eight crosses which segregated for (Rb, rb). All eight were low in the expected number of plants showing ribbon-grass, and three crosses, J-7, J-18, and J-21, showed P values which dropped below the .05 level. High seedling mortality,

Table 14. Segregation of rough (R) versus smooth (r) awns in the F_2 generation. Chi-square and P values based on a 3:1 ratio.

Cross	R	r	Total	X^2	D.F.	P
J-1	29	9	38	.04	1	.75-.90
J-2	93	24	117	1.25	1	.25-.50
J-5	170	53	223	.19	1	.50-.75
J-6	216	61	277	1.31	1	.25-.50
J-7	191	74	265	1.21	1	.25-.50
J-8	282	117	399	3.97	1	.03-.05*
J-9	59	18	77	.11	1	.50-.75
J-11	212	82	294	1.31	1	.25-.50
J-14	103	28	131	.85	1	.25-.50
J-16	239	90	329	.97	1	.25-.50
J-18	258	65	323	4.12	1	.03-.05*
J-19	68	20	88	.24	1	.50-.75
J-22	227	79	306	.11	1	.50-.75
Sum of 13 chi-square				15.68	13	.25-.50
Total	2147	720	2867	.00	1	> .95
Interaction				15.68	12	.10-.25

Table 15. Segregation of normal (Rb) versus ribbon-grass (rb) in the F_2 generation. Chi-square and P values are based on a 3:1 ratio.

Cross	Rb	rb	Total	X^2	D.F.	P
J-6	343	113	456	.01	1	.90-.95
J-7	250	52	302	4.95	1	.03-.05[a]
J-8	345	99	444	1.73	1	.10-.25
J-10	320	94	414	1.16	1	.25-.50
J-14	100	27	127	.95	1	.25-.50
J-18	313	56	369	18.34	1	< .01[a]
J-20	308	95	403	.44	1	.50-.75
J-21	357	48	405	35.21	1	< .01[a]
Sum of five chi-squares				4.29	5	.25-.50
Total	1416	428	1844	3.15	1	.05-.10
Interaction				1.14	4	.75-.90

[a] Crosses omitted from the sum of chi-squares, total, and interaction.

effect of environment, as well as gene penetration have all been postulated to explain poor ratios obtained by previous workers (Heiner, 1958; Doney, 1961; Tehrani, 1966). The three crosses mentioned all had one parent in common, Bt-126. This is an entirely glossy plant, and perhaps the accumulation of these mutants in the same cross weakens the plants to the extent that few survive. Crosses involving this parent have been omitted from the sum of chi-squares, totals, and interaction chi-squares. Cross J-1 should have segregated for (Rb, rb), but due to the very small size of this cross (one family) no (rb) plants were detected. Overall, it appears ribbon-grass is recessive and conditioned by a single gene.

Normal (Ge) versus glossy (ge) ear. When this study was undertaken, the author was of the opinion that there was one gene responsible for glossy sheath (gs) and another for glossy ear (ge). However, it was soon noted that every plant with a glossy sheath also had a glossy ear, but there were plants with glossy ear only. A search of the literature soon revealed that (gs) does indeed condition the plant for glossy sheath and spike, and a separate gene (ge) is responsible for glossy spike alone. Unfortunately, due to this misunderstanding, every cross involving (ge) also carried (Gs, gs) which made it impossible to study the inheritance of (ge) alone or in relation to other characters, for linkage.

Glossy Leaf in Combination with Other Characters

Table 16 shows no relationships between glossy leaf and (n) in linkage group 1, as expected, if (gl) is indeed in group 4 as has been reported.

Table 17 gives (gl) in combination with the characters in linkage group 2. Glossy leaf appears to be independent of (E, e), (Tr, tr), and (Li, li). One cross, J-22, shows a low P value based on a 9:3:3:1 ratio, but when broken down by family, none fall below the .05 level. Thus it is concluded that glossy leaf is independent of all the factors studied in group 2.

Glossy leaf in combination with factors in linkage group 4 are presented in Table 18. Glossy leaf appears linked with (K, k) and (Z, z) but not with (Gs, gs). Glossy leaf appeared in combination with (K, k) in only one cross,

Table 16. Non-glossy (Gl) versus glossy (gl) leaves in relation to factors in linkage group 1, in the F_2 generation. P values based on a 9:3:3:1 ratio.

