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An Investigation of Certain Linkage Relationships in Barley

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AN INVESTIGATION OF CERTAIN LINKAGE RELATIONSHIPS IN BARLEY

by

Parichehr Ahmadian Tehrani

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of the requirements for the degree

of

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P. Ahmadian
Parichehr Ahmadian Tehrani

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INTRODUCTION

Barley is one of the world's most important food and feed crops. It is adapted to a wide range of environments. According to Harlan and Martini (1936) barley is grown from north of the Artic Circle to the sands of the Sahara, and from the slopes of Mt. Everest to the lower delta of the Nile.

Considerable progress has been made in its improvement through plant breeding. Barley is one of the best cultivated crop plants for use in genetic studies. It is a diploid plant from the family Gramineae with seven pairs of chromosomes. The cultivated species are interfertile and have a large number of readily distinguishable genetic characters. Approximately 370 characters are recognized (Nilan, 1964).

Many of barley's genes have been mapped and assigned to one of the seven chromosomes. Linkage groups in barley have been designated in a number of ways. A Roman numeral was used extensively in the earlier studies to identify each linkage group. More recently an Arabic number system has been used. This system was adopted by the Fourth Annual Barley Research Worker's Conference and will be followed in this study.

The study involves 24 contrasting factors and was undertaken to determine the location of certain genes already reported in specific linkage groups and, if possible, to assign several previously unassigned genes to linkage groups. Of the 24 factor pairs studied, six have not yet been assigned to a chromosome. The inheritance and linkage associations of these unassigned genes receive major emphasis in this study.

REVIEW OF LITERATURE

The literature on the genetics of barley is very extensive and has been reviewed by many investigators. Some of the literature reviewed here was summarized by Smith (1951), Buckley (1930), Robertson (1933, 1937), Robertson et al. (1947, 1955, 1965), and Nilan (1964).

Individual Character with Their Linkage Groups

This review will be restricted to the 24 characters examined in the present study. The characters will be considered by linkage groups.

Linkage group 1

Covered (N) versus naked (n) caryopsis. The naked or hull-less character is reportedly inherited as a single recessive gene (Hayes and Garber, 1927; Buckley, 1930; Robertson, 1933; Das, 1957; Heiner, 1958; Imam, 1959; Doney, 1961; Shaheen, 1961; Oldham, 1962). Robertson (1937) and Das (1957) found that (N, n) is in chromosome 3, whereas it has been reported by Hayes and Garber (1927), Buckley (1930), Robertson (1933, 1965), Das (1957), Heiner (1958), Imam (1959), Doney (1961), Kramer and Blander (1961), Oldham (1962), and Nilan (1964), that genes for this character are located in chromosome 1. These divergent findings might be reconciled by the fact that Kramer, Veryl and Hanson (1954) reported linkage groups III and VII to be separate arms of chromosome 1.

Linkage group 2

Normal (E) versus long awned (e) outer glume. Long awned outer glume is recessive and has been reported by Hor (1924), Heiner (1958), Imam (1959), and Doney (1961) to be inherited as a single gene. However, Gill (1951) and Doney (1961) also observed two factor inheritance. Many induced mutations for this character have been reported (Nilan, 1964). There have frequently been associated with increased yield.

Normal (Tr) versus triple awned (tr) lemma. It is indicated by Anderson (1958), Heiner (1958) and Imam (1959) that triple-awned lemma is monofactorially inherited. Two factor pairs were reported to be involved in the inheritance of this character by Nilan (1964). According to Shands, Kramer and Patterson (1964) normal versus triple-awned lemma is linked with (V^t, V, v) which are located in the long arm of chromosome 2.

Deficiens (V^t) versus two-rowed (V) versus six-rowed (v) spike. The row number on the spike is controlled by a single gene, with two-rowed dominant over six-rowed (Gill, 1951; Das, 1957; LeBaron, 1959; Shaheen, 1961; Oldham, 1962; Bray, 1963; Necas, 1963). Woodward (1947) reported that the deficiens character behaves as an allele of the factors conditioning two-rows versus six-rows, and is at least partially dominant. Oldham (1962) found that deficiens is dominant over the two-row factor. The factor pair (V, v) is reportedly linked with the factor pair (Pr, pr) for purple versus white straw color (Robertson, 1933). Woodward (1947) found that deficiens (V^t) versus non deficiens (V^d) is also linked with the factor pair (Pr, pr), thus constituting further evidence that the (V^t) gene for deficiens is an allele to the (V, v) genes.

There is an allelic series (I^h), (I), and (i) for fertility of lateral florets. This series is in linkage group 4 and tends to modify the effect of the allelic series (V^t), (V) and (v). However, the fertility alleles (I^h, I, or i) and row number alleles (V^t, V, and v) are in different linkage groups (Robertson, 1933; Woodward, 1947).

Lax (L) versus dense (l) spike. This character has been reported by most workers to be inherited as a single gene with lax dominant over dense spike (Isom, 1951; Heiner, 1958; Doney, 1961; Oldham, 1962). Nilan (1964), however, reported that Aziz, Mir, and Necas observed a multiple factor inheritance for this character. Smith (1951) reported that factors for lax versus dense spike are located in linkage groups 1, 2, and 4, whereas Woodward (1957) concluded that the genes for this character are located in groups other than 1.

Purple (Pau) versus normal (pau) auricle. Purple auricle is apparently determined by a single factor pair, with purple dominant over normal auricle (Doney, 1961; Doney and Woodward, 1963; Nilan, 1964). Purple auricle was found to be linked with purple straw (Pr), with purple lemma and pericarp (Re_2) (Doney and woodward, 1963), and with the deficiens spike (V^t) (Woodward, 1947; Doney and Woodward, 1963).

Purple (Pr) versus normal (pr) stem. According to Imam (1959), LeBaron (1959), and Doney (1961), purple stem is dominant over normal stem color and is determined by one gene pair. Gill (1951) and Heiner (1958) reported that two complementary factor pairs are involved in the expression of this character. The factor or factors responsible for this character were found to be linked with the factor pair (V, v) (Robertson, 1933), and with the factor pair (V^t, V^d) (Woodward, 1947). Smith (1951), Robertson (1933), and Robertson et al. (1955) reported that the factor or factors determining purple stem color are located in chromosome 1.

Normal (Li) versus liguleless (li). The "liguleless" characteristic in barley refers to the condition wherein the leaves have no ligule. This character is apparently conditioned by a single gene with the liguleless condition recessive (Heiner, 1958; Imam, 1959; Doney, 1961; Oldham, 1962). Nilan (1964) reported that Takahashi et al. found an F_2 ratio of one normal, two intermediate, and one liguleless. It has been reported by Robertson et al. (1955) that the gene pair (Li, li) is located in chromosome 1; however, in the linkage summary compiled by Robertson et al. (1965), the liguleless factor is supposed to be located on chromosome 2.

Purple (Re_2) versus normal (re_2) lemma and pericarp. Purple lemma and pericarp is dominant over normal. It is reported by Buckley (1930), Daane (1931), Gill (1951), Anderson (1958), Heiner (1958), Imam (1959), and Doney (1961) that purple lemma is inherited monofactorially; but Woodward and Thieret (1953) and Oldham (1962) found evidence for two factor inheritance. Woodward and Thieret (1953) and Woodward (1957) found an F_2 segregation of 9 purple to 7 white, indicating that purple is dominant over white. It was reported by Buckley (1930) and Robertson et al. (1955) that the gene pairs for purple pericarp are in chromosome 1, whereas

Nilan (1964) and Robertson et al. (1965) indicated that (Re_2, re_2) is located in chromosome 2.

Linkage group 4

Blue (Bl) versus non-blue (bl) aleurone. According to Buckley (1930) and Nilan (1964) blue versus non-blue aleurone is inherited monofactorially, with blue dominant over white. Myler and Stanford (1942) and Oldham (1962) obtained two factor inheritance for this character. One of these two factors was found to be linked with the hooded versus awned character. The second factor appears to be linked with (N, n) for covered versus naked caryopsis (Myler and Stanford, 1942). They obtained an F_2 segregation ratio of 9 blue to 7 white. Buckley (1930) and Robertson et al. (1955) reported that one of the genes for this character is in chromosome 3, whereas Nilan (1964) and Robertson, et al. (1965) indicated that (Bl, bl) is located in chromosome 4, and the second factor for blue versus non-blue aleurone is in chromosome 1.

Hooded (K) versus awned (k) spike. The hooded spike condition has been reported to be dominant over awned (Hayes and Garber, 1927; Buckley, 1930; Al-jibouri, 1953; Albrechtsen, 1957; Shaheen, 1961; Oldham, 1962). Nilan (1964) reported that Walker, Kasha and Miller found a recessive factor (kr) for hoods. He noted that some workers have observed monofactorial inheritance and others have found two factor pairs involved in the inheritance of this character. Woodward (1955) and Woodward and Rasmusson (1957) found that two pairs were responsible for hoods and awns, whereas Hayes and Garber (1927) and Shaheen (1961) reported this character to be controlled by single gene. The factor pair (K, k) was found by Robertson (1933) to be linked with the factor pair (I, i) with 15.12 per cent crossing over.

Normal (Z) versus zoned (z) leaf. It was reported by Immer and Henderson (1943), Gill (1951), Wheatley (1955), Woodward (1957), Heiner (1958), LeBaron (1959), Doney (1961), and Oldham (1962) that normal (Z) leaves are dominant over zoned leaves. These workers all observed a monofactorial segregation for this character. However, Wheatley (1955), Heiner (1958), LeBaron (1959), and Doney (1961) obtained low probability values for a 3:1 segregation, and suggested that it was due to the high mortality of zoned leaf plants.

