Osler, Robert Donald

ABSTRACT

INHERITANCE OF RACHIS INTERNODE LENGTH IN CROSSES OF ACCORDIAN RACHIS

The need for a variety of barley that does not shatter when being combine harvested has been realized for some time. It is believed that internode length, since this factor regulates the degree of compactness or laxness in the barley head, and brittle rachis, are the two main factors controlling the degree of shattering in any one particular variety. With this knowledge, plant breeders would have a better understanding of the inheritance of factors affecting shattering which would thus enable them to more clearly plan their breeding programs.

<u>The problem</u>

What is the mode of inheritance of rachis internode length?

<u>Problem analysis</u>.--1. How many genetic factor pairs are involved?

2. On which chromosome or chromosomes are these genetic factors located?

<u>Delimitation</u>.--This investigat

data obtained from crosses of Accordian

extremely lax barley variety with five relatively compact barley varieties, namely: 1. Coast III, 2. Colsess I, 3. Colsess V, 4. Nigrinudum I, and 5. Minnesota 90-5. The data presented in the thesis was limited to that obtained in 1947 and 1948 from parental stocks, F_1 and F_2 generations.

Methods and Materials

Since seven linkage groups (chromosome pairs) have been found in cultivated barley, the barley varieties used in the crossing program were chosen with the idea of testing each linkage group. Through use of these linkage group testers it was hoped that it would be possible to locate the factors controlling the inheritance of rachis internode length within their respective linkage group.

Accordian Rachis is a two-rowed, naked, rough awned, short haired rachilla barley with a white aleurone. Accordian Rachis originated from one of twin kernels. This specific kernel produced a plant normal in size and other characteristics, with the exception of an extremely unusual rachis (Figure 1). The individual rachis segments are very long as compared to those of normal cultivated barley and are curved in such a way that the effect is a zigzag rachis which is elastic under tension. Accordian Rachis was used in all the crosses in order to determine the inheritance of the difference in length between

Fig. 1.--Accordian Rachis (long rachis internode type) and Minnesota 90-5 (short rachis internode type). Other parental types not shown have slightly longer rachis internodes than Minnesota 90-5 but were classified as short rachis internode varieties.

extremely lax types (Accordian Rachis) and short internode types. It was believed that this extreme laxity of spike exhibited by Accordian Rachis when crossed with the other five varieties as named previously, would make it possible to locate the factors controlling the inheritance of rachis internode length in their respective linkage groups.

In order to determine if there was a significant difference in rachis internode length between Accordian Rachis and the five varieties with which it was crossed, a statistical comparison of parental mean rachis internode lengths was made. The extremely high t values obtained when the statistical comparison was completed showed that the shorter mean internode length values for Coast III, Colsess I, Colsess V, Minnesota 90-5, and Nigrinudum I, when compared to Accordian Rachis were highly significant.

The barley crosses were made at the Colorado Experiment Station at Fort Collins, Colorado in 1946 and 1947. One half the seeds resulting from these crosses were planted in the field evenly spaced in four-foot rows in 1947. When these plants had matured, they were pulled individually. Measurement data was then secured in a manner described later in this abstract from each of these F_1 plants as well as for 25 plants of each parent. The procedure carried out in 1947 was repeated in 1948 with the additional planting of the seeds resulting from the F_1

plants grown in 1947. At maturity, individual plants of the parents, F_1 and F_2 generations were harvested and measured as in 1947. Wherever possible, from 4 to 6 spikes from each F_2 plant were saved to provide a population from which a random sample could be obtained to plant in 1949. This procedure was necessary in order to check in the F_3 generation the F_2 genotypes and the hypothesis made in 1948.

After discarding the bottom and top four internodes of the head being measured, at least ten internodes were measured to obtain an internode length for that particular head. Care was taken to select the head from the longest culm for measurement and only one head per plant was measured. Figure two is a photograph of the equipment used to measure any rachis which was too crooked to be measured with an ordinary millimeter rule. The rachis to be measured was first stripped of its florets and then placed inside the photographic print press which is shown at the top of the photograph. The rachis being measured was held in the press by a piece of glass frosted on one side. This rough side made it possible to measure the rachis by following the outline of the rachis with the map measureing device shown at the bottom of Figure two. Data comparisons between F_1 and F_2 generations or between any of the parental lines and the F_1 and F_2 generation was

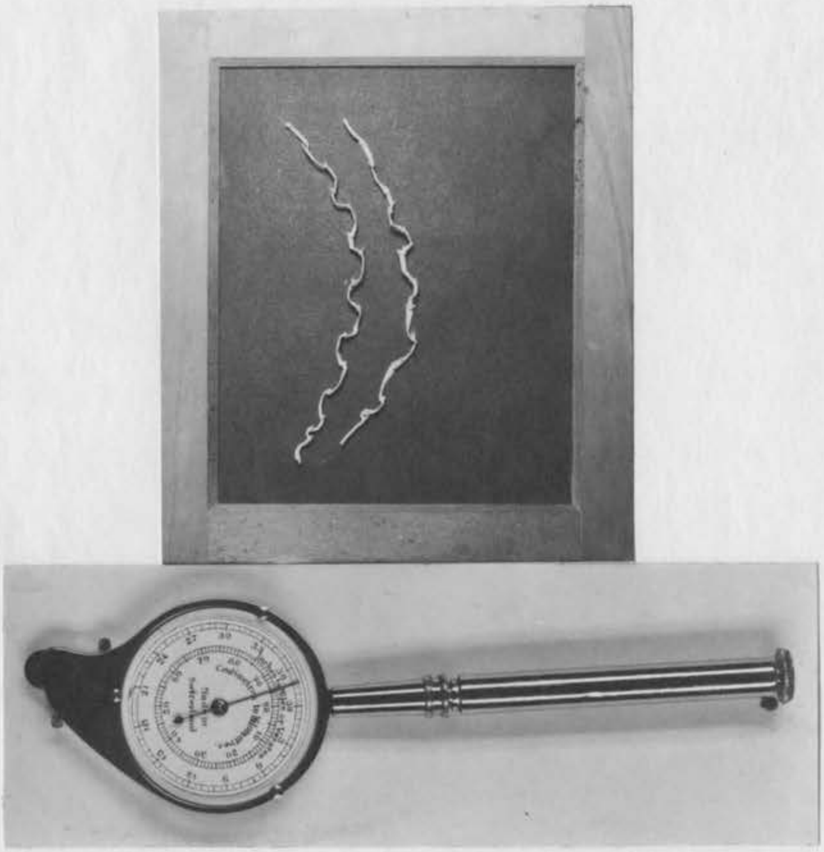

Fig. 2.--Special apparatus used to obtain measurements. Upper photograph shows a wooden frame enclosing two barley rachises as held in place by a frosted glass. Lower photograph shows a Universal Map Measurer used in tracing the curved rachis internodes.

done using parental, F_1 or F_2 measurements obtained during the same season.

The observed data on qualitative characters segregating in the F_2 was compared to calculated theoretical ratios and tested for goodness of fit by use of the X^2 (Chi square) test when two or more phenotypic classes were involved.

To check the F_2 data for possible linkage of factors controlling rachis internode length with the qualitative characters studied, mean rachis internode lengths for comparable qualitative character classes were tested for significant differences by use of the "t" test.

In order to obtain a theoretical distribution for the F_2 rachis internode measurement data, the Castle formula was used to estimate the number of factor pairs involved in the parental differences.

Discussion

Comparison of parental mean internode lengths for 1947 and 1948 supports the findings of Harlan and Wexelsen where they found that density may vary significantly in different seasons.

Data supported Neatby's and Wexelsen's findings in that one or more factors controlling inheritance of rachis internode length is located in linkage group I. Data also supported Wexelsen where he found indications that another factor controlling inheritance of rachis internode length was located in linkage group V.

The data did not completely support any one of the three types of F_1 behavior reported by earlier workers. Crosses of Colsess I, Colsess V and Minnesota 90-5 X Accordian Rachis in both 1947 and 1948 plus crosses of Coast III X Accordian Rachis in 1948 show partial dominance for short rachis internode over long rachis internode. Results from crosses of Nigrinudum I and Coast III X Accordian Rachis in 1947 agree with results reported by Hayes and Harlan where they found a case of almost complete dominance of short rachis internode over long rachis internode. The other four crosses gave mean rachis internode lengths in the F_1 generation which show partial dominance for short rachis internode over long rachis internode.