Cross	Phase	AB	Ab	aB	ab	Total	P
		(Gl, gl) in relation to (N, n)					
J-1	Coupling	29	6	0	3	38	.03-.05*
J-2	Coupling	73	30	7	6	116	.50-.75
J-5	Coupling	144	31	42	6	223	.50-.75
J-7	Coupling	178	48	31	8	265	.75-.90
J-10	Repulsion	199	70	57	12	338	.10-.25
J-12	Repulsion	198	73	36	15	322	.90-.95
J-13	Coupling	184	72	51	15	322	.25-.50
J-15	Repulsion	52	16	17	4	89	.50-.75
J-16	Coupling	239	53	30	6	328	.25-.50
J-18	Coupling	214	65	33	11	323	.50-.75
J-19	Coupling	60	18	7	3	88	.50-.75
J-21	Coupling	205	78	43	12	338	.25-.50

*Significant at the 5 percent level.

Table 17. Non-glossy (Gl) versus glossy (gl) leaves in relation to factors in linkage group 2, in the F_2 generation. P values based on a 9:3:3:1 ratio.

Cross	Phase	AB	Ab	aB	ab	Total	P
		(Gl, gl) in relation to (E, e)					
J-7	Repulsion	180	46	35	4	265	.50-.75
J-14	Coupling	86	25	13	4	128	.75-.90
		(Gl, gl) in relation to (Tr, tr)					
J-2	Repulsion	60	18	30	10	118	.75-.90
J-16	Coupling	133	49	108	40	330	.50-.75
J-17	Coupling	84	34	37	17	172	.50-.75
J-22	Repulsion	143	42	91	30	306	.75-.90
		(Gl, gl) in relation to (Li, li)					
J-6	Coupling	153	64	44	16	277	.50-.75
J-8	Coupling	255	89	38	17	399	.50-.75
J-10	Coupling	228	56	53	17	354	.25-.50
J-14	Repulsion	82	29	12	6	129	.50-.75
		(Gl, gl) in relation to (Gp, gp)					
J-2	Repulsion	82	22	8	5	117	.25-.50
J-16	Repulsion	221	73	22	13	329	.25-.50
J-22	Repulsion	(By families)					
a		18	6	3	1	28	> .95
b		18	9	4	1	32	.25-.50
c		25	10	1	0	36	.50-.75
d		14	6	5	0	25	.10-.25
e		29	10	12	0	51	.05-.10
f		20	5	7	1	33	.50-.75
g		14	14	3	1	32	.05-.10
h		23	7	4	1	35	> .95
i		23	9	2	0	34	.50-.75
Totals (J-22)		184	76	41	5	306	.01-.03*

*Significant at the 5 percent level.

Table 18. Non-glossy (Gl) versus glossy (gl) leaves in relation to factors in linkage group 4, in the F_2 generation. P values and % recombination based on a 9:3:3:1 ratio.

Cross	Phase	AB	Ab	aB	ab	Total	P	% Recomb.
		(Gl, gl) in relation to (K, k)						
J-13	Coupling	(By families)						
a		30	5	1	9	45	< .01	11 ± 5
b		27	4	0	4	35	< .01	15 ± 7
c		23	3	2	8	36	< .01	14 ± 6
d		18	6	2	7	33	< .01	22 ± 8
e		35	2	3	8	48	< .01	12 ± 5
f		29	5	4	2	40	.25-.50	36 ± 10
g		33	3	2	8	46	< .01	12 ± 5
h		30	3	1	5	39	< .01	12 ± 5
Totals		225	31	15	51	322	.01	16 ± 2
		(Gl, gl) in relation to (Z, z)						
J-10	Repulsion	(By families)						
a		14	17	5	0	36	< .01	26 ± 15
b		31	9	6	1	47	.75-.90	42 ± 12
c		26	12	6	0	44	.10-.25	36 ± 13
d		28	11	8	0	47	.10-.25	34 ± 13
e		19	7	16	0	42	< .01	27 ± 14
f		21	13	10	0	44	.01-.03	26 ± 14
g		30	8	10	0	48	.10-.25	37 ± 12
h		29	9	8	0	46	.10-.25	38 ± 12
Totals		198	86	69	1	354	< .01	13 ± 5