Infertile intermedium (I) versus non-intermedium (i). Nilan (1964) reported that Murty and Jain studied the inheritance of fertility of lateral florets and found two types of segregation. In one cross a single gene difference was observed (VVii X vvii). In another cross the segregation was best explained by a two-gene difference (VVii X vvI^hI^h).

Woodward (1949) described a multiple allelic series for the inheritance of fertility of the lateral florets, (v, V^d, V, V^t). He suggested that this series interacts with the (I^h, I, i) series in linkage group IV to give different degrees of fertility of the lateral florets. In the presence of (i, i) the lateral florets are relatively infertile, but when either (I^h, I^h) or (I, I) combinations accompany the heterozygous (V, v) genotype, the spike shows considerable to almost complete fertility. Fertile intermedium usually produces two or more lateral kernels per spike, usually located in the upper half or near the center of the spike (Woodward, 1947).

Robertson (1933) reported that the factor pairs (I, i) and (K, k) are linked and that these factors are independent of the allelic series for six-row, two-row, and deficiens. Woodward (1957), however, found in a series of crosses that (I) failed to show linkage with (K), (Gl), (Z), and (Bl).

Normal (Gl) versus glossy (gl) leaf. This character is one of the most common mutant types induced in barley, and according to Nilan (1964) all of the mutants are recessive and show monohybrid segregation. Heiner (1958), Imam (1959), and Doney (1961) obtained very low probability values when fitting observed segregation to a 3:1 ratio. They attributed this to poor germination or to a differential seedling mortality of glossy-leaved plants. Oldham (1962) obtained a reasonably good ratio of 3 non-glossy to 1 glossy-leaved plant.

Linkage group 5

Black (B) versus white (b) lemma and pericarp. Black lemma and pericarp is dominant over white. A monohybrid mode of inheritance has been reported by Hayes and Garber (1927), Woodward and Thieret (1953), Woodward (1957), Heiner (1958), Doney (1961), and Nilan (1964). Das (1957) found that the (B) versus (b) segregation, significantly deviated from a 3:1 ratio and more closely fit a 9:7 ratio. He concluded that lemma and pericarp color is controlled by two gene pairs.

Normal (Trd) versus third (trd) outer glume. The third outer glume is a recessive character and appears to be monofactorially inherited (Konzak, 1953; Heiner, 1958; Nilan, 1964). This character has been reported to be linked with (B,b) (Konzak, 1953; Ramage and Peterson, 1960).

Linkage group 7

Rough (R) versus smooth (r) awns. It has been reported by Hayes and Garber (1927), Daane (1931), and Doney (1961) that rough is dominant to smooth awns and is conditioned by a single gene pair. Other researchers (Heiner, 1958; Imam, 1959; Oldham, 1962) have observed a single factor ratio in some crosses and two factor segregation in other crosses. Nilan (1964) reported that two factor pairs are involved in the inheritance of this character. He indicated that one of the genes shows linkage with genes on chromosome 7, while other genes concerned with rough versus smooth awns were associated with genes in chromosome 2, or in chromosome 4. Kramer and Blander (1961), Oldham (1962), Nilan (1964), Robertson et al. (1965) reported that the (R,r) locus is located in chromosome 7.

Long (S) versus short (s) rachilla hairs. According to Gill (1951), Das (1957), Woodward (1957), Heiner (1958), and Doney (1961) this character is monofactorially inherited, with long dominant over short rachilla hairs. Nilan (1964) reported that Patterson and Shands found that the segregation of short and long rachilla hairs in F_2 poorly fits a 3:1 ratio. It is suggested by Konzak that the genes responsible for rachilla hairs may also determine glume hairs or may be linked closely with the glume hair factor (Nilan, 1964). Most workers are of the opinion that the factor pair (S,s) for long versus short rachilla hairs is located on chromosome 7 (Ramage and Peterson, 1960; Kramer and Blander, 1961; Nilan, 1964; Robertson et al.

1965). However, Buckley (1930) found an association between the (S, s) locus and other genes known to be on chromosome 2.

Unassigned genes

Normal (Rb) versus ribbon-grass (rb). Gill (1951), Wheatley (1955), Heiner (1958), Doney (1961), and Oldham (1962) reported that normal versus ribbon-grass is inherited as a single gene difference with normal dominant over ribbon-grass. Oldham (1962) is of the opinion that some plants which carry genes for ribbon-grass do not show it. Also, the expression of the character appears to be influenced to a considerable extent by environment, e. g., cold, stormy weather accentuates it. Woodward (1957) observed that (Rb, rb) is inherited independently of the following factor pairs: (N, n) for covered versus naked caryopsis on chromosome 1; (Re_2, re_2) for normal versus purple lemma and pericarp, (V, v) for non-six-row versus six-row, (E, e) for normal versus long-awned glume, and (Tr, tr) for normal versus triple awn on chromosome 2; (Bl, bl) for normal versus blue aleurone in chromosome 4; (B, b) for black versus white lemma and pericarp on chromosome 5; (Gs, gs) for normal versus glossy stem and (Gp, gp) for normal versus grandpa plants (unassigned).

Normal (Gp) versus grandpa (gp). Heiner (1958), Imam (1959), Doney (1961), and Oldham (1962) reported that grandpa is controlled by a single recessive gene. The rather poor fit to a 3:1 ratio that all these workers observed was considered to be due to the high seedling mortality and late maturity of grandpa plants. It was reported by Robertson et al. (1965) that the factor pair (Gp, gp) is inherited independently of (N, n) on chromosome 1; of (V, v), (E, e), (Tr, tr), (Li, li) for normal versus liguleless on chromosome 2; of (Bl, bl), (K, k) for hooded versus awned, (Gl, gl) for normal versus glossy leaf on chromosome 4; of (R, r) for rough versus smooth awned, and (S, s) for long versus short rachilla hairs on chromosome 7; and of (Rb, rb) for normal versus ribbon-grass (unassigned).

Long (Gh) versus short (gh) outer glume hair. It was reported by Gill (1951), Al-jibouri (1953), Heiner (1958), Imam (1959), and Oldham (1962) that long outer glume hair is dominant over short, and the inheritance of this character is governed by a single gene pair. Doney (1961) observed a single factor difference in one cross and two factor segregation in another cross. It was concluded by Rasmusson (1956) that two or more genes are involved in the inheritance of this character. The factor pair (Gh, gh), in relation to (Li, li), showed a recombination value of 36.2 per cent in a study reported by Woodward (1957).

Nilan (1964) reported that Konzak found an identity between the genes controlling the length of rachilla hairs and those controlling the length of outer glume hair. He concluded that the genes responsible are either identical or are so close to each other that no crossing-over occurs.

Normal (Gs) versus glossy (gs) stem. "Glossy stems" are characterized by the lack of waxy coating. Normal is dominant over glossy stem and has been reported to be inherited monofactorially (Gill, 1951; Wheatley, 1955; Heiner, 1958; Imam, 1959; LeBaron, 1959; Doney, 1961; Oldham, 1962). According to Robertson et al. (1965) the factor pair for normal versus glossy stem (Gs, gs) is inherited independently of (N, n) on chromosome 1; of (V, v), (Re_2, re_2), (Pr, pr) for normal versus purple straw on chromosome 2; of (Bl, bl) on chromosome 4; of (B, b) on chromosome 5; of (R, r), (S, s) on chromosome 7; and of (Rb, rb) (unassigned). They suggested that the factor pair (Gs, gs) is located on chromosome 1. Woodward (1957), however, found that (Gs, gs) showed a tendency to be linked with genes known to be located in group IV.

Normal (Ge) versus glossy (ge) spike. There is a reduction of wax on the spikes of glossy-spike plants. This character is reportedly recessive and is controlled by a single gene (Nilan, 1964). The factor pair (Ge, ge) shows a recombination percentage of 41.0, in relation to factor pair (E, e), and 24.5 per cent in relation to factor pair (K, k) (Woodward, 1957). It was reported by Robertson et al. (1965) that gene pair (Ge, ge) is inherited independently of (N, n) on chromosome 1; of (V, v), (Re_2, re_2), (E, e), (Li, li) on chromosome 2; of (Bl, bl) on chromosome 4; and of (R, r) on chromosome 7.

Normal (Ga) versus short (ga) glume awns. Awns on the outer glumes vary considerably in length. Long-awned outer glumes are attached to a large wide outer glume. They may be nearly equal in length to the regular awns. On normal plants the glumes are narrow while the awns, resembling hairs, vary from one-half the glume length to three or more times the glume length. These have been called (Gh) versus (gh) by LeBaron (1959) and Doney (1961), while Robertson et al. (1965) chose to call them (E_2) versus (e_2). LeBaron (1959) and Doney (1961) found a linkage between normal versus short glume awn and (N, n) and (Br, br) on chromosome 1. Robertson et al. (1965) assigned this gene pair to chromosome 1. The symbol (Ga, ga) has been suggested by Dr. R. W. Woodward (personal communication) for glume awns in place of the symbols (E_2, e_2). He also suggested the use of (Gh, gh) for glume hairs to distinguish these from glume awns. The symbols (Ga, ga) and (Gh, gh) will be used in this study.