Statistical analysis of F_2 data from all five F_2 segregations support the findings of Wexelsen and Neatby who found evidence of the occurrence of transgressive segregation.

Linkage investigations.--Indications of linkage in Coast III, Colsess I, and Colsess V X Accordian Rachis crosses was found in linkage group I between the factors controlling number of rows and factors controlling rachis internode length. Data for Nigrinudum I X Accordian Rachis crosses indicated linkage was occurring between factors controlling intermedium versus non-intermedium located in linkage group IV and factors controlling rachis internode length. Indications of linkage were found in crosses of Minnesota 90-5 X Accordian Rachis between factors controlling intermedium versus non-intermedium located in linkage group IV, and factors controlling long versus short-haired rachilla located in linkage group V in respect to factors controlling rachis internode length in these crosses. Independent inheritance was found between the factor pairs for short versus long internode and black versus white floral bracts (group II), covered versus naked caryopsis (group III), hooded versus awned lemma (group IV), rough versus smooth awns (group V), and green versus chlorina plants (group VII).

Number of factor pairs differentiating the short and long rachis internode parents.--Measurement class totals for the Nigrinudum I and Minnesota 90-5 X Accordian Rachis crosses indicated a difference of six pairs of factors while the Colsess I and Colsess V X Accordian Rachis crosses indicated a difference of three pairs of factors and the Coast III X Accordian Rachis crosses indicated a difference of five pairs of factors as the best assumption upon which to base further study in respect to rachis internode length. At least three of these factor pairs are located in different linkage groups.

Suggestions for further study

Theoretically, the best method would be to select random samples of each F_2 measurement class as given in Tables 7, 10, 12, 14, 16 and plant them in the field in the spring of 1949 in conjunction with all six parents. Measurements of individual F_3 plants would be made as in previous years and the data would be analyzed to ascertain the breeding behavior of each F_2 measurement class. Knowledge of F_3 breeding behavior should make possible the formulation of conclusions concerning linkage of factors controlling the qualitative characters with factors controlling rachis internode length as well as the number of factors by which Accordian Rachis differs from the other parental varieties in respect to rachis internode length.

Such a procedure as outlined above would, however, be impossible to carry out due to lack of time and money. Therefore, in order to use the above method the field planting would probably be limited to one entire family--the choice as to which family to plant being dependent upon which would give the most information as determined by thorough study of F_2 data from all five of the crosses.

THESIS

INHERITANCE OF RACHIS INTERNODE LENGTH IN CROSSES OF ACCORDIAN RACHIS

Submitted by

Robert Donald Osler

In partial fulfillment of the requirements for the Degree of Master of Science in Agronomy

Colorado A & M College

Fort Collins, Colorado

COLORADO AGRICULTURAL AND MECHANICAL COLLEGE

April 5, 1949

WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR

SUPERVISION BY ROBERT DONALD OSLER

ENTITLED INHERITANCE OF RACHIS INTERNODE LENGTH IN CROSSES OF ACCORDIAN RACHIS

BE ACCEPTED AS FULFILLING THIS PART OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

CREDITS 12

Committee on Graduate Work

David W Robertson H. H. Stonaker Jas L. Fults
Major Professor Minor Professor

David W Robertson
Head of Department

W. R. Horlacher
Dean of Division

Committee on Final Examination

Examination Satisfactory

L W Durrell — H H Stonaker
Jas L. Fults — David W Robertson
Bruford Olsen — Robert O. Bock

David H Morgan
Dean of the Graduate School

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Chapter I

INTRODUCTION

The need for a variety of barley that does not shatter when being combine-harvested has been realized for sometime. It is believed that internode length, since this factor regulates the degree of compactness or laxness in the barley head, and brittle rachis are the two main factors controlling the degree of shattering in any one particular variety. With this knowledge plant breeders would have a better understanding of the inheritance of factors affecting shattering which would thus enable them to more clearly plan their breeding programs.

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What is the mode of inheritance of rachis internode length?

Problem analysis.--1. How many genetic factor pairs are involved?

2. On which chromosome or chromosomes are these genetic factors located?

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Chapter II

REVIEW OF LITERATURE

Seven linkage groups have been established in cultivated barley, the literature for which has been reviewed by Robertson, Wiebe, and Immer (11), 1941, and Robertson, Wiebe, and Shands (12), 1947. Since a complete review of literature is beyond the scope of this thesis, the reader is referred to the above two references for any information regarding qualitative characters studied in this research problem. The literature review presented in this thesis is limited to those studies which have previously investigated the mode of inheritance of rachis internode length in barley and will be discussed under appropriate headings.

Environmental effects

Harlan (4), 1914, after comparing rachis internode data for one given variety from one season or location as against the same variety grown in a different season or location concluded that spike density varies markedly with season and location. Wexelsen (16, 17), 1933, and 1934, found evidence supporting Harlan's conclusions and also found that border and spacing effects were very important factors controlling rachis internode length in any one given variety.

Linkage of rachis internode length with other plant characters

Although quite a lot of work has been done in inheritance of rachis internode length in barley, only Neatby (10), 1929, and Wexelsen (16), 1933, presented any actual data showing any indications of linkage. Neatby (10), 1929, crossed Guy Mayle X Canadian Thorpe and found linkage between number of rows and rachis internode length. The same cross gave no indication of linkage between the factors controlling adherence of glumes and the factors controlling rachis internode length.

Wexelsen (16), 1933, found an indication of linkage between rachis internode length and rough versus smooth awns in a cross of Machine X C.I. 4252. In another cross (Asplund X Abed Binder) Wexelsen found indications of linkage of rachis internode length with number of rows.

The possibility of linkage of rachis internode length and other quantitative characters has been reported in but two papers. Harlan (4), 1914, in a study of twenty varieties of barley, found a direct correlation between density and earliness while Hayes and Harlan (5), 1920, reported no correlation between rachis internode length and plant vigor in crosses among Jet, Zeocriton, Pyramidatum, Manchuria, Hanna, Steigum, and Reid Triumph barleys.

F_1 behavior

Each of the papers mentioning the behavior of F_1 plants in regard to rachis internode length may be placed in one of three groups as follows: 1. lax dominant over dense; 2. dense dominant over lax; and 3. intermediate between the two parents. Spillman cited by Biffen (1), 1907, Hayes and Harlan (5), 1920, and Wexelsen (17), 1934, reported crosses where the F_1 progeny was intermediate between the parents in respect to rachis internode length. Hayes and Harlan (5), 1920, reported a case of almost complete dominance of dense over lax in a cross of Manchuria X Svanhals. Biffen (1), 1907, reported a case of almost complete dominance of lax over dense in a cross of Zeocriton X Nutans barleys.

Number of factors involved in inheritance of rachis internode length

One, two or as many as six main factors plus several minor factors have been proposed by various investigators to explain segregations. Hayes and Harlan (5), 1920, found that in respect to rachis internode length the crosses Manchuria X Svanhals and Pyramidatum X Jet differed by one main factor; the cross Hanna X Reid Triumph differed by two main factors; the cross Hanna X Zeocriton differed by three main factors. Hayes and Harlan also concluded that in addition to the main factors found to be present, modifying factors were also evident, as did Neatby (10), 1929, and von Ubisch (13), 1919, as cited by Wexelsen (17), 1934.

In a cross of Guy Mayle X Canadian Thorpe in addition to the modifying factors mentioned previously, Neatby (9), 1929, obtained a segregation indicating the inheritance of density of spike was governed by one main factor.

Wexelsen (16, 17), 1933 and 1934, has made one of the most extensive studies of the inheritance of rachis internode length and found differences of one main factor in a cross of Machine X Abed Binder; two main factors in crosses of Asplund X Abed Binder, Asplund X Machine, and Machine X C.I. 4252 in respect to rachis internode length. Wexelsen stated that probably as many as five factors were concerned with inheritance of rachis internode length.

Vik and Lunden (14), 1928, cited by Wexelsen (17), 1934, crossed Asplund X Machine and obtained a two factor segregation for short versus long rachis internode.

Lunden (8), 1931, cited by Wexelsen (17), 1934, crossed Asplund X DS 295 and obtained a two factor segregation.

von Ubisch (13), 1919, cited by Wexelsen (17), 1934, found that as the range between lax and dense parent increased, so did the number of factors. Note the following:

H.34 (2.57 mm.) X H.37 (3.43 mm.) gave a one factor segregation.