Table 18. Continued

Cross	Phase	AB	Ab	aB	ab	Total	P
		(Gl, gl) in relation to (Gs, gs)					
J-6	Repulsion	155	62	45	15	277	.50-.75
J-7	Repulsion	159	68	28	11	266	.50-.75
J-8	Coupling	262	82	39	16	399	.25-.50
J-10	Coupling	219	51	49	21	381	.05-.10
J-12	Repulsion	205	66	37	14	322	.25-.50
J-13	Repulsion	192	64	49	17	322	.90-.95
J-14	Repulsion	83	28	13	4	128	.90-.95
J-15	Repulsion	56	12	16	6	90	.25-.50
J-16	Coupling	222	72	22	13	329	.25-.50
J-18	Repulsion	206	74	29	14	323	.50-.75
J-19	Repulsion	58	20	8	2	88	.75-.90
J-20	Repulsion	218	61	69	22	370	.50-.75
J-21	Repulsion	207	76	41	14	338	.50-.75
J-22	Coupling	200	60	39	7	306	.25-.50

and showed 16 percent recombination in the coupling phase, as compared with a range of from 10 percent to 34.5 percent reported in the literature (Immer and Henderson, 1943; Woodward, 1957a). It also appeared in only one cross in combination with (Z, z) with 13 percent recombination in the repulsion phase. A range of from three percent (Immer and Henderson, 1943) to 34.5 percent recombination (Woodward, 1955) is reported in the literature. The few linkage relationships reported between (gl) and (gs) (Woodward, 1955, 1957b; Albrechtsen, 1957; Tehrani, 1966) show them to be quite widely separated. Perhaps this is why a relationship was not detected here.

Table 19 gives (gl) in combination with factors in linkage group 5. The two crosses which carried glossy leaf and (B, b) showed good P values for independence. Only one cross segregated for (gl) and (trd), but it indicated the two to be independent also.

The two crosses segregating for (gl) and (o) are found in Table 20. There appears to be no association between these two genes.

Table 21 contains the data from crosses between glossy leaf and rough versus smooth awns, located in linkage group 7. Independence is indicated, as would be expected.

Data from glossy leaf in combination with factors not yet assigned to linkage groups are presented in Table 22. No relationship was found between (gl) and (rb), although the literature contains at least one report (Woodward, 1955) of a loose linkage between these two genes.

Table 19. Non-glossy (Gl) versus glossy (gl) leaves in relation to factors in linkage group 5, in the F_2 generation. P values based on a 9:3:3:1 ratio.

Cross	Phase	AB	Ab	aB	ab	Total	P
		(Gl, gl) in relation to (B, b)					
J-12	Coupling	204	67	41	10	322	.50-.75
J-20	Repulsion	157	55	45	16	273	> .95
		(Gl, gl) in relation to (Trd, trd)					
J-12	Repulsion	210	61	39	12	322	.50-.75

Table 20. Non-glossy (Gl) versus glossy (gl) leaves in relation to factors in linkage group 6, in the F_2 generation. P values based on a 9:3:3:1 ratio.

Cross	Phase	AB	Ab	aB	ab	Total	P
		(Gl, gl) in relation to (O, o)					
J-5	Repulsion	147	47	26	3	223	.25-.50
J-6	Repulsion	163	54	45	15	277	> .95

Table 21. Non-glossy (Gl) versus glossy (gl) leaves in relation to factors in linkage group 7, in the F_2 generation. P values based on a 9:3:3:1 ratio.

Cross	Phase	AB	Ab	aB	ab	Total	P
		(Gl, gl) in relation to (R, r)					
J-6	Repulsion	165	52	53	7	277	.05-.10
J-7	Repulsion	164	62	27	12	265	.90-.95
J-19	Repulsion	63	8	12	5	88	.05-.10
J-22	Repulsion	191	69	36	10	306	.50-.75

Table 22. Non-glossy (Gl) versus glossy (Gl) leaves in relation to factors unassigned to linkage groups, in the F_2 generation. P values based on a 9:3:3:1 ratio.

Cross	Phase	AB	Ab	aB	ab	Total	P
		(Gl, gl) in relation to (Rb, rb)					
J-6	Coupling	162	55	47	13	277	.50-.75
J-8	Coupling	261	83	49	6	399	.10-.25
J-10	Coupling	217	59	63	15	354	.75-.90
J-14	Repulsion	87	24	16	2	129	.50-.75

As has been explained, it was impossible to study (ge) in combination with other factors in this study.