MATERIALS AND METHODS

The crosses for this study were made by Dr. R. W. Woodward in 1963. The F_2 plants were grown in 1964 in rows two feet apart. Plants were spaced about 2-3 inches apart in rows on the North Logan Experimental Farm. Each cross was made up of several families, each family deriving from separate F_1 plants.

Characters which were visible only before maturity, e.g., grandpa (gp), glossy leaf (gl), glossy stem (gs), zoned leaf (z), purple auricle (pau), ribbon grass (rb), and purple lemma and pericarp (re_2), were tied with different colored string at the stage of growth when the character was most evident. Each family was pulled at maturity and bundled and labeled for further study in the laboratory. Plants were classified individually for different phenotypic characters.

The data were tabulated and each family was analyzed for inheritance of the individual characters. Characters were also studied two at a time in order to detect independence or association. After analysis by individual family, families were grouped together and characters were analyzed by crosses. The data for all crosses were then analyzed as a total.

Chi-square values were calculated to test observed inheritance patterns against hypothesized ratios. The probability values for chi-squares were taken from Snedecor (1962). Recombination percentages for indicating independence or association of characters studied two at a time, were computed by the product method reported by Fisher and Balmukend (1928) and described by Immer (1930).

Characters Used in This Study and Their Gene Symbols

A total of twenty–four pairs of contrasting characteristics were examined in the study. The gene symbols and their linkage groups are those suggested by Robertson et al. (1947, 1955, 1965) and Nilan (1964).

Linkage group 1

Covered versus naked caryopsis	N, n

Linkage group 2

Deficiens versus two-rowed versus six-rowed spikes	V^t, V, v
Normal versus long-awned outer glume	E, e
Lax versus dense spike	L, l
Normal versus triple awned lemma	Tr, tr
Normal versus liguleless	Li, li
Purple versus normal auricle	Pau, pau
Purple versus normal lemma and pericarp	Re_2, re_2
Purple versus normal stem	Pr, pr

Linkage group 4

Hooded versus awned spike	K, k
Normal versus zoned leaf	Z, z

Normal versus glossy leaf	Gl, gl
Blue versus non-blue aleurone	Bl, bl
Non-intermedium versus infertile intermedium versus fertile intermedium	i, I, I^h
Linkage group 5	
Black versus white lemma and pericarp	B, b
Normal versus third outer glume	Trd, trd
Linkage group 7	
Rough versus smooth awns	R, r
Long versus short rachilla hairs	S, s
Unassigned factor pairs	
Long versus short outer-glume hair	Gh, gh
Normal versus glossy stem	Gs, gs
Normal versus short glume awns	Ga, ga
Normal versus grandpa plant	Gp, gp
Normal versus ribbon-grass leaves	Rb, rb

Crosses and Parents

The study involved 22 crosses. The crosses, their parentage and the characters for which the crosses were segregating, plus a few segregating factors for which the parental genotypes are not known, are listed in Table 1.

Table 1. Crosses, parents and their segregating characters

Cross	Parentage	Segregating characters	Segregating characters for which parental genotypes are not known
B 1992	T818	K R gh I Gp E L	
	T919	k r Gh i gp e l	
B 1994	T357	gh Re_2 Pau Gs	(N, n), (I^h, i)
	T137	Gh re_2 pau gs	
B 1997	T305	R gh Bl n Gp E L	
	T919	r Gh bl N gp e l	
B 1999	T337	k Z s N	(Pr, pr), (Re_2, re_2) (I, i), (Gh, gh), (Ga, ga)
	T388	K z S n	
B 2005	T542	r s ga	(B, b)
	T298	R S Ga	
B 2010	T241	s Ga	(B, b), (Ge, ge), (I, I^h)
	T629	S ga	
B 2014	T 29	n R s I	
	T363	N r S i	

Table 1. Continued.

Cross	Parentage	Segregating characters	Segregating characters for which parental genotypes are not known
B 2080	T258	k Gl bl N E L Li Gs	(V^t, V), (Ga, ga)
	T1087	K gl Bl n e l li gs	
B 2083	T780	k Z L Li b gh gs	(Ga, ga), (E, e)
	T1097	K z l li B Gh Gs	
B 2084	T939	K R Bl gh n gs E l I	(Rb, rb)
	T938	k r bl Gh N Gs e L i	
B 2085	T876	E r Gh	(Li, li), (B, b)
	T943	e R gh	
B 2087	T938	k Gl i N e L r Gh Gs bl	(Rb, rb)
	T939	K gl I n E l R gh gs Bl	
B 2092	T993	rb v N e l li tr	(K, k), (B, b), (Gl, gl)
	B298Ge	Rb V n E L Li Tr	
B 2093	T 951	k V N E l Li Gh Rb	(Gl, gl), (B, b)
	T1087	K v n e L li gh rb	

Table 1. Continued

Cross	Parentage	Segregating characters	Segregating characters for which parental genotypes are not known
B 2095	T1087	e v K gl re_2 l Li Gh	(Ga, ga), (Pr, pr), (B, b)
	T148	E V k Gl Re_2 L Li gh	
B 2099	T258	b v re_2	(Gh, gh), (Ga, ga)
	T329	B V^t Re_2	
B 2100	T800	k Gl V^t e L li B Gh gs	
	T956	K gl V E l Li b gh Gs	
B 2102	T258	b v Gh re_2 Ga	(S, s)
	T309	B V^t gh Re_2 ga	
B 2103	T780	k V L Li tr b gh gs	(E, e)
	T1097	K V^t l li Tr B Gh Gs	
B 2107	T1087	e v K gl gs b S gh li trd	(Ga, ga)
	T115	E V k Gl Gs B s Gh Li Trd	
B 2108	T800	k Gl v e li B gs Ga	(S, s)
	T956	K gl V E Li b Gs ga	

EXPERIMENTAL RESULTS AND DISCUSSION

The results of this study are arranged in the same order as the Review of Literature.

Inheritance of Individual Characters

Linkage group 1

Covered (N) versus naked (n) caryopsis. The results of the segregation of covered versus naked caryopsis are presented in Table 2. A single gene difference would account for the segregation pattern in almost all crosses.

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

Cross	N	n	Total	X^2	P
B 1994	201	73	274	.039	.750-.900
B 1997	111	41	152	.315	.500-.750
B 1999	497	150	647	1.138	.250-.500
B 2012	310	116	426	1.129	.250-.500
B 2014	306	112	418	.717	.250-.500
B 2080	300	127	427	5.121	.010-.025
B 2084	340	100	440	1.212	.250-.500
B 2087	472	147	619	.517	.250-.500
B 2092	101	49	150	4.702	.025-.050
B 2093	273	104	377	1.344	.100-.250
Sum of 10 chi-squares				16.234	.050-.100
Total	2911	1019	3930	1.807	.100-.250
Interaction chi-square				14.427	.100 .250

Linkage group 2

Normal (E) versus long-awned (e) outer glume. Monofactorial inheritance with normal being dominant over long-awned glume would explain the segregation pattern observed in most of the crosses shown in Table 3. Crosses B 2103 and B 2108 fell below the .05 probability level, however. Both had too few plants with long-awned outer glumes. The sum and interaction chi-aquares barely fell within the acceptable probability range. By omitting these two crosses better chi-square and P values were obtained for the sum and interaction.

Table 3. Segregation of normal (E) versus long-awned (e) outer glume. Chi-square and P values are based on a 3:1 ratio.

Cross	E	e	Total	X^2	P
B 1992	253	95	348	.981	.250-.500
B 1997	111	41	152	.315	.500-.750
B 2080	325	102	427	.282	.500-.750
B 2083	88	40	128	2.666	.100-.250
B 2084	326	114	440	1.939	.100-.250
B 2085	238	75	313	.180	.500-.750
B 2087	485	134	619	2.846	.050-.100
B 2092	117	33	150	.720	.250-.500
B 2093	284	93	377	.221	.500-.750
B 2095	363	122	485	.618	.250-.500
B 2100	481	184	665	2.526	.100-.250
B 2103	337	87	424	4.541	.025-.050[a]
B 2107	280	98	378	.173	.500-.750
B 2108	490	135	625	3.853	.025-.050[a]
Sum of 14 chi-squares				21.861	.050-.100
Sum of 12 chi-squares				13.467	.250-.500
Total	4178	1353	5531	.853	.250-.500
Total	3351	1131	4482	.131	.500-.750
Interaction chi-square				21.008	.050-.100
Interaction chi-square				13.336	.250-.500

[a] Crosses which are omitted from the second set of sum, total and interaction chi-squares and P values.

Normal (Tr) versus triple-awned (tr) lemma. Table 4 shows the F_2 data for normal versus triple-awned lemma. The probability values indicate a single gene pair is likely involved in the inheritance of this character.

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

Cross	Tr	tr	Total	X^2	P
B 2092	115	35	150	.222	.500-.750
B 2103	200	80	280	1.904	.100-.250
Sum of 2 chi-squares				2.126	.250-.500
Total	315	115	430	.697	.250-.500
Interaction chi-square				1.429	.100-.250

Deficiens (V^t) versus two-rowed (V) versus six-rowed (v) spike. Tables 5 and 6 suggest a simple mode of inheritance with deficiens dominant over two-rowed and two-rowed dominant over six-rowed spike. However, in cross B 2100 (Table 7), deficiens appears to be recessive. The author cannot explain the reason for this. The low chi-square obtained in cross B 2092 might be attributed to its small number which makes it less reliable than the other crosses. This cross was left out in the calculation of sum and total chi-squares.