H.37 (3.15 mm) X H. Spont (5.75 mm.) gave a two factor segregation.

H.34 (2.57 mm.) X H.40 (5.75 mm.) gave a three factor segregation.

Huber (6), 1929, cited by Wexelsen (17), 1934 crossed *H. distichum* var. *nigricans* X *H. distichum* var. *erectum* and obtained a two factor segregation with one factor being stronger than the other.

Transgressive segregation

In the cross Asplund X Sacramento, Wexelsen (17), 1934, obtained homozygous lines in the F_2 and F_3 generations which were significantly longer and shorter than the parents, thus indicating that transgressive segregation was occurring. Neatby (10), 1929, in the cross Canadian Thorpe X Guy Mayle and Huber (6), 1929, cited by Wexelsen (17), 1934, in the cross *H. distichum* var. *nigricans* X *H. distichum* var. *erectum* also obtained types which were indicative of the occurrence of transgressive segregation. Biffen (1), 1907, found that planting of a long or short extreme measurement class usually demonstrated homozygosity.

Chapter III

METHODS AND MATERIALS

Since seven linkage groups (chromosome pairs) have been found in cultivated barley, the barley varieties used in the crossing program were chosen with the idea of testing each linkage group. Note Table 1.

Table 1.--BARLEY LINKAGE GROUPS LISTING BARLEY VARIETIES USED AS TESTERS.

Linkage group number	Barley variety testers
I	Coast III, Colsess I, Colsess V
II	Minnesota 90-5, Nigrinudum I
III	Coast III, Colsess I, Colsess V, Minnesota 90-5
IV	Colsess I, Colsess V, Minnesota 90-5, Nigrinudum I
V	Minnesota 90-5
VI	Colsess I, Nigrinudum I
VII	Coast III, Colsess V

Through use of these linkage group testers it is hoped that it will be possible to locate the factors controlling the inheritance of rachis internode length within their respective linkage group.

Symbols for genetic characters

The factor pairs listed in Table 2 were involved in one or more of the five varietal crosses and the nomenclature as suggested by Robertson, Wiebe, and Shands (12), 1947, has been followed.

Table 2.--GENETIC SYMBOLS AND NOMENCLATURE.

Linkage group number	Symbols	Character pairs
I	Vv	Non-6-row vs. 6-row
II	Bb	Black vs. white floral bracts
III	Nn	Covered vs. naked caryopsis
IV	Kk	Hoods vs. awns
	Ii	Intermedium vs. non-intermedium
V	Rr	Rough vs. smooth awns
	Ss	Long vs. short-haired rachillas
VI	$A_c a_c$	Green vs. albino seedling color
	$A_n a_n$	Green vs. albino seedling color
VII	$F_c f_c$	Green vs. chlorina seedling color
	$Y_c y_c$	Green vs. virescent seedling color

Genetic description of Varieties

Accordian Rachis is a two-rowed, naked, rough awned, short haired rachilla barley with a white aleurone. According to Martini and Harlan (9), 1942, Accordian Rachis originated from one of twin kernels. This specific kernel produced a plant normal in size and other characteristics, with the exception of an extremely unusual rachis (Figure 1). The individual rachis segments are very long as compared to those of normal cultivated barley and are curved in such a way that the effect is a zigzag rachis which is elastic under tension. Accordian Rachis was used in all the crosses because while the other barley varieties used show compactness of spike (a function of internode length) in varying degrees, Accordian Rachis is an extreme type, i.e., the extremely long internodes as shown in Figure I give Accordian Rachis a very lax spike. It was believed that this extreme laxity of spike exhibited by Accordian Rachis when crossed with the other varieties as named previously will make it possible to locate the factors controlling the inheritance of rachis internode length in their respective linkage groups.

A factorial description of Accordian Rachis, together with the lines crossed with it, is given in Table 3.

Fig. 1.--Accordian Rachis (long rachis internode type) and Minnesota 90-5 (short rachis internode type). Other parental types not shown have slightly longer rachis internodes than Minnesota 90-5 but were classified as short rachis internode varieties.

Table 3.--FACTOR PAIRS FOUND IN THE DIFFERENT BARLEY VARIETIES

Variety	Symbols for characters											
	Vv	Bb	Nn	Kk	Ii	Blbl	Rr	Ss	$A_c a_c$	$A_n a_n$	$Y_c y_c$	$F_c f_c$
Accordian Rachis	VV	bb	nn	kk	ii	blbl	RR	ss	$A_c A_c$	$A_n A_n$	$Y_c Y_c$	$F_c F_c$
Coast III	vv	bb	NN	kk	II	BlBl	RR	ss	$A_c A_c$	$A_n A_n$	$Y_c y_c$	$F_c F_c$
Colsess I	vv	bb	NN	KK	II	BlBl	RR	ss	$A_c a_c$	$A_n A_n$	$Y_c Y_c$	$F_c F_c$
Colsess V	vv	bb	NN	KK	II	BlBl	RR	ss	$A_c A_c$	$A_n A_n$	$Y_c Y_c$	$f_c f_c$
Minnesota 90-5	VV	BB	NN	kk	ii	----	rr	SS	$A_c A_c$	$A_n A_n$	$Y_c Y_c$	$F_c F_c$
Nigrinudum I	VV	BB	nn	kk	II	----	RR	ss	$A_c A_c$	$A_n a_n$	$Y_c Y_c$	$F_c F_c$

In order to show the difference in rachis internode length between Accordian Rachis and the five varieties with which it was crossed, a statistical comparison was made by the method described by Leonard and Clark (7:60-1), 1939. Since a "t" value of two or more is interpreted as showing there is a significant difference in the two values being compared, the extremely high "t" values given in Table 4 show that shorter mean internode length values for Coast III, Colsess I, Colsess V, Minnesota 90-5, and Nigrinudum I when compared to Accordian Rachis are highly significant.

Table 4.—COMPARISON OF RACHIS INTERNODE LENGTHS BETWEEN ACCORDIAN RACHIS AND EACH OF THE OTHER FIVE PARENTS

Variety or strain	Mean rachis internode lengths in mm. 1947	1948	t values 1947	1948
Accordian Rachis	9.61 ± 0.1298	9.43 ± 0.1179	42.18	45.28
Coast III	3.95 ± 0.0336	3.96 ± 0.0266		
Accordian Rachis	9.61 ± 0.1298	9.43 ± 0.1179	44.88	45.73
Colsess I	3.69 ± 0.0225	3.81 ± 0.0344		
Accordian Rachis	9.61 ± 0.1298	9.43 ± 0.1179	43.14	46.82
Colsess V	3.76 ± 0.0396	3.83 ± 0.0204		
Accordian Rachis	9.61 ± 0.1298	9.43 ± 0.1179	55.77	58.05
Minnesota 90-5	2.47 ± 0.0383	2.54 ± 0.0124		
Accordian Rachis	9.61 ± 0.1298	9.43 ± 0.1179	33.35	42.30
Nigrinudum I	4.04 ± 0.1050	3.77 ± 0.0630		

Methods used in making and handling crosses

The barley crosses in this research problem were made at the Colorado Experiment Station at Fort Collins, Colorado in 1946 and 1947. One half the seeds resulting from these crosses were planted in the field evenly spaced in four-foot rows in 1947. When these plants had matured, they were pulled individually. Measurement data were then secured in a manner described later in this thesis from each of these plants as well as at least 25 plants of each parent. The procedure carried out in 1947 was repeated in 1948 with the additional planting of the seeds resulting from the F_1 plants grown in 1947. At maturity, individual plants of parents, F_1 and F_2 generations were harvested and measured as in 1947. Wherever possible, from 4 to 6 spikes from each F_2 plant were saved to provide a population from which a random sample could be obtained to plant in 1949. This procedure was necessary in order to check in the F_3 generation phenotypic classifications and hypothesis made in 1948 from the F_2 segregation.