Glossy Sheath and Spike in Combination with Other Characters

Table 23 gives the data for glossy sheath and spike in combination with (N, n), which was the only factor studied in linkage group 1. One cross, J-13, gave a low P value, but the individual families within the cross indicated that the two factors involved are likely independent.

Table 23. Normal (Gs) versus glossy (gs) sheath and spike in relation to factors in linkage group 1, in the F_2 generation. P values based on a 9:3:3:1 ratio.

Cross	Phase	AB	Ab	aB	ab	Total	P
		(Gs, gs) in relation to (N, n)					
J-1	Coupling	24	7	5	2	38	.50-.75
J-2	Coupling	55	29	27	7	118	.10-.25
J-5	Repulsion	128	41	43	15	227	.75-.90
J-7	Coupling	149	38	61	18	266	.75-.90
J-10	Repulsion	212	70	60	12	354	.10-.25
J-11	Repulsion	185	50	66	17	318	.75-.90
J-12	Repulsion	175	67	59	21	322	.75-.90
J-13	Repulsion	183	58	52	29	322	.75-.90
J-15	Repulsion	56	16	14	4	90	> .95
J-16	Coupling	218	35	64	13	330	.25-.50
J-18	Coupling	177	60	74	15	326	.05-.10
J-19	Repulsion	50	16	17	5	88	.90
J-21	Coupling	186	66	66	24	342	.90-.95

*Significant below the 5 percent level.

Glossy sheath and spike also appeared to be independent of three out of four characters in linkage group 2, as indicated by the data in Table 24. (Gs, gs) was found to be independent of (E, e), (Tr, tr), and (Li, li). Imam (1959) reported a weak linkage between (Gs, gs) and (Li, li).

Table 24. Normal (Gs) versus glossy (gs) sheath and spike in relation to factors in linkage group 2, in the F_2 generation. P values based on a 9:3:3:1 ratio.

Cross	Phase	AB	Ab	aB	ab	Total	P	% Recomb.
		(Gs, gs) in relation to (E, e)						
J-7	Repulsion	146	40	69	10	265	.25-.50	
J-14	Repulsion	74	24	26	7	131	.50-.75	
		(Gs, gs) in relation to (Tr, tr)						
J-2	Repulsion	62	22	28	6	118	.25-.50	
J-16	Repulsion	173	67	68	22	330	.50-.75	
J-22	Repulsion	171	72	52	11	306	.05-.10	
		(Gs, gs) in relation to (Li, li)						
J-6	Repulsion	145	60	52	20	277	.75-.90	
J-8	Repulsion	216	85	77	21	399	.10-.25	
J-10	Coupling	225	57	56	16	354	.50-.75	
J-14	Coupling	70	29	26	7	132	.25-.50	
		(Gs, gs) in relation to (Gp, gp)						
J-2	Repulsion	57	25	32	2	116	< .005*	33 ± 8
J-16	Repulsion	177	68	67	18	330	.10-.25	
J-22	Repulsion	203	56	24	23	306	< .005*	25 ± 5

*Significant at the 5 percent level.

Two of the three crosses segregating for (gs) and (gp) showed loose linkages, while one cross showed independence. These three crosses were also segregating for the grandpa characteristic which confused the classification of the glossyness of the spike.

Since the gene for glossy sheath and spike has been reported by a number of workers (Nilan, 1964; Haus et al. , 1971) to be in linkage group 4, linkage relationships between (gs) and factors in this group would not be unexpected. However, Table 25 shows that only one cross indicated an association between (gs) and (k) and even this cross (J-4) showed independence for each of the families. Several loose linkages have been reported between (gs) and (k) (Woodward, 1955, 1957a).

Two crosses segregated for (gs) and (z). One family of cross J-10 gave a low P value for a 9:3:3:1 ratio which caused the P value for the cross as a whole to fall below the .05 level. Several authors (Woodward, 1955, 1957b; Albrechtsen, 1957; Tehrani, 1966) have reported (gs) to be linked to (z), however.

Table 26 shows (Gs, gs) to be independent of both factors studied in group 5, (B, b) and (Trd, trd). The author found no reports in the literature of linkages between (gs) and either of these two factors.

