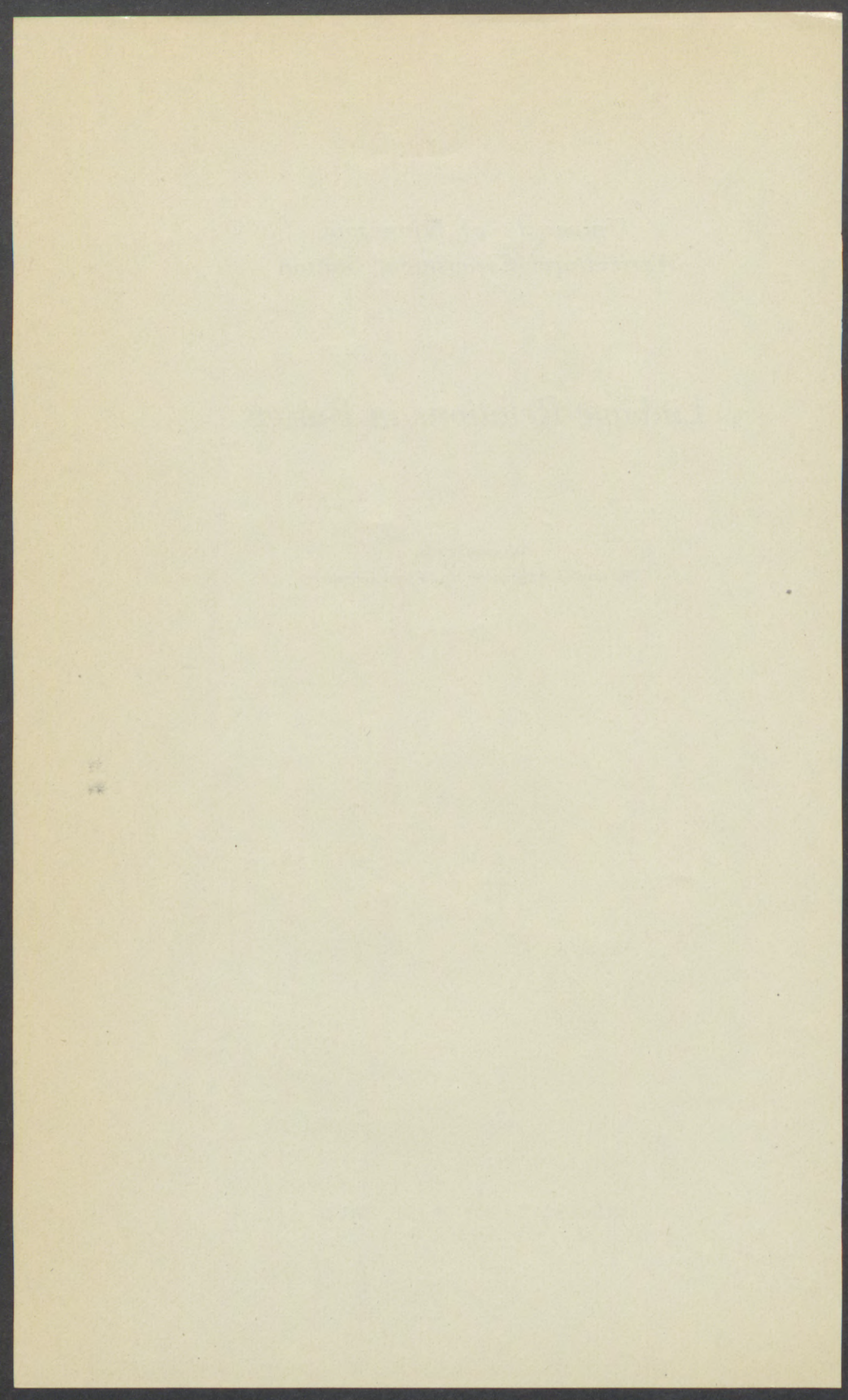


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Linkage Relations in Barley

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LINKAGE RELATIONS IN BARLEY

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INTRODUCTION

Chlorophyll-deficient seedlings appear in several cultivated crops. They have been reported frequently in corn, barley, sorghum, timothy, red clover, rye, and in other crops to a less extent. In most cases they die as soon as the plant food stored in the endosperm has been exhausted. There are several forms of chlorophyll deficiency. Some seedlings contain very little chlorophyll, if any; others show more, the plants ranging in color from a pale green to the normal shade. Recessive types exhibiting some chlorophyll may later appear normal and grow to maturity. Albino, xantha, chlorina, superchlorina, virescent, and lutescens have been used to designate the different forms of deficiency.