Experimental methods

Measuring techniques.--Measurement data were obtained by the same general methods used by Hayes and Harlan (5), 1920, Wexelsen (16, 17), 1934, and Webster (15), 1947. After discarding the bottom and top four internodes of the head being measured, at least ten internodes were measured to obtain an internode length for that particular head. Care was taken to select the head from the longest culm for measurement and only one head per plant was measured. Extreme variability of the bottom and top four internodes makes their use prohibitive in rachis internode studies according to Hayes and Harlan (5), 1920, and Webster (15), 1947. Figure 2 is a

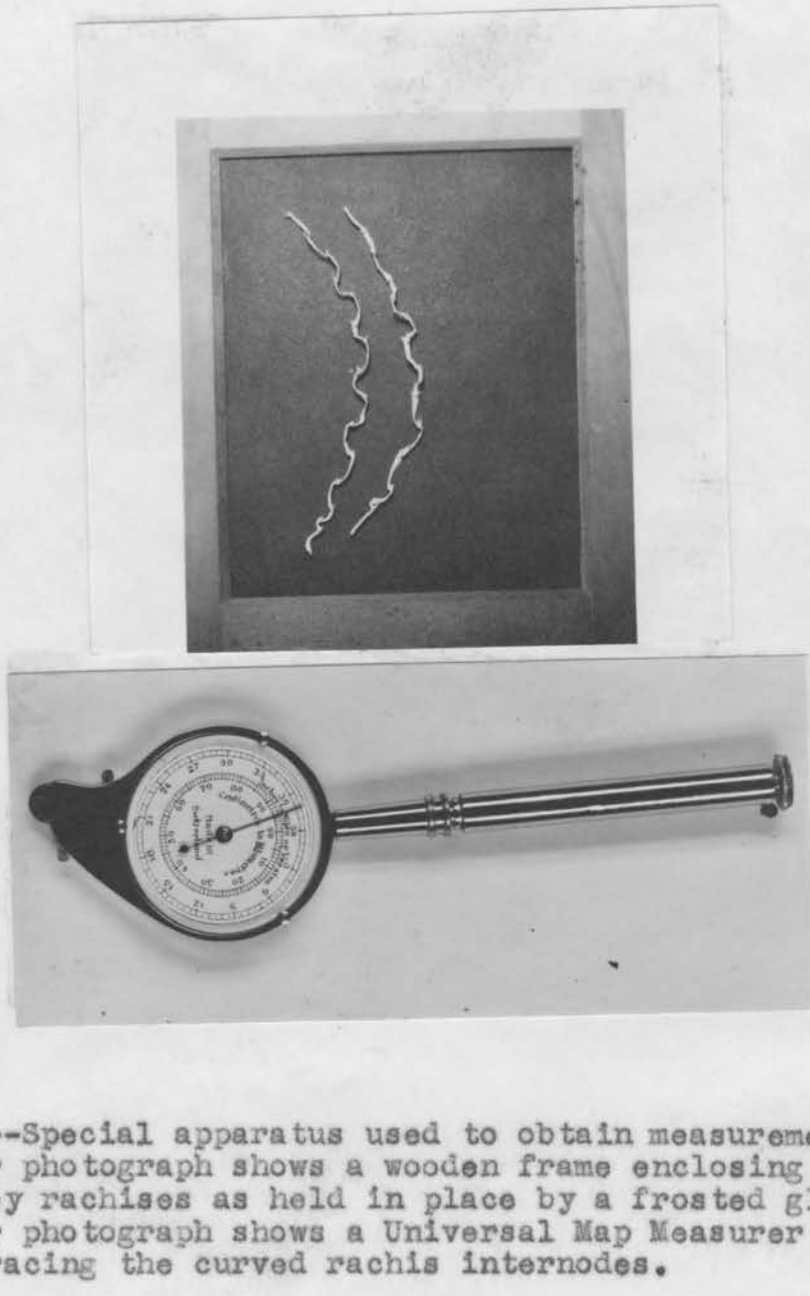

Fig. 2.--Special apparatus used to obtain measurements. Upper photograph shows a wooden frame enclosing two barley rachises as held in place by a frosted glass. Lower photograph shows a Universal Map Measurer used in tracing the curved rachis internodes.

SAMPLE DATA SHEET*

Varities in cross: Minnesota 90-5 and Accordian Rachis

Cross number: II-46-175-8

No. of plant	Length[1/] in cm.	No. of[2/] internodes	Internode[3/] length
2998	3.8	14	2.71
2999	4.0	12	3.33
3000	4.2	10	4.2
3001	3.8	12	3.17
3002	6.4	12	5.33
3003	4.6	16	2.88
3004	3.9	12	3.25

* Reproduced from actual F_2 data obtained September 1948.

1/ Measurements of entire rachis excluding bottom and top four internodes.

2/ Number of internodes actually measured per head.

3/ Expressed in millimeters.

Fig. 3.--Sample of original data sheet

photograph of the equipment used to measure any rachis which was too crooked to be measured with an ordinary millimeter rule. The rachis to be measured was first stripped of its florets and then placed inside the photographic print press which is shown at the top of the photograph. The rachis to be measured was held in the press by a piece of frosted glass. This rough side made it possible to measure the rachis by following the outline of the rachis with the map measuring device shown at the bottom of Figure 2. The length of rachis measured and the actual number of internodes measured was recorded in a data sheet as shown in Figure 3.

Data comparisons between F_1 and F_2 generations or between any of the parental lines and the F_1 or F_2 generation were made using parental, F_1, or F_2 measurements obtained during the same season. This procedure was necessary since, according to several investigators, differences in environment from one year to the next may bring about considerable variation in internode length within one variety when data obtained in one year is compared with that of another year.

Statistical Analysis

The observed data on qualitative characters segregating in the F_2 were compared to calculated theoretical ratios and tested for goodness of fit by use of the

X^2 (Chi-square) test when two or more phenotypic classes were involved. The general formula for X^2 is as follows:

$$X^2 = S\left[\frac{(O-C)^2}{C}\right]$$

where O equals the observed frequency for a particular phenotypic class and C the calculated theoretical number for the same class based on the hypothesis that the data follow some certain distribution. It is obvious that the more closely the observed number agrees with the calculated, the smaller will be the X^2 value. The method of interpretation of X^2 values as to their significance was the same as that used by Fisher (3), 1934.

For the purpose of illustration, Table 7 under experimental results, will be used. The X^2 values in the next to last column of the table were obtained for each phenotypic classification by applying the formula for X^2 as previously given. Thus, for the black class, X^2 equals $\frac{(390-399.75)^2}{399.75}$. The theoretical value 399.75 is obtained by adding the observed frequency for black and white and multiplying by three-fourths. Similarly, one-fourth equals 133.25. The X^2 value .951 for black and white segregation was obtained by the summation of the X^2 values for both black and white. The last column at the right hand margin of Table 7 was obtained from Fisher's (3), 1934, tables of X^2 where P is a number showing the

probability due to chance alone of obtaining a X^2 value as great or greater than was actually obtained. For example, the P value for the black and white classes 0.340 means that a poorer fit (larger X^2 value) could be expected 34 out of every 100 trials.

The observed data on rachis internode length was treated by the statistical methods described by Leonard and Clark (7), 1939, and as used by Wexelsen (16, 17), 1933 and 1934. To check the F_2 data for possible linkage of factors controlling rachis internode length with the qualitative characters studied, the data were treated statistically and summarized in Table 9 under experimental results. For purposes of illustration, note the statistical constants given for the two phenotypic classes, black and white, in Table 9. In order to check whether the mean rachis internode length for the black class (4.436 mm.) was significantly longer than the mean rachis internode length for the white class (4.429 mm.) a value for t was computed by the following formula:

$$t = \frac{X_1 - X_2}{\sqrt{(\sigma_{\bar{x}_1})^2 + (\sigma_{\bar{x}_2})^2}} = \frac{4.436 - 4.429}{\sqrt{.48^2 + .093^2}} = 0.007$$

Since 0.007 is less than 1.96 (the .05 level of significance), the mean rachis internode lengths can not be said to differ significantly.

In order to obtain a theoretical distribution for the F_2 rachis internode measurement data, the Castle formula (2), 1921, was used to estimate the number of factor pairs involved in the parental differences. This formula assumes additive gene action, genes of equal effects, the absence of dominance, and that the parents represent the genetic extremes. The formula used is as follows:

$$\% = 100 \frac{S'F_2 - S'F_1}{\bar{x}_1 - \bar{x}_2}$$

Where: $S'F_2$ = standard deviation of the F_2

$S'F_1$ = standard deviation of the F_1

$\bar{x}_1$ = Mean rachis internode length of long rachis internode parent

$\bar{x}_2$ = Mean rachis internode length of short rachis internode parent

The percentage value thus obtained, according to Castle (2), 1921, then represents the percent the F_2 genetic variability is of the range between the long and short rachis internode parent. This percentage value, when compared with a table prepared by Castle, tells the number of factor pairs differentiating the two parents in respect to rachis internode length. In using this method of determination of number of factor pairs it was realized that the basic assumptions upon which the formula is based are not completely fulfilled in these data. In regard to additive gene action and genes having equal effects, the available data was not discriminatory.