Glossy sheath and spike was also found to be independent of the gene for orange lemma, in linkage group 6. Table 27 presents the data from the two crosses segregating for these genes.

Table 25. Normal (Gs) versus glossy (gs) sheath and spike in relation to factors in linkage group 4, in the F_2 generation. P values based on a 9:3:3:1 ratio.

Cross	Phase	AB	Ab	aB	ab	Total	P
		(Gs, gs) in relation to (K, k)					
J-4	Repulsion	(By families)					
a		30	6	10	3	49	.50-.75
b		50	10	15	3	78	.90-.95
Totals		80	16	25	6	127	< .01*
J-9	Coupling	205	63	53	14	335	.75
J-13	Coupling	180	61	60	21	322	.90-.95
		(Gs, gs) in relation to (Z, z)					
J-10	Repulsion	(By families)					
a		14	16	5	1	36	.03-.05*
b		27	10	10	0	47	.10-.25
c		25	12	7	0	44	.10-.25
d		30	9	6	2	47	.90
e		26	6	9	1	42	.50-.75
f		28	10	3	3	44	.25-.50
g		30	7	10	1	48	.50-.75
h		24	8	13	1	46	.10-.25
Totals		204	78	63	9	354	.01-.03*
J-11	Repulsion	183	52	68	15	318	.25-.50

*Significant at the 5 percent level.

Table 26. Normal (Gs) versus glossy (gs) sheath and spike in relation to factors in linkage group 5, in the F_2 generation. P values based on a 9:3:3:1 ratio.

Cross	Phase	AB	Ab	aB	ab	Total	P
		(Gs, gs) in relation to (B, b)					
J-12	Coupling	190	60	55	17	322	> .90
J-20	Coupling	213	75	60	23	371	.75-.90
		(Gs, gs) in relation to (Trd, trd)					
J-12	Repulsion	187	55	62	18	322	> .95

Table 27. Normal (Gs) versus glossy (gs) sheath and spike in relation to factors in linkage group 6, in the F_2 generation. P values based on a 9:3:3:1 ratio.

Cross	Phase	AB	Ab	aB	ab	Total	P
J-5	Coupling	127	42	49	9	227	.10-.25
J-6	Coupling	155	50	53	19	277	.50-.75

In crosses involving (gs) and (r) (linkage group 7), two showed a slight relationship at the cross level, but when these crosses were presented by families, they showed independence.

Glossy sheath and spike was also found to be independent of the gene for ribbon-grass (unassigned). Crosses segregating for these two genes are presented in Table 29.

Table 28. Normal (Gs) versus glossy (gs) sheath and spike in relation to factors in linkage group 7, in the F_2 generation. P values based on a 9:3:3:1 ratio.

Cross	Phase	AB	Ab	aB	ab	Total	P
		(Gs, gs) in relation to (R, r)					
J-1	Coupling	25	6	4	3	38	.10-.25
J-2	Repulsion	66	16	26	8	116	.50-.75
J-5	Coupling	136	41	45	11	233	.50-.75
J-6	Coupling	159	46	57	15	277	.75-.90
J-7	Repulsion	(By families)					
a		27	16	10	2	55	.10-.25
b		17	8	6	1	32	.25-.50
c		27	9	9	2	47	.50-.75
d		23	6	14	4	47	> .95
e		15	8	13	4	40	.50-.75
f		18	12	12	2	44	.05-.10
Totals (J-7)		127	59	64	15	265	.03-.05*
J-11	Repulsion	144	60	58	22	284	.75-.90
J-18	Coupling	187	44	77	15	284	.75-.90
J-19	Repulsion	(By families)					
a		24	7	14	1	46	.10-.25
b		21	12	8	1	42	.10-.25
Totals (J-19)		45	19	22	2	88	.03-.05*
J-22	Repulsion	132	53	95	26	306	.10-.25

*Significant at the 5 percent level

Table 29. Normal (Gs) versus glossy (gs) sheath and spike in relation to factors unassigned to linkage groups, in the F_2 generation. P values based on a 9:3:3:1 ratio.