Chlorophyll-deficient plants have little economic value. However, the genetic factors responsible for them are of considerable importance in the study of linkage relations of plant characters.

The chlorophyll-deficient character used in this study was found in the University Farm plots. The strain was given the culture number B17. As the strain carried several other recessive characters, it was excellent parental material to use in genetic studies. This paper summarizes previous knowledge of linkage relations in barley and presents new data on linkage with particular reference to the chlorophyll deficiency in B17.

REVIEW OF LITERATURE

The review of literature on the genetics of barley is confined to characters that have been used by investigators in studies of linkage relations.

Inheritance of Differential Characters

Chlorophyll deficiencies.—Nilsson-Ehle (25) describes six different chlorophyll deficiencies in barley, three of which were albino, two were yellow, and one was of chlorina type. Each behaved as a simple Mendelian recessive when crossed with a normal green plant. The three albinos were, however, genotypically different. Hallqvist

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(9) reports a chlorophyll-defective type that depends on temperature for its expression. No chlorophyll was developed at 0° to 10° C.; at 12° to 15° C. some green pigment could be detected at the tips of the blades. However, the plants died at an early stage. This type of defective proved to be a simple Mendelian recessive character. Hallqvist (9) later reports the results of his investigations with chlorophyll-deficient types, three of which were classed as albinos, two as xanthas, two as virescents, and one each as chlorina, superchlorina, and lutescens. The albinos, when intercrossed, gave ratios in F_2 of 9 green to 7 albino, indicating that complementary factors were involved. In crosses involving virescent and xantha, an F_2 ratio of 9:3:4 of green to xantha to virescent was obtained. Albino 3 was found to be linked with chlorina and also with albino 4. Kiessling (19) reported a chlorophyll-defective mutation that behaved as a simple Mendelian recessive.

An albino form is reported by Collins (3) that grows to maturity and produces seed at temperatures above 45° F. In crosses with normal green plants, a segregation of 3 green to 1 albino was obtained in F_2 , showing a single factor difference.

Robertson (26) worked with three different chlorophyll deficiencies. An albino form appeared in three strains of Colseess, namely, I, II, and III, and was designated as $A_c a_c$. A second form, $A_t a_t$, was found in Trebi; the third, a xantha type, $X_c x_c$ appeared in Colseess IV. His results showed each deficiency to be inherited as a simple Mendelian recessive. One strain, Colseess II, carried two complementary factors for chlorophyll color but further studies with this strain are not included in this report.

McGregor (21) reports a chlorophyll-deficient factor in Manchuria 184, which later proved to be identical with the chlorophyll-deficient factor found in the Colseess strains used by Robertson. Segregation in the F_2 indicated a single factor difference.

Fertility of lateral florets.—Biffen (1) found a single factor difference between *vulgare* and *distichon*. Robertson (26), Tedin and Tedin (28), Neatly (24), McGregor (21), and Buckley (2) obtained similar results. Biffen crossed *vulgare* with *deficiens* and found that the segregation in F_2 could be explained on the basis of a single factor difference. His cross of *deficiens* with *distichon* gave like results.

Many of the investigators in the genetics of barley have studied the inheritance of the fertility of the lateral florets. The results obtained from crossing two-rowed varieties with six-rowed differ. An explanation for some of the varying results is made by Harlan and Hayes (13) in interpreting the data from crossing two-rowed and six-rowed varieties. In most cases an intermediate condition in the F_1 was obtained and the lateral florets were awned and were very low

in fruitfulness. Segregation in F_2 could be explained on a single factor difference, as reported by Biffin.

In a cross between Manchuria, a six-rowed barley, and Svanhals, a two-rowed variety, the F_1 lateral florets were slightly fruitful with intermediate awns. The F_2 generation was classified, on the basis of the results obtained in F_3 , as follows:

1. Those that bred true for the six-rowed character.
2. Those that segregated, giving six-rowed, awned, intermediate forms with very high fruitfulness of the lateral florets and *intermedium* forms in a 1:2:1 ratio.
3. *Intermedium* forms that bred true, giving few or no awns on lateral florets and producing approximately 50 per cent of barren lateral florets.
4. Those that gave all forms as in F_2 .
5. Those that produced intermediates and two-rowed types.
6. Those that produced six-rowed, awned intermediates with little or no fruitfulness in the lateral florets and two-rowed forms in a 1:2:1 ratio.
7. Those that bred true for the two-rowed condition.