However, in respect to the other two assumptions, the data show that dominance is present and indicates that the parents do not represent the genetic extremes.

Chapter IV

EXPERIMENTAL RESULTS

This chapter of the thesis has been divided into five separate sections. Each section presents data obtained from one of the five different varietal crosses along with a discussion of the findings. For the sake of clarity Tables 5 and 6 have been prepared to present a summary of data comparing all F_1 generations with both the short and long rachis internode parents.

Nigrinudum I X Accordian Rachis

Examination of the t values given in Table 6 for these crosses shows that the genes controlling inheritance of rachis internode length which are contributed to the F_1 by the short rachis internode parent are dominant over the genes contributed by the long rachis internode parent. Data for mean internode lengths as given in Table 5 also illustrate the almost complete dominance of the genes for short rachis internode as stated in the discussion of Table 6.

The F_2 plants from the crosses of Nigrinudum I X Accordian Rachis were classified into four phenotypic groups and a rachis internode length was then obtained for

Table 5.--MEAN RACHIS INTERNODE LENGTHS OF PARENTS AND F_1 PLANTS

Variety or cross	Mean rachis internode length in millimeters	
	1947	1948
Nigrinudum I	4.04 ± 0.1050	3.77 ± 0.0315
Accordian Rachis	9.61 ± 0.1298	9.43 ± 0.1179
F_1	4.06 ± 0.0422	------------
Coast III	3.95 ± 0.0336	3.96 ± 0.0266
Accordian Rachis	9.61 ± 0.1298	9.43 ± 0.1179
F_1	3.95 ± 0.0235	4.12 ± 0.0356
Colsess I	3.69 ± 0.0225	3.81 ± 0.0345
Accordian Rachis	9.61 ± 0.1298	9.43 ± 0.1179
F_1	4.37 ± 0.0266	4.60 ± 0.0592
Colsess V	3.76 ± 0.0396	3.83 ± 0.0204
Accordian Rachis	9.61 ± 0.1298	9.43 ± 0.1179
F_1	4.45 ± 0.0362	4.44 ± 0.0475
Minnesota 90-5	2.47 ± 0.0383	2.54 ± 0.0124
Accordian Rachis	9.61 ± 0.1298	9.43 ± 0.1179
F_1	3.42 ± 0.0310	3.26 ± 0.0407

each plant as described under materials and methods. The observed data were then organized into a frequency distribution according to phenotypic class as well as rachis internode length class.

Table 6.--COMPARISON OF F_1 PROGENY WITH PARENTS

Cross	t values: Between short rachis internode parent and F_1		Between long rachis internode parent* and F_1	
	1947	1948	1947	1948
Nigrinudum I X Accordian Rachis	0.18	----	40.72**	----
Coast III X Accordian Rachis	0.00	3.60**	42.91**	43.07**
Colsess I X Accordian Rachis	18.99**	11.53**	39.49**	36.62**
Colsess V X Accordian Rachis	12.85**	11.80**	38.25**	39.20**
Minnesota 90-5 X Accordian Rachis	19.67**	16.94**	46.40**	49.44**

*Accordian Rachis
**Less than .01

Table 7 gives the observed frequencies for all qualitative characters studied in this cross plus theoretical frequencies as follows: theoretical values for a 3:1 ratio of black versus white glumes and caryopsis; theoretical values for a 3:1 ratio of intermedium versus non-intermedium; X^2 and P values for the qualitative characters. Table 8 presents the observed and calculated ratios in

Table 7.—OBSERVED AND CALCULATED DATA OF F_2 SEGREGATION OF QUALITATIVE CHARACTERS IN NIGRINUDUM I X ACCORDIAN RACHIS CROSSES.

Phenotypic class	Measurement class limits in mm.													
	3.707 or less	3.707 to 3.833[1]	3.833 to 4.735	4.735 to 5.625	5.625 to 6.515	6.515 to 7.415	7.415 to 8.305	8.305 to 9.198	9.198 to 9.670[2]	9.670 or more	Phenotypic class totals	Theoretical totals[3]	X^2	P
	1	2	3	4	5	6	7	8	9	10				
Black	63	50	191	47	27	5	3	3	0	1	390	399.75	0.951	0.34
White	26	15	77	12	8	1	1	1	0	2	143	133.25		
Intermedium	64	53	203	40	19	1	0	3	0	0	383	399.75	2.807	0.096
Non-intermedium	25	12	65	19	16	5	4	1	0	3	150	133.25		

1/ Class limits set by establishing limits twice the standard error on both sides of mean rachis internode length of Nigrinudum I

2/ Parental class corresponding to long rachis internode parent with limits determined by methods discussed in footnote #1

3/ Based on expected 3:1 ratio

regard to rachis internode length where the ratios are based on the assumption that the two parents differed by six factor pairs in respect to the inheritance of rachis internode length.

The P values for the four qualitative characters show that the parents do differ by one factor pair in respect to inheritance of black and white glume color and in respect to intermedium versus non-intermedium. The low value of P in regard to intermedium versus non-intermedium is undoubtedly attributable to the difficulty encountered in classification. Data in Table 8 for the Nigrinudum I X Accordian Rachis crosses show a definite piling up of measurements around the short rachis internode parental class. By use of Castle's formula (2), 1921, it was determined that the parents differed by six pairs of factors in respect to rachis internode length. X^2 and P values show a good fit between the observed distribution and a theoretical frequency distribution based on an assumption of a six factor pair difference. Since the observed class limits were arbitrary and the basic data does not completely fit the original assumptions made by Castle (2), 1921, in deriving his formula, the good fit obtained between observed and theoretical must only be considered an indication of the number of factors involved. However, the good fit obtained led to the belief that the six factor hypothesis was the best assumption upon which to base

Table 8.—OBSERVED AND CALCULATED DATA OF F_2 SEGREGATION OF RACHIS INTERNODE MEASUREMENTS FOR ALL FIVE CROSSES.

Distribution	Measurement class 1/											
	1	2	3	4	5	6	7	8	9	10	X^2	P
Accordian Rachis							3	12	11	14		
Nigrinudum I	12	13	15									
F_2 Obs.	89	65	268	59	35	6	4	4	0	3	2.015	0.733
F_2 Calc. 2/	94.86	347.83		70.27		17.57			3.47			
Coast III	16	12	10									
F_2 Obs.	221	141	359	88	44	20	13	9	3	4	0.898	0.826
F_2 Calc. 3/	214.04	594.58			79.28			14.10				
Colsess I	15	8	19									
F_2 Obs.	38	17	160	57	25	18	5	2	1	18	--	<.001
F_2 Calc. 4/	143.86		143.86		47.95					5.33		
Colsess V	15	13	13									
F_2 Obs.	115	56	332	84	45	27	13	14	7	14	--	<.001
F_2 Calc. 4/	298.27		298.27		99.42					11.04		
Minnesota 90-5	15	13	17									
F_2 Obs.	11	10	401	139	40	27	5	8	0	1	--	<.001
F_2 Calc. 2/	342.79			190.44	84.64		21.16		2.98			

1/ Refer to table of F_2 for particular measurement class limits of each particular cross.
2/ Calculated on assumption of six factor pair difference between parents.
3/ Calculated on assumption of five factor pair difference between parents.
4/ Calculated on assumption of three factor pair difference between parents.

further study.

Statistical analysis of data for the crosses of Nigrinudum I X Accordian Rachis to check for possible linkage of factors controlling inheritance of rachis internode length with any of the qualitative characters studied in these particular crosses is presented in Table 9.

Table 9.--LINKAGE DATA FOR PROGENY OF NIGRINUDUM I X ACCORDIAN RACHIS CROSSES.