Lax (L) versus dense (l) spike. A single factor pair generally appears to be involved on the inheritance of this character, with lax dominant over dense spike (Table 8). The families in cross B 2103 had high chi-square values which do not fit the expected 3:1 ratio. The author believes that it is

Table 5. Segregation of deficiens (V^t) versus two-rowed (V) spike. Chi-square and P values are based on a 3:1 ratio.

Cross	V^t	V	Total	X^2	P
B 2080	333	94	427	2.031	.100-.250
B 2093	100	50	150	5.555	.010-.025[a]
B 2093	240	73	313	.469	.250-.500
B 2095	342	143	485	5.202	.010-.025
B 2103	307	117	424	1.522	.100-.250
B 2107	278	100	378	.427	.500-.750
Sum of 6 chi-squares				15.206	.010-.025
Sum of 5 chi-squares				9.651	.050-.100
Total	1600	577	2177	2.627	.100-.250
Total	1500	527	2027	1.078	.250-.500
Interaction chi-square				12.479	.025-.050
Interaction chi-square				8.573	.050-.100

[a] This cross was omitted from the second set of sum, total, and interaction chi-squares and P values.

Table 6. Segregation of two-rowed (V) versus six-rowed (v) spike. Chi-square and P values are based on a 3:1 ratio.

Cross	V	v	Total	X^2	P
B 2099	571	168	739	2.025	.100-.250
B 2102	392	107	499	3.367	.050-.100
B 2108	468	157	625	.026	.750-.900
Sum of 3 chi-squares				5.418	.100-.250
Total	1431	432	1863	3.260	.050-.100
Interaction chi-square				2.158	.250-.500

Table 7. Segregation of two rowed (V) versus deficiens (V^t) spike. Chi-square and P values are based on a 3:1 ratio.

Cross	V	V^t	Total	X^2	P
B 2100	491	174	665	.482	.250-.500

Table 8. Segregation of lax (L) versus dense (l) spike. Chi-square and P values are based on a 3:1 ratio.

Cross	L	l	Total	X^2	P
B 1992	195	63	258	.046	.250-.500
B 1997	117	35	152	.315	.500-.750
B 2080	317	110	427	1.319	.250-.500
B 2083	94	34	128	.166	.500-.750
B 2084	327	113	440	.109	.500-.750
B 2087	347	116	463	.0007	$>$ .900
B 2092	103	47	150	3.208	.050-.100
B 2093	269	108	377	2.674	.100-.250
B 2095	388	97	485	6.466	.010-.025
B 2100	492	173	665	.365	.500-.750
B 2103	354	70	424	16.301	$<$ .005[a]
Sum of 11 chi-squares				30.969	$<$ .005
Sum of 10 chi-squares				14.668	.100-.250
Total	3007	962	3969	1.229	.250-.500
Total	2653	892	3545	.049	.750-.900
Interaction chi-square				29.740	$<$ .005
Interaction chi-square				14.619	.100-.250

[a] Crosses which are omitted from the second set of sum, total and interaction chi-squares and P values.

because of poor classification. If cross B 2103 is left out of the computation, the sum and interaction chi-squares fall within the acceptable range.

Purple (Pau) versus normal (pau) auricle. Table 9 shows the F_2 data for the segregation of purple versus normal auricle. A monofactorial mode of inheritance with purple dominant to normal auricle would seem probable.

Table 9. Segregation of purple (Pau) versus normal (pau) auricle. Chi-square and P values are based on a 3:1 ratio.

Cross	Pau	pau	Total	X^2	P
B 1994	202	72	274	.238	.500-.750

Purple (Pr) versus normal (pr) stem. Two crosses involved in this study segregated for this character. In cross B 1999 purple seems to be dominant over normal, whereas in cross B 2095 purple stem appears to be recessive. Data for the two crosses are presented separately in Tables 10a and 10b. Segregation patterns for both crosses fall within the probability limits of a 9:7 ratio, but the dominance relationship is reversed in the two crosses.

Table 10a. Segregation of purple (Pr) versus normal (pr) stem. Chi-square and P values are based on a 9:7 ratio.

Cross	Pr	pr	Total	X^2	P
B 1999	313	279	592	2.745	.050-.100

Table 10b. Segregation of purple (Pr) versus normal (pr) stem. Chi-square and P values are based on a 7:9 ratio.

Cross	Pr	pr	Total	X^2	P
B 2095	168	194	362	1.041	.250-.500

<u>Normal (Li) versus liguleless (li)</u>. The data in Table 11 suggest that normal is dominant over liguleless and that a monohybrid mode of inheritance is operating. Croses B 2107 and B 2080 show low probability values. Errors in classification might be responsible for the large chi-square in these crosses. As most of the crosses fit a 3:1 ratio very well, by omitting these two crosses, the sum, total, and interaction chi-squares also agree with a 3:1 segregation ratio for (Li, li).

Table 11. Segregation of normal (Li) versus liguleless (li). Chi-square and P values are based on a 3:1 ratio.

Cross	Li	li	Total	X^2	P
B 2080	338	89	427	6.152	.010-.025[a]
B 2083	91	37	128	1.041	.250-.500
B 2085	230	83	313	.384	.500-.750
B 2092	115	35	150	.005	$>$ .900
B 2093	287	90	377	.255	.500-.750
B 2095	370	115	485	.429	.500-.750
B 2100	509	156	665	.842	.250-.500
B 2103	318	106	424	.000	$>$ .900
B 2107	258	120	378	9.174	$<$ .005[a]
B 2108	454	171	625	1.856	.100-.250
Sum of 10 chi-squares				19.138	.025-.050
Sum of 8 chi-squares				3.812	.750-.900
Total	2970	1002	3972	.108	.500-.750
Total	2384	793	3177	.002	$>$.900
Interaction chi-square				19.030	.010-.025
Interaction chi-square				3.810	.750-.900

[a] Crosses which are omitted from the second set of sum, total and interaction chi-squares and P values.

Purple (Re_2) versus normal (re_2) lemma and pericarp. The expected 9:7 ratio for purple versus normal lemma and pericarp was not observed in any of the crosses involving this character. Crosses B 1999 and B 2095 gave a ratio of 6:10 indicating purple recessive to normal (Table 12a), whereas other workers have found purple to be dominant over normal. Crosses B 1994, B 2099, and B 2102 indicate that purple is dominant over normal, but they did not show a 9:7 ratio. Ratios of 10:6 for cross B 1994, and 13:3 for two other crosses were obtained (Tables 12b and 12c). Although there was little agreement among crosses, two gene pairs appeared to be involved in the segregation of this character in all crosses. It is quite possible that the difficulty in classifying this character is largely responsible for the observed variation.

Table 12a. Segregation of purple (Re_2) versus normal (re_2) lemma and pericarp. Chi-square and P values are based on a 6:10 ratio.

Cross	Re_2	re_2	Total	X^2	P
B 1999	260	387	647	1.990	.100-.250
B 2095	191	294	485	.732	.250-.500
Sum of 2 chi-squares				2.722	.250-.500
Total	451	681	1132	2.646	.100-.250
Interaction chi-square				.076	.750-.900

Table 12b. Segregation of purple (Re_2) versus normal (re_2) lemma and pericarp. Chi-square and P values are based on a 10:6 ratio.

Cross	Re_2	re_2	Total	X^2	P
B 1994	175	99	274	.218	.500-.750

Table 12c. Segregation of purple (Re_2) versus normal (re_2) lemma and pericarp. Chi-square and P values are based on a 13:3 ratio.

Cross	Re_2	re_2	Total	X^2	P
B 2099	602	137	739	.031	.750-.900
B 2102	385	114	499	5.494	.010-.025
Sum of 2 chi-squares				5.525	.050-.100
Total	987	251	1238	1.888	.100-.250
Interaction chi-squares				3.637	.050-.100

Linkage group 4

Blue (Bl) versus non-blue (bl) aleurone. Two factor pairs appear to be involved in the inheritance of blue versus non-blue aleurone (Table 13). A 7:9 ratio was obtained in most crosses, with non-blue dominant over blue, whereas most other workers have suggested that blue is dominant over non-blue.

Hooded (K) versus awned (k) spike. The data for hooded versus awned spikes are shown in Table 14. Hooded appears to be dominant over awned. These data support others who have suggested single factor inheritance for this character.

Table 13. Segregation of blue (Bl) versus non-blue (bl) aleurone. Chi-square and P values are based on a 7:9 ratio.

Cross	Bl	bl	Total	X^2	P
B 1997	71	81	152	.541	.250-.500
B 2080	164	263	427	4.951	.025-.050
B 2084	90	93	183	2.184	.100-.250
B 2087	275	344	619	.118	.500-.750
Sum of 4 chi-squares				7.794	.050-.100
Total	600	781	1381	.051	.750-.900
Interaction chi-square				7.743	.050-.100

Table 14. Segregation of hooded (K) versus awned (k) spike. Chi-square and P values are based on a 3:1 ratio.