These results were explained on a two-factor basis. The six-rowed parent contained both factors for six-rowed and for *intermedium* in a homozygous condition, the *intermedium* factor being hypostatic to the six-rowed factor.

Indications of a single factor difference were obtained by crossing *intermedium* with six-rowed. Such crosses gave intermediates of high fertility in F_1 . Awness forms with very low fruitfulness in F_1 were secured by crossing *intermedium* with two-rowed. The degree of fruitfulness of the lateral florets of *intermedium* types was considered to be modified by minor factors that were sometimes present.

Griffie (8), in his studies of the inheritance of the fertility of the lateral florets, obtained results similar to those of Harlan and Hayes. In a cross of *H. deficiens steudellii* with Manchuria the F_1 greenhouse plants were indistinguishable from the *deficiens*. However, under field conditions many of the F_1 plants showed slight glume and palea development in the lateral florets. The F_2 generations could be easily grouped into three types, *deficiens*, intermediates, and six-rowed, the ratio being approximately 1:2:1. The classification was confirmed in the F_3 . The only sure method of differentiating between homozygous *deficiens* plants and heterozygous was by the progeny test.

In another cross, Svanhals x Lion, the F_1 plants resembled the two-rowed parent but the glumes of the lateral florets were more pointed and bore small awns. In classifying the F_2 plants, four groups were used, six-rowed, *intermedium*, intermediates, and two-rowed. The

six-rowed and intermedium plants bred true in F_3 . Of the plants classed as two-rowed in F_2 , two-thirds gave segregation in F_3 , some producing two-rowed, intermediates, and six-rowed; some two-rowed and intermedium; others produced all the types found in F_2 . About one-fourth of all the F_2 plants were six-rowed. The lines that segregated for two-row vs. six-row gave a ratio of approximately 3:1 two-rowed and intermediate to six-rowed. Griffée explains such results by the same hypothesis that was advanced by Harlan and Hayes.

Robertson (26), in crosses between six-rowed forms with two-rowed and *deficiens* types, used similar explanations for the inheritance of fruitfulness as advanced by Harlan and Hayes, and by Griffée. The six-rowed parents, Colsess and Trebi, were considered to have the genotypic condition of vvII, in which the factor for intermedium, or I, was hypostatic to v. The two-rowed parent had the genotypic condition VVii.

Ubisch (29) uses two factors to explain the results obtained from crosses involving *vulgare* and *distichon*. Six-rowed has the constitution zzww, intermedium zzWW, and two-rowed ZZWW. The expression of Z is responsible for the two-rowed; W produces the intermedium. On this hypothesis the two-rowed parent carries the intermedium factor in a hypostatic condition.

Gillis (7) considers three factors necessary to explain the differences in the fertility of the lateral florets. In addition to the two factors used by Ubisch, a third factor, D, for fertility of lateral florets is added. This third factor is in the dominant condition in intermedium and recessive in *deficiens*. Thus a two-rowed homozygous form would be of the genotypic condition, ZZWWDD, while *deficiens* would carry the formula, ZZWWdd. Six-rowed varieties might contain either D or d. On this basis *deficiens*, six-rowed, and two-rowed do not form an allelomorph series.

Engledow (5) (6), and Hor (17) conclude that *vulgare*, *distichon*, and *deficiens* form an allelomorph series.

The investigations on the inheritance of the fertility of the lateral florets of barley may be summarized as follows:

Deficiens, *distichon*, and *vulgare* form an allelomorph series but the intermedium of low fertility reported by Harlan and Hayes (13), Griffée (8), and Robertson (26) is not an allelomorph of the above mentioned series.

Black vs. white glumes.—In crosses of black and white hulled varieties, Biffen (1), Kezer and Boyack (19), Griffée (8), Hayes and Garber (15), Ubisch (29), Hor (17), Robertson (26), Sigfusson (27), McGregor (21), and Buckley (2) found F_1 to be black and the F_2 generation to segregate in ratio of 3 black to 1 white. A single factor

difference explains the results. Buckley (2) has contributed considerable evidence on the inheritance of color in the glumes and the caryopsis.

In crosses involving black vs. white glumes and black vs. red pericarp color, black was found to be dominant and a ratio of 3 black to 1 not black was secured in the F_2 generation showing simple Mendelian inheritance. Black in the glumes and pericarp appears to be dependent upon the same genetic factor.

Purple vs. white glumes.—Observations by Biffen (1) and Buckley (2) show that in the F_1 purple is dominant to white. In the F_2 a ratio of 3 purple to 1 white is obtained, indicating a single factor difference.