Cross	Phase	AB	Ab	aB	ab	Total	P
		(Gs, gs) in relation to (Rb, rb)					
J-6	Repulsion	236	22	25	6	277	.05-.10
J-8	Coupling	228	73	82	16	399	.10-.25
J-10	Coupling	219	57	61	17	354	.75
J-14	Coupling	66	22	38	6	132	.05-.10
J-20	Coupling	231	57	63	20	371	.25-.50

SUMMARY AND CONCLUSIONS

The F_2 generation of 22 crosses was studied to determine the inheritance of 15 contrasting characters, with special emphasis on glossy leaf (gl), glossy sheath and spike (gs), and glossy ear (ge). (gl) and (gs) were each studied in combination with the other factors to determine possible linkage relationships. The inheritance and linkages of (ge) were not determined due to the masking effect of (gs) in each cross.

All factors studied, except (ge), appeared to be monofactorially inherited. Glossy leaf appeared to be linked with (K, k) and (Z, z) in linkage group 4, and independent of (N, n), (E, e), (Tr, tr), (Li, li), (Gp, gp), (Gs, gs), (Trd, trd), (O, o), (R, r), and (Rb, rb).

Glossy sheath and spike appeared linked with (Gp, gp) (Linkage group 3) in two out of three crosses and independent of (N, n), (E, e), (Tr, tr), (Li, li), (K, k), (Z, z), (Gl, gl), (B, b), (Trd, trd), (O, o), (R, r), and (Rb, rb). The apparent linkage between (gs) and (gs) is probably due to a masking effect of the grandpa characteristic.

LITERATURE CITED

Albrechtsen, R. S. 1957. Hood elevation and awn length studies in barley. Unpublished M.S. thesis. Utah State University Library, Logan, Utah.

Al-Jibouri, H. A. 1953. Inheritance of ten characters in barley crosses. Unpublished M.S. thesis. Utah State University Library, Logan, Utah.

Andersen, W. R. 1958. Linkage relationships of located and unlocated genetic testers in certain normal and translocation stocks of barley. Unpublished M.S. thesis. Utah State University Library, Logan, Utah.

Buckley, G. F. H. 1930. Inheritance in barley with special reference to the color of caryopsis and lemma. Scientific Agriculture 10:460-491.

Byington, F. J. 1940. Inheritance studies and possible linkage relationships in barley involving five factor pairs. Unpublished M.S. thesis. Utah State University Library, Logan, Utah.

Daane, A. 1931. Linkage relations in barley. Minnesota Experiment Station Technical Bulletin 78.

Das, K. 1957. Partial sterility in a line of X-ray irradiated barley. Indian Journal of Genetics and Plant Breeding 17:58-64.

Doney, D. L. 1961. An inheritance and linkage study of barley with special emphasis on purple pigmentation of the auricle. Unpublished M.S. thesis. Utah State University Library, Logan, Utah.

Fisher, R. A., and B. Balmukand. 1928. The estimation of linkage from the offspring of selfed heterozygotes. Journal of Genetics 20:79-92.

Gill, T. S. 1951. Inheritance of 16 barley characters and their linkage relationships. Unpublished M.S. thesis. Utah State University Library, Logan, Utah.

Gustafsson, A., A. Hagburg, and G. Pirsson. 1969. A proposed system of symbols for the collection of barley mutants at Svalov. Hereditas 62:409-413.

Haus, T. E., R. T. Ramage, and T. Tsuchiya. 1971. Barley Genetics Newsletter I:1-199.

Heiner, R. E. 1958. Linkage and inheritance studies in barley (Hordeum). Unpublished M.S. thesis. Utah State University Library, Logan, Utah.

Imam, A. G. I. 1959. Inheritance and linkage studies in selected crosses of cultivated barley (Hordeum vulgare L.). Unpublished M.S. thesis. Utah State University Library, Logan, Utah.

Immer, F. R., and M. T. Henderson. 1943. Linkage studies in barley. Genetics 28:419-440.

Isom, W. H. 1951. Inheritance and linkage relationships in twenty-two barley characters. Unpublished M.S. thesis. Utah State University Library, Logan, Utah.

Jenkins, C. J. 1950. Inheritance of certain characters and the linkage relationships of factors in chromosome IV in barley. Unpublished M.S. thesis. Utah State University Library, Logan, Utah.

Kasha, K. and G. W. R. Walker. 1960. Several recent barley mutants and their linkages. Canadian Journal of Genetics and Cytology 5:200-219.

Konzak, C. F. 1953. The third outer glume character in barley. Journal of Heredity 44:103-105.