Cross	K	k	Total	X^2	P
B 44	484	168	652	.204	.500-.750
B 1992	258	90	348	.138	.500-.750
B 1999	476	171	647	.705	.250-.500
B 2080	317	110	427	.132	.500-.750
B 2083	89	39	128	2.041	.100-.250
B 2084	342	98	440	1.745	.100-.250
B 2087	472	147	619	.517	.250-.500
B 2092	116	34	150	.435	.500-.750
B 2093	276	101	377	.644	.250-.500
B 2095	346	139	485	3.464	.050-.100
B 2100	474	191	665	4.912	.025-.050
B 2107	294	84	378	1.555	.100-.250
B 2108	465	160	625	.120	.500-.750
Sum of 13 chi-squares				16.612	.100-.250
Total	4409	1532	5941	1.962	.100-.250
Interaction chi-square				14.650	.250-.500

Normal (Z) versus zones (z) leaf. Zoned leaf reduces vigor and results in a high mortality for many of the plants that are homozygous recessive. Two of the three crosses were deficient in zoned leaf plants and deviated significantly from a 3:1 ratio (Table 15). The high chi-squares are probably due to the seedling mortality of zoned-leaf plants.

Table 15. Segregation of normal (Z) versus zoned (z) leaf. Chi-square and P values are based on a 3:1 ratio.

Cross	Z	z	Total	X^2	P
B 44	486	166	652	.073	.750-.900
B 1999	556	91	647	41.261	$<.005$
B 2083	118	10	128	20.166	$<.005$
Sum of 3 chi-squares				61.500	$<.005$
Total	1160	267	1427	30.105	$<.005$
Interaction chi-square				31.395	$<.005$

Fertile intermedium (I^h) versus infertile intermedium (I) versus non-intermedium (i). The genes involved in fertility of lateral florets (I^h, I, i) are reported to be alleles. Segregation data for the three characters, taken two at a time are given in Tables 16, 17, and 18. The data are somewhat erratic but indicate that these characters might be controlled by two gene pairs with non-intermedium dominant over infertile intermedium and infertile intermedium, and non-intermedium dominant over fertile intermedium. Most other workers have suggested a single gene difference

Table 16a. Segregation of non-intermedium (i) versus infertile intermedium (I). Chi-square and P values are based on a 13:3 ratio.

Cross	i	I	Total	X^2	P
B 44	516	136	652	1.903	.100-.250

Table 16b. Segregation of non-intermedium (i) versus infertile intermedium (I). Chi-square and P values are based on a 10:6 ratio.

Cross	i	I	Total	X^2	P
B 2014	272	146	418	1.179	.250-.500

Table 17a. Segregation of infertile intermedium (I) versus fertile intermedium (I^h). Chi-square and P values are based on a 13:3 ratio.

Cross	I	I^h	Total	X^2	P
B 1992	283	65	348	.001	$>$.900
B 2084	365	75	440	.837	.250-.500
B 2087	268	44	312	4.423	.025-.050
Sum of 3 chi-squares				5.261	.100-.250
Total	916	184	1100	2.954	.050-.100
Interaction chi-square				2.307	.250-.500

for the inheritance of (I^h, I, i). The difficulty in making an accurate classification for (I^h) versus (I), and (I) versus (i) might be the cause of the rather poor fits. Most of the crosses fit a 13:3 or 10:6 ratio (Tables 16a, 16b, 17a, and 17b). The 13:3 ratio is possible when class (1) and one of the (3) classes are not distinguishable from class (9), in a basic 9:3:3:1 dihybrid ratio. A 10:6 ratio could occur when both (3) classes are indistinguishable and class (1) appears like class (9) (Dr. E. J. Gardner, personal communication). There were two crosses involved in the study of (i) versus (I). Cross B 44 segregated in a 13:3 ratio and cross B 2014 in a 10:6 ratio. In relation to (I) and (I^h) (Table 17a), all crosses showed a 13:3 ratio except cross B 2010 which segregated in a 10:6 ratio. This cross was left out of the sum, total, and interaction chi-squares, and is presented in Table 17b.

Non-intermedium versus fertile intermedium showed a 15:1 segregation ratio with non-intermedium dominant over fertile intermedium (Table 18).

Table 17b. Segregation of infertile intermedium (I) versus fertile intermedium (I^h). Chi-square and P values are based on a 10:6 ratio.

Cross	I	I^h	Total	X^2	P
B 2010	112	55	167	1.485	.100-.250

Table 18. Segregation of non-intermedium (i) versus fertile intermedium (I^h). Chi-square and P values are based on a 15:1 ratio.

Cross	i	I^h	Total	X^2	P
B 1994	256	18	274	.048	.750-.900
B 1999	603	44	647	.334	.500-.750
Sum of 2 chi-squares				.382	.750-.900
Total	859	62	921	.365	.500-.750
Interaction chi-square				.017	$>$ .900

Table 19. Segregation of normal (Gl) versus glossy (gl) leaf. Chi-square and P values are based on a 3:1 ratio.

Cross	Gl	gl	Total	X^2	P
B 2080	351	76	427	11.810	$<$ .005
B 2087	373	95	468	5.515	.010-.025
B 2092	113	37	150	.008	$>$ .900
B 2093	307	70	377	8.319	$<$ .005
B 2095	383	102	485	4.075	.025-.050
B 2100	270	56	326	10.638	$<$ .005
B 2107	260	53	313	10.863	$<$ .005
B 2108	501	124	625	8.875	$<$ .005
Sum of 8 chi-squares				60.103	$<$ .005
Total	2558	613	3171	54.342	$<$ .005
Interaction chi-square				5.761	.500-.750

Normal (Gl) versus glossy (gl) leaf. Table 19 contains the data for the segregation of normal versus glossy leaf. A very low probability value based on 3:1 ratio was obtained. In almost all instances the poor fits were due to a deficiency of glossy-leaved plants. Poor germination or differential seedling mortality of glossy-leaved plants, as is commonly reported in the literature, might serve as an explanation for the low P values.

Linkage group 5

Black (B) versus white (b) lemma and pericarp. The data in Table 20 show reasonable chi-square values for a 3:1 ratio, indicating a simple Mendelian pattern of inheritance for this character, with black dominant over white lemma and pericarp.

Normal (Trd) versus third (trd) outer glume. This character was present in only one of the crosses involved in this study. Although the data are limiting, they suggest a single gene difference for normal versus third outer glume (Table 21).

Linkage group 7

Rough (R) versus smooth (r) awns. The results of the segregation of rough versus smooth awns are presented in Table 22. According to the literature this character can be inherited either monofactorially or by two factor pairs. A very low probability value was obtained for all crosses when tested against a 3:1 ratio. However, by assuming two factor inheritance for (R, r), a reasonably good 13:3 segregation ratio was obtained for all crosses except cross B 1997. The small numbers in this cross may have contributed

Table 20. Segregation of black (B) versus white (b) lemma and pericarp. Chi-square and P values are based on a 3:1 ratio.

Cross	B	b	Total	X^2	P
B 2005	118	50	168	2.032	.100-.250
B 2010	130	37	167	.720	.250-.500
B 2083	97	31	128	.042	.750-.900
B 2085	236	77	313	.026	.750-.900
B 2092	109	41	150	.535	.250-.500
B 2093	230	83	313	.384	.500-.750
B 2095	93	30	123	.024	.750-.900
B 2099	563	176	739	.552	.250-.500
B 2100	504	161	665	.221	.500-.750
B 2102	383	116	499	.818	.250-.500
B 2103	325	99	424	.616	.250-.500
B 2107	279	99	378	.285	.500-.750
B 2108	465	160	625	.193	.500-.750
Sum of 13 chi-squares				6.448	.900-.950
Total	3532	1160	4692	.192	.500-.750
Interaction chi-square				6.256	.900-.950

Table 21. Segregation of normal (Trd) versus third (trd) outer glume. Chi-square and P values are based on a 3:1 ratio.

Cross	Trd	trd	Total	X^2	P
B 2107	145	34	179	3.443	.050-.100

to its high chi-square value. Cross B 1997 was eliminated from calculation of one set of sum, total, and interaction chi-squares.

Table 22. Segregation of rough (R) versus smooth (r) awns. Chi-square and P values are based on a 13:3 ratio.

Cross	R	r	Total	X^2	P
B 44	152	31	183	.393	.500-.750
B 1992	286	62	348	.199	.500-.750
B 1997	105	47	152	14.780	$<.005^a$
B 2005	143	25	168	1.650	.100-.250
B 2012	341	85	426	.404	.500-.750
B 2014	324	94	418	3.833	.050-.100
B 2084	154	29	183	1.012	.250-.500
B 2085	248	65	313	.835	.250-.500
B 2087	127	24	151	.808	.250-.500
Sum of 9 chi-squares				23.914	$<.005$
Sum of 8 chi-squares				9.134	.250-.500
Total	1880	462	2342	1.465	.100-.250
Total	1775	415	2190	.057	.750-.900
Interaction chi-square				22.449	$<.005$
Interaction chi-square				9.077	.100-.250

[a] Crosses which are omitted from the second set of sum, total and interaction chi-squares and P values.

Long (S) versus short (s) rachilla hairs. The data for the segregation of this character are shown in Table 23. Long hairs dominate short rachilla hairs. Inheritance generally appears to be controlled by a single gene. Crosses B 2014 and B 2108 had low P values. Poor classification in these crosses may be the cause. In the computation of one set of sum, total, and interaction chi-squares these crosses were omitted. The result was smaller chi-squares and higher P values.

Table 23. Segregation of long (S) versus short (s) rachilla hairs. Chi-square and P values are based on a 3:1 ratio.