Phenotypic Class	Mean rachis internode length in mm.	t value
Black	4.436 ± 0.048	0.007
White	4.429 ± 0.093	
Intermedium	4.306 ± 0.038	3.01
Non-intermedium	4.761 ± 0.113	

Since the long rachis internode parent (Accordian Rachis) is genetically white and non-intermedium, a linkage of any of the factors controlling length of rachis internode with either of these two characters should result in that particular phenotypic class having a longer mean rachis internode length than does its alternate class (plants having black glumes as compared to plants having white glumes). Study of the t values given in Table 8 shows no indication of linkage between factors controlling length of rachis internode with factors controlling black versus white glumes. If there is a linkage between the factors controlling intermedium versus non-intermedium and factors controlling internode length, the phenotypic class non-intermedium in the F_2 generation would be expected to have a longer mean rachis internode value than the intermedium class. The t value 3.01 shows that the mean internode length of the non-intermedium class is significantly longer than for the intermedium class indicating linkage.

Coast III X Accordian Rachis

Examination of 1947 F_1 progeny and parental data for these crosses as presented in Tables 5 and 6 shows very nearly the same relationships as discussed for the Nigrinudum I X Accordian Rachis crosses in that the factors for short rachis internode length were dominant over the factors for long rachis internode length. The 1948 data for this cross were different from the 1947 data in that the genes for short rachis internode were not completely dominant over the factors for long rachis internode. However, the data show that the factors for short rachis internode have more effect than the factors for long rachis internode.

The F_2 plants from the crosses of Coast III X Accordian Rachis were classified into five phenotypic groups before proceeding to obtain and analyze the data or to form a frequency distribution as described in the discussion of the Nigrinudum I X Accordian Rachis crosses. Table 10 gives the observed frequencies for all qualitative characters studied in this cross plus theoretical frequencies as follows: theoretical values for a 1:2:1 ratio of 2-row, intermediate, and 6-row; theoretical values for a 3:1 ratio of naked versus covered caryopsis; X^2 and P values for the qualitative characters. Table 8 presents the observed and calculated ratios on rachis internode lengths where the ratios are based on the assumption that the two parents differed by five pairs of factors in respect to the inheritance of rachis internode length.

The P value for the segregation of 2-row, intermediate, and 6-row ($<$.001) indicates a poor fit to the expected 1:2:1 ratio. However, since all the literature as reviewed by Robertson, Wiebe, and Shands (12), 1947, indicates such a 1:2:1 ratio in the F_2 for this character, the poor fit must be accounted for by the difficulty in classification. The P value for the segregation of covered versus naked caryopsis indicates that the two parents differ by one factor pair in this respect. Data in Table 8 for the Coast III X Accordian Rachis crosses again show a definite piling up of measurements around the short rachis internode parental class. Study of the measurement class frequencies through application of Castle's formula (2), 1921, led to the belief that the data would best fit a five factor difference hypothesis. While this assumption

Table 10.—OBSERVED AND CALCULATED DATA OF F_2 SEGREGATION OF QUALITATIVE CHARACTERS IN COAST III X ACCORDIAN RACHIS CROSSES.

Phenotypic class	Measurement class limits in mm.										Pheno-typic class totals	Theoretical totals 3/	X^2	P
	3.906 or less	3.906 to 4.014 1/	4.014 to 4.876	4.876 to 5.740	5.740 to 6.601	6.601 to 7.467	7.467 to 8.330	8.330 to 9.198	9.198 to 9.670 2/	9.670 or more				
	1	2	3	4	5	6	7	8	9	10				
2-row	44	20	44	13	7	12	9	4	0	3	156	225.5		
Intermediate	128	86	181	52	27	5	2	3	3	1	488	451.0	29.139	<.001
6-row	49	35	134	23	10	3	2	2	0	0	258	225.5		
Covered	138	96	275	70	33	17	11	8	1	4	653	676.50	3.265	0.075
Naked	83	45	84	18	11	3	2	1	2	0	249	225.50		

1/ Short rachis internode parental class with class limits set by establishing limits twice the standard error on both sides of mean rachis internode length of Coast III.

2/ Long rachis internode parental class with class limits set as described in footnote #1 but using the standard error and mean of Accordian Rachis.

3/ Based on expected 1:2:1 and 3:1 ratios respectively.

may prove to be wrong, it seems to be the best assumption upon which to base further study. However, as stated previously during the discussion of Nigrinudum I X Accordian Rachis crosses, the good fit obtained between the observed and calculated frequency distributions for rachis internode length in Coast III X Accordian Rachis crosses must only be considered an indication of and not a proof for the number of factors involved.

Table 11 presents a summary of statistical analysis of data for the Coast III X Accordian Rachis crosses to check for possible linkage of factors controlling inheritance of rachis internode length with any of the qualitative characters studied in these particular crosses.

Table 11.--LINKAGE DATA FOR F_2 PROGENY OF COAST III X ACCORDIAN RACHIS CROSSES

Phenotypic class	Mean rachis internode length in mm.	t value
2-row	4.950 ± 0.126	
Intermediate	4.457 ± 0.043	3.514
6-row	4.475 ± 0.049	
Covered	4.622 ± 0.043	3.490
Naked	4.370 ± 0.058	

The t value for significance between mean rachis internode lengths for the 2-row class as compared to the 6-row class (3.514) indicates linkage between some of the factors controlling inheritance of rachis internode length and the factors controlling inheritance of number of rows. The P value (3.49) shows that the phenotypic class, covered caryopsis, has a longer mean rachis internode than does the naked caryopsis class. This fact cannot be assumed to be an indication of linkage but must be attributed to chance since, if linkage were occurring between the factors controlling adherence of glumes and factors controlling rachis internode length in these crosses, the naked class should have a significantly longer mean rachis internode length than the covered class.

Colsess I X Accordian Rachis

Study of the F_1 progeny and parental data for these crosses as given in Tables 5 and 6, shows that the F_1 progeny approaches the short parent in rachis internode length to a lesser degree than in the case of the two crosses discussed previously. Therefore, the factors controlling rachis internode length contributed by the short parent, have a less effect than the factors contributed by the long parent as compared to Nigrinudum I or Coast III X Accordian Rachis crosses. This fact shows that the factors controlling rachis internode length contributed by the short parent are partially dominant to those contributed by the long rachis internode parent.

The F_2 plants from the crosses of Colsess I X

Accordian Rachis were classified into seven phenotypic groups before proceeding to obtain and classify data as described in the discussion of Nigrinudum I X Accordian Rachis crosses. Table 12 gives the observed frequencies for all qualitative characters studied in this cross plus theoretical frequencies as follows: theoretical values for a 1:2:1 ratio of 2-row, intermediate, and 6-row; theoretical values for a 3:1 ratio of naked versus covered caryopsis; theoretical values for a 3:1 ratio of hooded versus awned lemma; X^2 and P values for comparison of observed and calculated frequencies of all qualitative characters studied in the Colsess I X Accordian Rachis crosses.

The P values for the three different ratios concerning the qualitative characters as given in Table 12 show a good fit in all three cases to calculated frequencies from expected ratios. The data in Table 12 show that in crosses of Colsess I X Accordian Rachis, the parents differ by one factor pair in respect to adherence of lemma and in respect to hooded versus awned lemma. Data in Table 8 for Colsess I X Accordian Rachis crosses, as in the two previous discussions of crosses (Nigrinudum I X Accordian Rachis and Coast III X Accordian Rachis), show a definite piling up of measurement data around the short rachis internode parental class. Study of the measurement class frequencies through application of Castle's formula (2), 1921, led to the belief that the data would best fit a

Table 12.—OBSERVED AND CALCULATED DATA FROM F_2 SEGREGATION OF QUALITATIVE CHARACTERS IN COLSESS I X ACCORDIAN RACHIS CROSSES.

Phenotypic class	Measurement class limits in mm.										Pheno-typic class totals	Theoreti-cal totals 3/	X^2	P
	3.742 or less	3.742 to 3.878 1/	3.878 to 4.765	4.765 to 5.655	5.655 to 6.545	6.545 to 7.425	7.425 to 8.315	8.315 to 9.198	9.198 to 9.670 2/	9.670 or more				
	1	2	3	4	5	6	7	8	9	10				
2-row	6	0	32	11	5	0	1	1	0	11	67	85.25		
Intermediate	22	7	78	32	16	14	2	1	1	7	180	170.50	5.33	0.074
6-row	10	10	50	14	4	4	2	0	0	0	94	85.25		
Covered	29	10	15	45	19	11	5	1	1	15	251	255.75	0.353	0.566
Naked	9	7	45	12	6	7	0	1	0	3	90	85.25		
Hooded	23	7	122	37	15	15	5	2	1	13	240	255.75	3.78	0.053
Awned	15	10	38	20	10	3	0	0	0	5	101	85.25		

1/ Short rachis internode parental class with class limits set by establishing limits twice the standard error on both sides of mean rachis internode length of Colsess I.