LeBaron, F. C. 1959. An inheritance and linkage study of 19 factor pairs in barley. Unpublished M.S. thesis. Utah State University Library, Logan, Utah.

Lundqvist, W. and D. Von Wettstein. 1962. Introduction of eceriferum mutants in barley by ionizing radiation and chemical mutagens. Hereditas 48:342-362.

Mather, K. 1943. Statistical analysis in biology. Mathuen and Company, London. 207 p.

Myler, J. L., and E. H. Stanford. 1942. Color inheritance in barley. Journal of the American Society of Agronomy 34:427-436.

Nilan, R. A. 1964. The cytology and genetics of barley. 1951-1962. Washington State University Press. 32(1). 287 p.

Oldham, J. D. 1962. A genetic study of linkage and inheritance in barley. Unpublished M.S. thesis. Utah State University Library, Logan, Utah.

Rasmusson, D. C. 1956. The inheritance of certain morphological characters of the barley spike. Unpublished M.S. thesis. Utah State University Library, Logan, Utah.

Robertson, D. W. 1933. Inheritance in barley. Genetics 18:148-159.

Robertson, D. W. 1937. Inheritance in barley. II. Genetics 22:443-451.

Robertson, D. W. 1939. Genetics of barley. American Society of Agronomy Journal 31:273-283.

Robertson, D. W. and O. H. Coleman. 1942. Location of glossy and yellow seedlings in two linkage groups. Journal of American Society of Agronomy 34:1028-1034.

Robertson, D. W., G. A. Wiebe, and F. R. Immer. 1941. A summary of linkage studies in barley. American Society of Agronomy Journal 33:47-64.

Robertson, D. W., G. A. Wiebe, and R. G. Shands. 1947. A summary of linkage studies in barley: Supplement I, 1940-1946. Journal of the American Society of Agronomy 39:464-473.

Robertson, D. W., G. A. Wiebe, and R. G. Shands. 1955. A summary of linkage studies in barley: Supplement II, 1947-1953. Journal of the American Society of Agronomy 47:418-425.

Robertson, D. W., G. A. Wiebe, R. G. Shands, and A. Hagberg. 1965. A summary of linkage studies in cultivated barley, Hordeum species: Supplement III, 1954-1963. Crop Science 5:33-43.

Smith, C. W. 1953. A linkage study of chromosome IV in barley. Unpublished M.S. thesis. Utah State University Library, Logan, Utah.

Smith, L. 1951. Cytology and genetics of barley. Botanical Review 17:1-355.

Snedecor, G. W. and W. G. Cochran. 1967. Statistical methods. 6th edition. The Iowa State University Press, Ames, Iowa. 593 p.

Sorensen, E. L. 1952. Inheritance and linkage relationships involving X-ray induced translocation stock in barley. Unpublished M.S. thesis. Utah State University Library, Logan, Utah.

Tehrani, P. A. 1966. An investigation of certain linkage relationships in barley. Unpublished M.S. thesis. Utah State University Library, Logan, Utah.

Walker, G. W. R., J. Dietrich, R. Miller, and K. Kasha. 1963. Linkages of barley mutants. Canadian Journal of Genetics and Cytology 5:200-219.

Waddoups, H. M. 1949. A study of semisterility and its linkage relationships in translocation stock in barley. Unpublished M.S. thesis. Utah State University Library, Logan, Utah.

Wheatley, G. W. 1955. Linkage relationships in group IV in barley. Unpublished M.S. thesis. Utah State University Library, Logan, Utah.

Woodward, R. W. 1941. Inheritance of melanin-like pigment in the glumes and caryopsis of barley. Journal of Agricultural Research 63:21-28.

Woodward, R. W. 1942. Linkage relationships between the allelomorphic series B, B^{mb}, B^2, and A_t a_t in barley. Journal of American Society of Agronomy 34:649-661.

Woodward, R. W. 1950. Annual report. Cereal Crops Division. United States Department of Agriculture.

Woodward, R. W. 1955. Annual report. Cereal Crops Division. United States Department of Agriculture.

Woodward, R. W. 1957a. Linkages in barley. Agronomy Journal 49:28-32.

Woodward, R. W. 1957b. Annual report. Cereal Crops Division. United States Department of Agriculture.

Woodward, R. W., and D. C. Rasmusson. 1957. Hood and awn development in barley determined by two genes. Agronomy Journal 49:92-94.