Cross	S	s	Total	X^2	P
B 1999	468	179	647	2.452	.100-.250
B 2005	127	41	168	.031	.750-.900
B 2010	115	52	167	3.355	.050-.100
B 2014	333	85	418	4.851	.025-.050[a]
B 2102	198	78	276	1.565	.100-.250
B 2107	275	103	378	1.019	.250-.500
B 2108	434	191	625	10.304	$<$ .005[a]
Sum of 7 chi-squares				23.577	$<$ .005
Sum of 5 chi-squares				8.422	.100-.250
Total	1950	729	2679	6.989	.005-.010
Total	1183	453	1636	.485	.250-.500
Interaction chi-square				16.588	.010-.025
Interaction chi-square				7.937	.050-.100

[a] Crosses which are omitted from the second set of sum, total and interaction chi-squares and P values.

Unassigned genes

Normal (Rb) versus ribbon-grass (rb) leaf. All crosses but one in Table 24 show a rather poor fit to a 3:1 ratio. In each instance there were fewer (rb) plants than expected. Since it has been reported that weather conditions affect the expression of this character and that (rb) plants suffer a relatively high seedling mortality, it is suspected by the author that a single gene difference is responsible for (Rb) versus (rb), even though the data do not generally support this hypothesis.

Table 24. Segregation of normal (Rb) versus ribbon-grass (rb) leaf. Chi-square and P values are based on a 3:1 ratio.

Cross	Rb	rb	Total	X^2	P
B 2084	346	94	440	3.103	.050-.100
B 2087	494	125	619	7.625	.005-.010
B 2092	116	34	150	.435	.500-.750
B 2093	322	55	377	21.794	$<$.005
Sum of 4 chi-squares				32.957	$<$.005
Total	1278	308	1586	26.337	$<$.005
Interaction chi-square				6.620	.050-.100

Table 25. Segregation of normal (Gp) versus grandpa (gp). Chi-square and P values are based on a 3:1 ratio.

Cross	Gp	gp	Total	X^2	P
B 1992	310	38	348	36.796	$<$.005
B 1997	137	15	152	18.561	$<$.005
Sum of 2 chi-squares				55.357	$<$.005
Total	447	53	500	55.296	$<$.005
Interaction chi-square				.061	.750-.900

Normal (Gp) versus grandpa (gp). The F_2 segregation data for (Gp, gp) are given in Table 25. The suggested 3:1 ratio fits the observed segregation very poorly. Here again, however, the author is of the opinion that a single gene difference is probably involved and that the lack of (gp) plants can be explained by high seedling mortality and late maturity of the grandpa plants.

Long (Gh) versus short (gh) outer glume hair. Segregation data for long versus short outer glume hair are presented in Table 26. Segregation in most of the crosses satisfactorily fits a 3:1 ratio. The high chi-square values obtained for crosses B 2085 and B 2099, which contributed heavily to the low total probability, may have resulted from difficulty in accurately classifying the character in these crosses.

Normal (Gs) versus glossy (gs) stem. Table 27 shows the data for the segregation of this character. A 3:1 ratio with normal dominant over glossy stem appears probable. Crosses B 2080 and B 2100 fell below the .05 probability level, probably due to misclassification. These two cross in large measure accounted for the large "sum" chi-square value. By omitting cross B 2080 in the calculation of sum, total, and interaction chi-squares, much better P values were obtained.

Glossy (Ge) versus normal (ge) spike. A 9:7 ratio was obtained for this character, suggesting that a two factor pair difference is involved. In cross B 44 glossy spike is dominant over normal spike, whereas in cross B 2010 normal appears to be dominant. Both crosses have the same segregation ratio, but the dominance relationship is reversed in the two crosses. The segregation data are recorded in Tables 28a and 28b.

Normal (Ga) versus short (ga) glume awns. The data in Table 29 generally indicate single gene inheritance with normal dominant over short glume awns. Crosses B 2080 and B 2083 gave low P values. The difficulty of classification is probably responsible.

Table 26. Segregation of long (Gh) versus short (gh) outer glume hair Chi-square and P values are based on a 3:1 ratio.

Cross	Gh	gh	Total	X^2	P
B 1992	253	95	348	.981	.250-.500
B 1994	203	71	274	1.216	.250-.500
B 1997	110	42	152	.561	.250-.500
B 2014	314	104	418	.031	.750-.900
B 2083	88	40	128	2.666	.100-.250
B 2084	134	49	183	.317	.500-.750
B 2085	219	94	313	4.226	.025-.050
B 2087	356	112	468	.284	.500-.750
B 2093	274	103	377	1.083	.250-.500
B 2095	363	122	485	.006	$<$ .900
B 2099	440	173	613	3.393	.050-.100
B 2100	481	184	665	2.526	.100-.250
B 2102	166	57	223	.181	.500-.750
B 2103	113	31	144	.926	.250-.500
B 2107	277	101	378	.596	.250-.500
Sum of 15 chi-square				18.993	.100-.250
Total	3791	1378	5169	7.586	.005-.010
Interaction chi-square				11.407	.500-.750

Table 27. Segregation of normal (Gs) versus glossy (gs) stem. Chi-square and P values are based on a 3:1 ratio

Cross	Gs	gs	Total	X^2	P
B 1994	207	67	274	.044	.750-.900
B 2080	351	76	427	11.810	$<$ .005[a]
B 2083	95	33	128	.042	.750-.900
B 2084	336	104	440	.436	.500-.750
B 2087	483	136	619	3.029	.050-.100
B 2100	402	106	508	4.629	.025-.050
B 2103	332	92	424	2.465	.100-.250
B 2107	187	57	244	.349	.500-.750
B 2108	453	172	625	2.116	.100-.250
Sum of 9 chi-squares				24.920	$<$ .005
Sum of 8 chi-squares				13.110	.100-.250
Total	2846	843	3689	9.080	$<$ .005
Total	2495	767	3262	3.845	.025-.050
Interaction chi-square				15.840	.025-.050
Interaction chi-square				9.265	.100-.250

[a] Crosses which are omitted from the second set of sum, total and interaction chi-squares and P values.

Table 28a. Segregation of glossy (Ge) versus normal (ge) spike. Chi-square and P values are based on a 9:7 ratio.

Cross	Ge	ge	Total	X^2	P
B 44	353	299	652	1.178	.250-.500

Table 28b. Segregation of glossy (Ge) versus normal (ge) spike. Chi-square and P values are based on 7:9 ratio.

Cross	Ge	ge	Total	X^2	P
B 2010	80	87	167	1.171	.250-.500

Table 29. Segregation of normal (Ga) versus short (ga) glume awns. Chi-square and P values are based on a 3:1 ratio.

Cross	Ga	ga	Total	X^2	P
B 1999	493	154	647	.495	.250-.500
B 2005	125	43	168	.032	.750-.900
B 2080	174	83	257	7.292	.005-.010
B 2083	49	29	78	6.168	.010-.025
B 2095	186	60	246	.048	.750-.900
B 2102	369	130	499	.294	.500-.750
Sum of 6 chi-squares				14.339	.025-.050
Total	1396	499	1895	1.794	.100-.250
Interaction chi-square				12.545	.025-.050

Factor Pairs Showing Linkage

Linkages obtained in group 2

Normal (Li) versus liguleless (li) in relation to other factor pairs. Possible linkages were found between (Li, li) in relation to (V^t, V, v) and (L, l). The data are presented in Table 30. A slight linkage between (Li, li) and (V^t, V, v) was obtained in 4 crosses. Evidence of linkage was also noted between (Li, li) and (L, l). In some crosses good recombination values suggest that these two factors are in the same chromosome. In the other crosses they showed near independence. Poor classification may be the cause.

Normal (E) versus long-awned (e) outer glume in relation to (V^t, V, v) and (L, l). As indicated in Table 30 linkages were obtained with (E, e) in relation to $(V^t, V\ v)$ and (L, l).

Deficiens (V^t) versus two-rowed (V) versus six-rowed (v) spike in relation to (L, l). Some relationship was found between (V^t, V) and (L, l) (Table 30). However, out of 6 crosses involving (V^t, V, v) and (L, l) only one cross showed linkage.

Purple (Re_2) versus normal (re_2) lemma and pericarp in relation to other factor pairs. Data in Table 30 point to possible linkage between (Re_2, re_2) and the (Pr, pr), and (E, e) loci. A very close linkage was obtained in one cross involving (Re_2, re_2) and (Pr, pr).

Linkages obtained in group 4

Hooded (K) versus awned (k) spike in relation to other factor pairs. The data in Table 31 show the relationship of hooded versus awned spike to

Table 30. Linkages obtained in group 2

Cross	Phase	XY	Xy	xY	xy	Total	Recomb. Per cent
(Li, li) in relation to (V^t, V)							
B 2080	Repulsion	257	81	76	13	427	41.5
B 2092	Repulsion	70	45	30	5	150	31.5
B 2093	Repulsion	175	59	66	13	313	42.5
B 2107	Repulsion	177	81	101	19	378	37.5
(Li, li) in relation to (V, v)							
B 2108	Repulsion	315	139	153	18	625	32.0
(Li, li) in relation to (L, l)							
B 2092	Repulsion	72	43	31	4	150	10.0
B 2093	Repulsion	190	97	79	11	377	32.5
B 2100	Repulsion	350	159	142	14	665	29.5
(E, e) in relation to (V^t, V)							
B 2092	Repulsion	72	45	28	5	150	33.0
B 2093	Repulsion	169	65	72	7	313	31.5
B 2107	Repulsion	191	89	87	11	378	32.5
(E, e) in relation to (V, v)							
B 2108	Repulsion	336	154	132	3	625	15.0
(E, e) in relation to (L, l)							
B 1992	Coupling	170	19	25	44	258	18.5
B 1997	Coupling	95	16	22	19	152	29.5
B 2084	Coupling	286	40	41	73	440	20.0
B 2087	Coupling	317	42	34	70	463	18.5
B 2092	Coupling	96	21	7	26	150	18.0
B 2093	Coupling	221	63	48	45	377	34.0
B 2100	Coupling	384	97	108	76	665	36.0
B 2103	Coupling	298	39	57	30	424	31.5
(V^t, V) in relation to (L, l)							
B 2093	Repulsion	167	74	51	21	313	31.5
(Re_2, re_2) in relation to (Pr, pr)							
B 1999	Coupling	262	91	17	222	592	<5.0
B 2095	Coupling	139	61	55	107	362	22.0
(Re_2, re_2) in relation to (E, e)							
B 2095	Coupling	241	53	122	69	485	31.0

(Z, z), (i, I, I^h) and (Gl, gl) in chromosome 4. Two crosses out of 3 showed close linkage between (K, k) and (Z, z). Cross B 2087 showed independent segregation with regard to (K, k) and (I^h, I). The other crosses involving these two factors gave evidence of linkage. Out of 3 crosses involving (K, k) and (Bl, bl) only cross B 2080 showed linkage between these factors. The linkage in this cross was very close, however. The difficulty in classification of (Bl, bl) might be the cause for the failure of the other two crosses to show linkage.