2/ Long rachis internode parental class with class limits set as described in footnote #1 but using the standard error and mean of Accordian Rachis.

3/ Based on expected 1:2:1, 3:1, and 3:1 ratios respectively.

three factor difference hypothesis. Although the observed and calculated ratios as given in Table 8 are not in close enough agreement to be a good fit when submitted to statistical tests, the three factor hypothesis seemed to be the best assumption on which to base further study. The difference between observed and theoretical values can be explained by the following:

1. One to several modifying factors may be and probably are present and would thus affect the rachis internode length considerably. This statement is in agreement with the findings of Hayes and Harlan (5), 1920, Neatby (10), 1929, and von Ubisch (13), 1919.

2. The arbitrary measurement class limits may overlap actual genetic class limits and some individuals may have been placed in the wrong class.

3. The basic data does not completely fit the original assumptions made by Castle (2), 1921, in deriving his formula.

Table 13 presents a summary of statistical analysis of data used to check for possible linkage of factors controlling inheritance of rachis internode length with the qualitative characters studied in the Colsess I X Accordian Rachis crosses.

Table 13.--LINKAGE DATA FOR F_2 PROGENY OF COLSESS I X ACCORDIAN RACHIS CROSSES

Phenotypic class	Mean rachis internode length in mm.	t value
2-row	5.605 ± 0.268	
Intermediate	5.054 ± 0.111	3.58
6-row	4.587 ± 0.095	
Covered	5.083 ± 0.102	0.75
Naked	4.896 ± 0.148	
Hooded	5.098 ± 0.104	0.87
Awned	4.882 ± 0.145	

Study of the three t values given in Table 13 shows no indication of linkage in the Colsess I X Accordian Rachis crosses between the factors controlling rachis internode length and either covered versus naked caryopsis or hooded versus awned lemma. However, the t value for significant difference between the mean rachis internode length of the 2-row class as compared to the 6-row class (3.58) does give an indication of linkage between the factors controlling number of rows and some of the factors controlling rachis internode length in this particular cross.

<u>Colsess V X Accordian Rachis</u>

Examination of the F_1 progeny and parental data for these crosses as given in Tables 5 and 6 shows that they do not differ in this respect from the F_1 data discussed for the Colsess I X Accordian Rachis crosses. The data show the F_1 progeny is behaving much the same as in the case of the Colsess I X Accordian Rachis crosses since the rachis internode length of the F_1 approaches the short parent in this respect to a lesser degree than in the case of the Nigrinudum I or Coast III X Accordian Rachis crosses. 1/

The F_2 plants from the crosses of Colsess V X Accordian Rachis were classified into nine phenotypic groups before proceeding to obtain and classify data as described in the discussion of Nigrinudum I X Accordian Rachis crosses. Table 14 gives the observed frequencies for all qualitative characters studied in these crosses plus theoretical frequencies and statistical analyses as follows: theoretical values for a 1:2:1 ratio of 2-row, intermediate, and 6-row; theoretical values for a 3:1 ratio of naked versus covered caryopsis; theoretical values for a 3:1 ratio of hooded versus awned lemma; theoretical values for a 3:1 ratio of green versus chlorina plant color; X^2 and P values for comparison of observed

1/For a more complete discussion the reader is referred to the first paragraph in the discussion of Colsess I X Accordian Rachis crosses.

Table 14.—OBSERVED AND CALCULATED DATA FROM F_2 SEGREGATION OF QUALITATIVE CHARACTERS IN COLSESS V X ACCORDIAN RACHIS.

Phenotypic class	Measurement class limits in mm.													
	3.789 or less	3.789 to 3.871 1/	3.871 to 4.758	4.758 to 5.645	5.645 to 6.532	6.532 to 7.420	7.420 to 8.307	8.307 to 9.198	9.198 to 9.670 2/	9.670 or more	Phenotypic class totals	Theoretical totals 3/	X^2	P
	1	2	3	4	5	6	7	8	9	10				
2-row	34	14	69	17	6	6	6	11	5	8	176	176.75		
Intermediate	41	31	170	38	30	19	3	3	2	5	342	353.50	1.226	0.548
6-row	40	11	93	29	9	2	4	0	0	1	189	176.75		
Covered	75	36	247	64	30	23	9	11	5	11	511	530.25	2.795	0.096
Naked	40	20	85	20	15	4	4	3	2	3	196	176.75		
Hooded	79	39	261	62	37	23	12	13	5	11	542	530.25	1.042	0.31
Awned	36	17	71	22	8	4	1	1	2	3	165	176.75		
Green	66	40	269	70	34	20	10	10	5	9	533	530.25	0.057	0.813
Chlorina	49	16	63	14	11	7	3	4	2	5	174	176.75		

1/ Short rachis internode parental class with class limits set by establishing limits twice the standard error on both sides of mean rachis internode length of Colsess V.

2/ Long rachis internode parental class with class limits set as described in footnote #1 but using the standard error and mean of Accordian Rachis.

3/ Based on expected 1:2:1, 3:1, 3:1, 3:1 ratios respectively.

and theoretical ratios.

The P values for the four different ratios concerning the qualitative characters as given in Table 14 show a good fit to calculated frequencies from expected ratios. In other words, Table 14 shows that in crosses of Colsess V X Accordian Rachis the parents differ by one factor pair in respect to each of the four qualitative characters studied which were: number of rows, adherence of lemma, whether lemma hooded or awned, and green versus chlorina seedling color. Data in Table 8 for Colsess V X Accordian Rachis crosses, as noted in discussions of the crosses Nigrinudum I, Coast III, and Colsess I X Accordian Rachis, show a piling up of measurements around the short rachis internode parental class. Thorough study of these measurement class frequencies through application of Castle's formula (2), 1921, led to the belief that the data would best fit a three factor difference hypothesis and even though the observed data give a very poor fit to calculated ratios, the three factor hypothesis seems to be the best assumption upon which to base further study.1/

1/For a discussion of the possible reasons for such a poor fit between observed and calculated measurement class frequencies the reader is referred to the first paragraph of the discussion of Colsess I X Accordian Rachis crosses.

A summary of statistical analysis of data used in checking for indications of linkage between factors controlling inheritance of rachis internode length with any of the qualitative characters studied in Colsess V X Accordian Rachis crosses is presented in Table 15.

Table 15.--LINKAGE DATA FOR F_2 PROGENY OF COLSESS V X ACCORDIAN RACHIS CROSSES.

Phenotypic class	Mean rachis internode length in mm.	t value
2-row	5.215 ± 0.153	4.38
Intermediate	4.781 ± 0.070	
6-row	4.490 ± 0.071	
Covered	4.858 ± 0.079	0.94
Naked	4.690 ± 0.100	
Hooded	4.874 ± 0.065	1.60
Awned	4.604 ± 0.104	
Green	4.826 ± 0.061	0.32
Chlorina	4.766 ± 0.126	

The t value for significant difference between mean rachis internode length for the 2-row and 6-row classes (4.38) indicates linkage between the factors controlling number of rows and some of the factors controlling rachis internode length in these particular crosses. The t values for significant difference between the mean rachis internode lengths of the other three qualitative characters (covered versus naked caryopsis, hooded versus awned lemma, and green versus chlorina seedlings) do not show any indication of linkage between them and the factors controlling length of rachis internode in the Colsess V X Accordian Rachis crosses.

Minnesota 90-5 X Accordian Rachis

Study of the data given for these crosses in Tables 5 and 6 shows the same results in general as were previously discussed for the crosses of Colsess I X Accordian Rachis and Colsess V X Accordian Rachis. The data show that the F_1 progeny is significantly different from the two parents in respect to mean rachis internode length and that the genes controlling inheritance of rachis internode length contributed by the short rachis internode parent are again partially dominant to those contributed by the long rachis internode parent.

Comparison of parental mean rachis internode values as given in Table 5 shows that the range between Minnesota 90-5 and Accordian Rachis is significantly greater than any of the other four crosses discussed in this paper. This fact would indicate, according to von Ubisch (13), 1919, that Minnesota 90-5 and Accordian

Rachis differ by a greater number of factors in respect to rachis internode length than do any of the other four crosses studied in this research problem.