Miyaka and Imai (22) grouped the F_2 progeny of a cross between purple and white lemma into three classes, namely dark purple, light purple, and white, and obtained the ratio 9:6:1. This is explained on a two-factor basis P_1p_2 , p_1P_2 being the genotypes of the light purple class, p_1P_2 of the dark purple class, and the p_1p_2 of the white class.

White vs. orange glumes.—In crossing two strains of barley, one having black and the other orange-colored glumes, a segregation of 3 white to 1 orange in F_2 was obtained by Buckley (2). A single factor difference explains the results.

Red vs. white pericarp.—In four crosses of red pericarp with white, Buckley (2) found that the F_1 was red and the F_2 segregated in a 3:1 ratio. In another cross in which both parents had white pericarp, the F_1 was red and the F_2 segregated in a 9 red to 7 white ratio, which indicated that complementary factors were involved. These are designated as R and O, with the latter as necessary for the expression of the former.

Blue vs. white aleurone.—Buckley (2) found the F_1 aleurone to be blue and the F_2 to segregate 3 blue to 1 white. White is here shown to be a simple recessive to blue. A cross of white with blue shows xenia in F_1 .

Hulled vs. naked.—Investigators are in accord on the mode of inheritance of the covering of the caryopsis. Biffen (1) found the hulled condition dominant in the F_1 generation; in the F_2 the plants segregated in the simple Mendelian ratio of 3 hulled to 1 hull-less. Later investigations by Hor (17), Harlan and Hayes (14), Griffee (8), Sigfusson (27), and McGregor (21) confirm these results.

Hooded vs. awned.—The investigations of Biffen (1), Kezer and Boyak (19), Hayes and Garber (14), Hor (17), Robertson (26), McGregor (21), and Buckley (2) show that there is but a single factor difference in crosses involving hoods and awns and that the hooded condition is dominant. Ubisch (30) arranges four groups in

the classification of the F_2 progeny of a cross between hooded and awned varieties. KKAA and KKaa plants are hooded; those of the constitution kkAA are long-awned and those kkaa are short-awned.

Rough vs. smooth awns.—Harlan (11) made a cross between a rough- and a smooth-awned variety. The F_1 generation was rough; in the F_2 generation the segregation obtained was 3:1 with rough dominant.

At the Minnesota station, Hayes et al. (16) report a segregation of 3:1 in the F_2 of a cross between a smooth and a rough variety, the rough-awned factor being dominant. Because of the wide variation in F_2 in the degree of roughness, an awn index was arranged, the value of which was obtained by dividing the length of the awn by the portion of the awn from the tip exhibiting large teeth at frequent intervals. In this way degrees of roughness and smoothness could be given values on which to base a classification. All plants with any degree of smoothness were placed in the smooth-awned group. Plants classed as smooth-awned in F_2 bred true for the smooth-awned condition in F_3 . There was segregation for degrees of smoothness in F_3 that was explained on a basis of minor modifying factors. Segregation for rough vs. smooth was explained on the hypothesis of a main single factor difference.

Griffie (8), employing a similar system, found that rough vs. smooth could be explained on a single factor basis. Plants with a higher index than 2 were called smooth and those between 1 and 2 were classed as intermediate smooth. As these classes appeared in approximately a 12:3:1 ratio, the results can be explained on the basis of two factors inherited independently. Factor R alone produces rough awns and is epistatic to S, which in the absence of R produces an intermediate smooth awn. The smooth-awned parent would be of the genetic constitution rrss.

Long- vs. short-haired rachilla.—Biffen (1) observed in crosses involving long- and short-haired rachillas that the F_1 generation was long haired and a segregation of 3 long to 1 short was obtained in the F_2 . This suggested a single factor difference. Similar results are reported by Hor (17), Engledow (4), Robertson (26), Sigfusson (27), Buckley (2) and McGregor (21).

Linkage Relationships

The following list of linkage relationships, reported by the investigators mentioned, gives the symbols used and the crossover percentage when this information was available.