Normal (Z) versus zoned (z) leaf in relation to (I^h, I, i). A relatively close linkage was obtained for (Z, z) in relation to fertile intermedium (I^h) versus non-intermedium (i) in cross B 1999. By way of contrast, cross B 44 showed a recombination value of 42.0. The difficulty in making an accurate classification for (I^h, I) and (I, i) might account for the divergent results. Data are shown in Table 31.

Normal (Gl) versus glossy (gl) leaf in relation to other factor pairs. Table 31 shows the data for the relationship of normal versus glossy leaf to (I^h, I), and (Bl, bl). Only cross B 2087 involved both (Gl, gl) and (I, I^h). A recombination value of 39.5 was obtained for this cross. Two crosses involved (Gl, gl) and (Bl, bl). Cross B 2080 showed a strong linkage, while weak linkage was indicated by cross B 2087. Misclassification of (Bl, bl) and/or excessive seedling mortality of glossy-leaved plants may have upset the linkage data in this latter cross.

Table 31. Linkages obtained in group 4

Cross	Phase	XY	Xy	xY	xy	Total	Recomb. Per cent
(K, k) in relation to (Z, z)							
B 1999	Repulsion	387	89	169	2	647	15.5
B 2083	Repulsion	79	10	39	0	128	21.5
(K, k) in relation to (i, I)							
B 44	Repulsion	349	135	167	1	652	<9.0
(K, k) in relation to (i, I^h)							
B 1999	Repulsion	437	39	166	5	647	32.5
(K, k) in relation to (I, I^h)							
B 2084	Coupling	295	47	72	26	440	39.0
(K, k) in relation to (Bl, bl)							
B 2080	Repulsion	165	152	98	12	427	<1.0
(K, k) in relation to (Gl, gl)							
B 2080	Repulsion	243	74	108	2	427	17.0
B 2087	Repulsion	273	82	100	13	468	38.5
B 2092	Repulsion	79	37	34	0	150	12.5
B 2093	Repulsion	207	69	100	1	377	12.5
B 2095	Repulsion	252	94	131	8	485	26.0
B 2100	Repulsion	182	49	88	7	326	33.5
B 2107	Repulsion	200	46	60	7	313	40.5
B 2108	Repulsion	351	114	150	10	625	29.0
(Z, z) in relation to (i, I)							
B 44	Repulsion	372	114	144	22	652	42.0
(Z, z) in relation to (i, I^h)							
B 1999	Repulsion	513	43	90	1	647	21.5
(Gl, gl) in relation to (I, I^h)							
B 2087	Coupling	105	16	30	10	161	39.5
(Gl, gl) in relation to (Bl, bl)							
B 2080	Coupling	247	104	16	60	427	14.0
B 2087	Coupling	227	146	49	46	468	41.5

Linkages obtained in group 5

Black (B) versus white (b) lemma and pericarp in relation to (Trd, trd). The data in Table 32 suggest that the genes for black versus white lemma and pericarp are in the same linkage group as (Trd, trd). The recombination value for these two characters was 12.5, indicating a close linkage.

Table 32. Linkages obtained in group 5

Cross	Phase	XY	Xy	xY	xy	Total	Recomb. Per cent
	(B, b) in relation to (Trd, trd)						
B 2107	Repulsion	102	34	43	0	179	12.5

Linkages obtained in group 7

Rough (R) versus smooth (r) awns in relation to (S, s). The data for the relationship of (R, r) to normal versus short rachilla hairs are given in Table 33. Cross B 2014 showed a fairly good linkage between (R, r) and (S, s), while cross B 2005 showed possibly a slight linkage. The difficulty in classifying both factors might be the cause for obtaining recombination values of 41.0 in cross B 2005.

Table 33. Linkages obtained in group 7

Cross	Phase	XY	Xy	xY	xy	Total	Recomb. Per cent
	(R, r) in relation to (S, s)						
B 2005	Repulsion	106	37	21	4	168	41.0
B 2014	Repulsion	245	79	88	6	418	29.5

New linkages suggested

Normal (Rb) versus ribbon-grass (rb) in relation to other factor pairs. The data for the relationship of (Rb, rb) to other factors are given in Table 34. One of two crosses involving (Rb, rb) and (R, r) shows a linkage between these two factors, with a 22.5 recombination value. A possible linkage was also noted between (Rb, rb) and (Li, li) in cross B 2093.

Normal (Gp) versus grandpa (gp) in relation to other factor pairs. Linkage associations involving (Gp, gp) and (E, e), (N, n), (L, l), (Bl, bl), and (I, I^h) are presented in Table 34. Of two crosses involving (Gp, gp) and (E, e) one showed evidence of linkage and one did not. Seedling mortality of (gp) plants may have influenced the results. As (Gp, gp) showed a closer linkage with (Bl, bl) and (I, I^h) in chromosome 4 than it did with genes in other linkage groups, it would appear that (Gp, gp) might be located in group 4.

Long (Gh) versus short (gh) outer glume hair in relation to other factor pairs. Table 34 gives the data for the relationship of long versus short outer glume hair to other factor pairs. A possible linkage between (Gh, gh) and (L, l) is indicated. One of two crosses involving (Gh, gh) and (Pr, pr) showed a linkage between these two genes with recombination value of 35.5. Out of 9 crosses only 3 showed linkage between (Gh, gh) and (B, b). Of 7 crosses only two showed linkage between (Gh, gh) and (V^t, V). All crosses involving (Gh, gh) and (I^h, I, i) with one exception, showed linkage between these two loci. Only one cross (B 1999) out of 5 showed linkage between (Gh, gh) and (Re_2, re). A very close linkage was obtained between (Gh, gh) and (Bl, bl), indicating that (Gh, gh) probably is in the same group as (Bl, bl).

Table 34. New linkages suggested

Cross	Phase	XY	Xy	xY	xy	Total	Recomb. Per cent
		(Rb, rb) in relation to (R, r)					
B 2084	Repulsion	117	28	37	1	183	22.5
		(Rb, rb) in relation to (Li, li)					
B 2093	Repulsion	237	85	50	5	377	32.5
		(Gp, gp) in relation to (E, e)					
B 1997	Coupling	103	34	8	7	152	36.5
		(Gp, gp) in relation to (N, n)					
B 1997	Coupling	102	35	8	7	152	37.5
		(Gp, gp) in relation to (L, l)					
B 1992	Coupling	179	48	16	15	258	33.5
B 1997	Coupling	109	28	8	7	152	34.0
		(Gp, gp) in relation to (Bl, bl)					
B 1997	Repulsion	72	65	9	6	152	20.0
		(Gp, gp) in relation to (I, I^h)					
B 1992	Repulsion	246	64	37	1	348	21.5
		(Gh, gh) in relation to (L, l)					
B 1992	Coupling	170	19	25	44	258	18.5
B 1997	Coupling	96	14	21	21	152	26.0
B 2083	Coupling	68	20	26	14	128	41.5
B 2084	Coupling	120	14	19	30	183	20.0
B 2087	Coupling	218	18	31	45	312	17.5
B 2093	Coupling	223	51	46	57	377	28.5
B 2095	Coupling	301	62	87	35	485	41.0
B 2100	Coupling	384	97	108	76	665	36.0
B 2103	Coupling	106	7	25	6	144	33.0
		(Gh, gh) in relation to (Pr, pr)					
B 1999	Repulsion	145	201	83	68	497	35.5
		(Gh, gh) in relation to (B, b)					
B 2099	Repulsion	408	32	66	107	613	15.0
B 2103	Repulsion	86	27	28	3	144	35.0
B 2102	Coupling	163	3	8	49	223	<5.0