LINKAGES

Group 1 Authority	Relations studied	Symbols used	Crossover percentage
Non-six-rowed vs. six-rowed in relation to			
Ubisch (29)	Toothed vs. untoothed lemma	Gg	16.6
Miyake and Imai (22)	Purple vs. colorless grain (1 factor)	Plpl	
	Awnless vs. awned lateral florets	Ii	
	Tall vs. short	Uu	
	Long- vs. short-awned (1 factor)	A ₂ b ₂	
Hor (17)*	Extended vs. narrow outer glume	Ee	40.5 ± 3.9
Griffee (8)	Early vs. late	Ee	42
	Resistance vs. susceptibility to <i>H. sativum</i>		Correlation
Tedin and Tedin (28)	Tall vs. short	Hh	Correlation
Neatby (24)	Tall vs. short (1 factor)		Correlation
	Dense vs. lax		Correlation
	Early vs. late (1 factor)		Correlation
	Long vs. short outer glume		Correlation
Buckley (2)	Purple vs. white-veined lemma (1 factor)	Cc	22.2
	Red vs. white pericarp (1 factor)	Rr	18.6
	Purple vs. white lemma	Pp	19.4
	Purple vs. white-veined lemma in relation to		
	Red vs. white pericarp	Rr	33.7
	Purple vs. white lemma	Pp	34.3
	Red vs. white pericarp in relation to		
	Purple vs. white lemma	Pp	0.5
	Early vs. late in relation to		
Griffee (8)	Resistance vs. susceptibility to <i>H. sativum</i>		Correlation
Group 2			
	Black vs. white lemma and pericarp in relation to		
Hor (17)	Rough vs. smooth	Rr	About 32
	Long- vs. short-haired rachilla	Ll	
Robertson (26)	Normal vs. albino seedlings	A _t a _t	22.3
Griffee (8)	Resistance vs. susceptibility to <i>H. sativum</i> (1 factor)		Correlation
Group 3			
	Hulled vs. naked in relation to		
Ubisch (30)	Hooded vs. long-awned	Aa	14.3
	Dense vs. lax (1 factor)	Ll	16.7
Miyake and Imai (22)	Dense vs. lax (one relation)	L ₁ l ₁	13.
	Dense vs. lax (a different cross)	L ₂ l ₂	23.
	Long- vs. short-awned (1 factor)	A ₁ a ₁	
	Hooded vs. awned (1 factor)	C ₁ c ₁	
Hor (17)	General vs. restricted pubescence on outer glume	Ss	23-27

* In most of Hor's crosses only small numbers were used.

Group 4 Authority	Relations studied	Symbols used	Crossover percentage
Hooded vs. awned in relation to			
Ubisch (30)	Dense vs. lax (1 factor)	L1	16-20
Robertson (26)	Normal vs. albino (Colsess)	A _{ca} c	45.1
Buckley (2)	Blue vs. white aleurone	B1b1	40.6
Normal vs. xantha seedlings in relation to			
Robertson (26)	Normal vs. albino seedlings	A _{ca} c	4-13
Group 5			
Rough vs. smooth in relation to			
Hor (17)	Long- vs. short-haired rachilla	L1	About 35
Griffee (8)	Resistance vs. susceptibility to <i>H. sativum</i>		Correlation
McGregor (21)	Long- vs. short-haired rachilla	Ss	42.7 ± 1.6
Sigfusson (27)	Long- vs. short-haired rachilla	L1	30.8
Long- vs. short-haired rachilla in relation to			
Buckley (2)	Red vs. white pericarp (1 factor)	Cc	34.7
	White vs. orange lemma	Brbr	39.1
Linkage not Placed			
Normal vs. albino seedlings (3) in relation to			
Nilsson-Ehle (25)	Normal vs. chlorina seedlings	Ff	5.
Hallqvist (11)	Normal vs. albino (4)		12.5
	Normal vs. chlorina		10.2
Normal vs. albino (4) in relation to			
	Normal vs. chlorina		3.8
Tall vs. short (1 factor) in relation to			
Neatby (24)	Early vs. late (1 factor)		Correlation
	Long vs. short outer glume (1 factor)		Correlation
	Early vs. late (1 factor) in relation to		Correlation
	Long vs. short outer glume (1 factor)		Correlation
Dense vs. lax in relation to			
	Long vs. short outer glume		Correlation

In the earlier studies of the genetics of barley some of the results reported are at variance with the findings of later investigators. Ubisch (29) reports linkage between hooded vs. long-awned and covered vs. naked. Miyake and Imai (22) find a similar linkage also. Later investigations, however, indicate quite definitely that hooded vs. awned and covered vs. naked belong to different groups. This is shown by the results obtained by Hor (17), Robertson (26), and Buckley (2).

Hor (17) places black vs. white lemma, rough vs. smooth, and long- vs. short-haired rachilla in the same group. While the latter two pairs of factors have been found linked by Sigfusson (27) and McGregor (21), also, independent inheritance of one or both of these factor pairs with black vs white is shown by Griffee (8), Robertson