Table 34. Continued

Cross	Phase	XY	Xy	xY	xy	Total	Recomb. Per cent
		(Gh, gh) in relation to (V^t, V)					
B 2093	Repulsion	160	64	80	9	313	33.0
B 2107	Repulsion	188	89	90	11	378	31.5
		(Gh, gh) in relation to (I, I^h)					
B 1992	Repulsion	199	54	84	11	348	40.0
B 2084	Repulsion	92	42	48	1	183	14.5
B 2087	Repulsion	192	44	76	0	312	12.0
		(Gh, gh) in relation to (i, I^h)					
B 1994	Coupling	187	16	69	2	274	31.0
B 1999	Repulsion	319	27	145	6	497	38.0
		(Gh, gh) in relation to (Re_2, re_2)					
B 1999	Repulsion	189	157	106	45	497	30.5
		(Gh, gh) in relation to (Bl, bl)					
B 1997	Repulsion	52	58	29	13	152	20.0
B 2084	Repulsion	58	76	35	14	183	<1.0
B 2087	Repulsion	186	170	87	25	468	<1.0
		(Gh, gs) in relation to (V^t, V)					
B 2107	Repulsion	129	58	49	8	244	36.0
		(Gs, gs) in relation to (Bl, bl)					
B 2080	Coupling	233	118	30	46	427	28.0
		(Gs, gs) in relation to (Z, z)					
B 2083	Repulsion	86	9	32	1	128	33.5
		(Gs, gs) in relation to (R, r)					
B 2084	Repulsion	114	26	40	3	183	34.5
		(Ge, ge) in relation to (K, k)					
B 44	Repulsion	241	112	243	56	652	29.0
		(Ge, ge) in relation to (B, b)					
B 2010	Repulsion	59	21	71	16	167	37.5
		(Ga, ga) in relation to (K, k)					
B 1999	Repulsion	343	150	133	21	647	36.0
B 2080	Repulsion	172	82	78	5	337	24.0
B 2083	Repulsion	50	38	29	1	118	14.5
B 2095	Repulsion	206	96	53	7	362	33.0
		(Ga, ga) in relation to (R, r)					
B 2005	Repulsion	103	22	40	3	168	37.0

Normal (Gs) versus glossy (gs) stem in relation to other factor pairs. The data in Table 34 show that two crosses gave evidence of a weak linkage between (Gs, gs) and (V^t, V, v). Cross B 2080 showed linkage between (Gs, gs) and (Bl, bl) with a recombination value of 28.0, but two other crosses did not show linkage. The misclassification of (Bl, bl) might be an explanation. Cross B 2083 was the only cross involving (Gs, gs) and (Z, z) which gave evidence of linkage between these two factors. It showed a recombination value of 33.5. One of two crosses showed linkage between (Gs, gs) and (R, r). It is suspected that (Gs, gs) is probably located in the same chromosome as (Bl, bl) and (Z, z).

Glossy (Ge) versus normal (ge) spike in relation to other factor pairs. Evidence of possible linkage between (Ge, ge) and the (K, k) and (B, b) loci can be observed in Table 34. The suggested linkage between (Ge, ge) and (B, b) is only slight and is based on relatively small numbers.

Normal (Ga) versus short (ga) glume awn in relation to other factor pairs. The data for the relationship of (Ga, ga) to (K, k) and (R, r) are given in Table 34. Relatively low recombination values were obtained for all crosses involved (Ga, ga) and (K, k), indicating a linkage between these two factors.

Factor Pairs Showing Independence

The following characters appeared to be independently inherited:

Factor pairs showing independence in group 2

Normal (Li) versus liguleless (li) independent of:

Normal versus long awned outer glume	E, e

Normal versus triple-awned lemma	Tr, tr
Purple versus normal stem	Pr, pr
Normal (E) versus long-awned (e) outer glume independent of:	
Normal versus triple-awned lemma	Tr, tr
Purple versus normal stem	Pr, pr
Lax (L) versus dense (l) spike independent of:	
Normal versus triple-awned lemma	Tr, tr
Purple versus normal stem	Pr, pr
Deficiens (V^t) versus two-rowed (V) versus six-rowed (v) spike independent of:	
Normal versus triple-awned lemma	Tr, tr
Purple versus normal stem	Pr, pr
Purple (Re_2) versus normal (re_2) lemma and pericarp independent of:	
Deficiens versus two-rowed versus six-rowed spike	V^t, V, v
Lax versus dense spike	L, l
Normal versus liguleless	Li, li

Factor pairs showing independence in group 4

Infertile intermedium (I) versus fertile intermedium (I^h) independent of:	
Non-blue versus blue aleurone	Bl, bl

Unassigned genes showing independence with regard to other factor pairs

Normal (Rb) versus ribbon-glass (rb) independent of:

Normal versus triple-awned lemma	Tr, tr
Hooded versus awned spike	K, k
Fertile versus infertile intermedium	I^h,I
Normal versus glossy leaf	Gl, gl
Non-blue versus blue aleurone	Bl, bl
Black versus white lemma and pericarp	B, b
Long versus short outer glume hair	Gh, gh
Normal versus glossy stem	Gs, gs

Normal (Gp) versus grandpa (gp) independent of:

Hooded versus awned spike	K, k
Rough versus smooth awns	R, r

Long (Gh) versus short (gh) outer glume hair independent of:

Hooded versus awned spike	K, k
Purple versus normal auricle	Pau, pau
Normal versus liguleless	Li, li
Long versus short rachilla hairs	S, s
Rough versus smooth awns	R, r
Normal versus third outer glume	Trd, trd
Covered versus naked caryopsis	N, n
Normal versus glossy stem	Gs, gs

Normal versus glossy leaf	Gl, gl
Normal versus grandpa plant	Gp, gp
Normal versus zoned leaf	Z, z

Normal (Gs) versus glossy (gs) stem independent of:

Hooded versus awned spike	K, k
Black versus white lemma and pericarp	B, b
Normal versus triple-awned lemma	Tr, tr
Normal versus liguleless	Li, li
Normal versus glossy leaf	Gl, gl
Normal versus long-awned outer glume	E, e
Lax versus dense spike	L, l
Covered versus naked caryopsis	N, n
Normal versus third outer glume	Trd, trd
Long versus short rachilla hairs	S, s
Fertile versus infertile versus non-intermedium	I^h, I, i
Purple versus normal auricle	Pau, pau
Purple versus normal lemma and pericarp	Re_2, re_2

Glossy (Ge) versus normal (ge) spike independent of:

Long versus short rachilla hairs	S, s
Normal versus zoned leaf	Z, z
Covered versus naked caryopsis	N, n
Fertile versus infertile versus non-intermedium	I^h, I, i
Rough versus smooth awns	R, r

Normal (Ga) versus short (ga) glume awns independent of:

Black versus white lemma and pericarp	B, b
Normal versus third outer glume	Trd, trd
Long versus short rachilla hairs	S, s
Deficiens versus two-rowed versus six-rowed spike	V^t, V, v
Normal versus liguleless	Li, li
Normal versus glossy leaf	Gl, gl
Normal versus zoned leaf	Z, z
Purple versus normal lemma and pericarp	Re_2, re_2
Purple versus normal stem	Pr, pr
Fertile versus non-intermedium	I^h, i
Lax versus dense spike	L, l
Covered versus naked caryopsis	N, n
Non-blue versus blue aleurone	Bl, bl

SUMMARY AND CONCLUSIONS

Twenty-two crosses in the F_2 generation were studied for the inheritance, linkage, and independence of twenty-four contrasting factors in barley.

Those factors for which monofactorial inheritance appeared most likely are:

N, n; Tr, tr; Li, li; V^t, V, v; E, e; L, l; Rb;rb; Pau, pau; K, k; Z, z; Gl, gl; Gp, gp; B, b; Trd, trd; R, r; S, s; Gh, gh; Gs, gs; Ga, ga.

A two factor pair difference is suggested for the following genes: Pr, pr; Bl, bl; Ge, ge; Re_2, re_2; i, I, I^h.

Good evidence was not obtained for the inheritance of (i, I), (I, I^h) and (Re_2, re_2) because of the difficulty involved in classifying these characters.

The unassigned genes examined in this study showed apparent association with certain genes from several of the known linkage groups. Evidence of possible linkage was obtained for the following combinations:

(Rb, rb) in relation to (R, r) in group 7.

(Gp, gp) in relation to (Bl, bl) and (i, I, I^h) in group 4.

(Gh, gh) in relation to (i, I, I^h) and (Bl, bl) in group 4.

(Gs, gs) in relation to (Bl, bl) and (Z, z) in group 4.

(Ge, ge) in relation to (K, k) in group 4.

(Ga, ga) in relation to (K, k) in group 4.

The following factor pairs were found to show independence:

(Li, li) in relation to (E, e), (Tr, tr), and (Pr, pr).

(E, e) in relation to (Tr, tr) and (Pr, pr).

(L, l) in relation to (Tr, tr) and (Pr, pr).

(V^t, V, v) in relation to (Tr, tr) and (Pr, pr).

(Re_2, re_2) in relation to (Pau, pau), (V^t, V, v), (L, l), and (Li, li).

(I, I^h) in relation to (Bl, bl).

(Rb, rb) in relation to (Tr, tr), (K, k), (I^h, I), (Gl, gl), (Bl, bl), (B, b), (Gh, gh), and (Gs, gs).

(Gp, gp) in relation to (K, k) and (R, r).

(Gh, gh) in relation to (K, k), (Pau, pau), (Li, li), (S, s), (R, r), (Trd, trd), (N, n), (Gs, gs), (Gl, gl), (Gp, gp), (Z, z), and (Ga, ga).

(Gs, gs) in relation to (K, k), (B, b), (Tr, tr), (Li, li), (Gl, gl), (E, e), (Ga, ga), (L, l), (N, n), (Trd, trd), (S, s), (I^h, I, i), (Pau, pau), and (Re_2, re_2).

(Ge, ge) in relation to (S, s), (Z, z), (N, n), (I^h, I, i), and (R, r).

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