The F_2 plants from the crosses of Minnesota 90-5 X Accordian Rachis were grouped into ten different phenotypic classes before proceeding with the obtaining and classification of data as described previously under the discussion of Nigrinudum I X Accordian Rachis crosses. Table 16 gives the observed frequencies for all qualitative characters studied in these particular crosses plus theoretical frequencies and statistical analyses as follows: theoretical frequencies for 3:1 ratios of black versus white glumes, covered versus naked caryopsis, rough versus smooth awns, long versus short rachilla hairs, and intermedium versus non-intermedium; X^2 and P values for comparison of observed and theoretical frequencies.

The P values as given in Table 16 show that in crosses of Minnesota 90-5 X Accordian Rachis, the parents differ by one factor pair in respect to each of four qualitative characters studied which were black versus white glumes and caryopsis, covered versus naked caryopsis, rough versus smooth awns, and long versus short haired rachilla. The X^2 value for intermedium versus non-intermedium (13.626) gives a very small P value indicating a poor fit to the expected 3:1 ratio. This fact can undoubtedly be attributed to difficulties encountered in

Table 16.—OBSERVED AND CALCULATED DATA FROM F_2 SEGREGATION OF QUALITATIVE CHARACTERS IN MINNESOTA 90-5 X ACCORDIAN RACHIS.

Phenotypic class	Measurement class limits in mm.										Pheno-typic class totals	Theoretical totals 3/	X^2	P
	2.516 or less	2.516 to 2.564 1/	2.564 to 3.675	3.675 to 4.775	4.775 to 5.885	5.885 to 6.985	6.985 to 8.085	8.085 to 9.198	9.198 to 9.670 2/	9.670 or more				
	1	2	3	4	5	6	7	8	9	10				
Black	10	9	299	102	34	20	4	6	0	1	485	481.5	0.102	0.755
White	1	1	102	37	6	7	1	2	0	0	157	160.5		
Covered	8	7	293	106	28	21	4	7	0	1	475	481.5	0.351	0.568
Naked	3	3	108	33	12	6	1	1	0	0	167	160.5		
Rough	8	8	312	108	28	20	4	4	0	1	493	481.5	1.099	0.296
Smooth	3	2	89	31	12	7	1	4	0	0	149	160.5		
Long	10	9	330	106	27	17	2	2	0	0	503	481.5	3.84	0.049
Short	1	1	71	33	13	10	3	6	0	1	139	160.5		
Intermedium	11	10	312	89	17	2	0	0	0	0	441	481.5	13.626	<0.001
Non-intermedium	0	0	89	50	23	25	5	8	0	1	201	160.5		

1/ Short rachis internode parental class with class limits set by establishing limits twice the standard error on both sides of mean rachis internode length of Minnesota 90-5.

2/ Long rachis internode parental class with class limits set as described in footnote #1 but using the standard error and mean of Accordian Rachis.

3/ Based on expected 3:1 ratios.

classification--a condition which can be rectified as soon as F_3 data are available. Data in Table 8 for Minnesota 90-5 X Accordian Rachis crosses show an even more definite piling up of measurements around the short rachis internode parental class than has been the case in any of the previous four crosses which have been discussed. Thorough examination of the measurement class totals through application of Castle's formula (2), 1921, led to the assumption that the data would best fit a six factor difference hypothesis and even though the observed data give a very poor fit to calculated ratios, the six factor hypothesis seems to be the best assumption upon which to base further study.1/

Table 17 presents a summary of the statistical analysis of data used in checking for indications of linkage between factors controlling inheritance of rachis internode length and any of the qualitative characters studied in crosses of Minnesota 90-5 X Accordian Rachis.

1/For a discussion of the possible reasons for such a poor fit between observed and calculated measurement class frequencies the reader is referred to the first paragraph of the discussion for Colsess I X Accordian Rachis crosses.

Table 17.--LINKAGE DATA FOR F_2 PROGENY OF MINNESOTA 90-5 X ACCORDIAN RACHIS CROSSES.

Phenotypic class	Mean rachis internode length in mm.	t value
Black	3.735 ± 0.048	0.25
White	3.702 ± 0.086	
Covered	3.753 ± 0.054	0.52
Naked	3.650 ± 0.144	
Rough	3.693 ± 0.049	0.75
Smooth	3.837 ± 0.105	
Long	3.596 ± 0.042	4.10
Short	4.198 ± 0.133	
Intermedium	3.409 ± 0.032	7.08
Non-intermedium	4.422 ± 0.111	

The t values 0.25, 0.52, and 0.75 for black versus white glumes and caryopsis, for covered versus naked caryopsis, and for rough versus smooth awns, respectively, do not give any indication of linkage between the factors controlling them and the factors controlling rachis internode length in this particular cross. The t values for significant difference between mean rachis internode length for the long versus short rachilla hairs and intermedium versus non-intermedium classes which, according to Table 16 are 4.10 and 7.08, respectively, do indicate presence of linkage between the factors controlling them and some of the factors controlling inheritance of rachis internode length in Minnesota 90-5 X Accordian Rachis crosses.

Linkage investigations

Study of F_2 data in regard to possible linkages between certain qualitative characters and the factors controlling rachis internode length for the five crosses studied in this research problem is summarized in Table 18.

Table 18 shows that in crosses of Coast III, Colsess I, and Colsess V X Accordian Rachis some of the factors differentiating the parents in respect to rachis internode length are located in linkage group I. Data in Table 18 also show that in crosses of Nigrinudum I and Minnesota 90-5 X Accordian Rachis some of the factors differentiating the parents in respect to rachis internode length are located in linkage group IV. Further study of Table 18 shows that in crosses of Minnesota 90-5 X Accordian Rachis some of the factors controlling differences in rachis internode length are located in linkage group V. In summary, Table 18 shows that at least three different groups of factors are involved in the inheritance of rachis internode length but final conclusions must await the availability of F_3 data not only in respect to

Table 18.—INDICATIONS OF LINKAGE FOR THE FIVE CROSSES

Linkage Group	Phenotypic Classes	Accordian Rachis crossed with Nigrinudum I $\bar{X}$*	t	Coast III $\bar{X}$*	t	Colsess I $\bar{X}$*	t	Colsess V $\bar{X}$*	t	Minnesota 90-5 $\bar{X}$*	t
	2-row			4.950		5.605		5.215			
I	Intermediate			4.467	3.514	5.054	3.58	4.781	4.38		
	6-row			4.475		4.587		4.490			
	Black glumes	4.436								3.735	
II			0.007								0.25
	White glumes	4.429								3.702	
	Covered caryopsis			4.622		5.083		4.858		3.753	
III					3.49**		0.75		0.94		0.52
	Naked caryopsis			4.370		4.896		4.690		3.650	
	Hooded lemma					5.098		4.874			
							0.87		1.60		
	Awned lemma					4.882		4.604			
IV											
	Intermedium	4.306								3.409	
			3.01								7.08
	Non-intermedium	4.761								4.422	

Table 18.—INDICATIONS OF LINKAGE FOR THE FIVE CROSSES.—Continued

Linkage Group	Phenotypic Classes	Accordian Rachis crossed with									
		Nigrinudum I		Coast III		Colsess I		Colsess V		Minnesota 90-5	
		$\bar{X}$*	t	$\bar{X}$*	t	$\bar{X}$*	t	$\bar{X}$*	t	$\bar{X}$*	t
	Rough awns									3.693	0.75
	Smooth awns									3.837	
V											
	Long haired rachilla									3.596	4.10
	Short haired rachilla									4.198	
VI		***				***					
	Green seedling							4.826	0.32		
VII				***							
	Chlorina seedling							4.766			

* Mean rachis internode length in millimeters

** Although significant, this t value is not an indication of linkage as pointed out in the discussion of this particular cross

*** Seedling lethals which must be carried into the F_3 generation in order to obtain data for linkage studies those characters already studied but also in respect to the Nigrinudum I, ($A_n a_n$) Coast III, ($Y_c y_c$) and Colsess I, ($A_c a_c$) seedling characters which, since they are lethal when homozygous, do not lend themselves to linkage studies in the F_2.

Chapter V

DISCUSSION

The data as presented in Chapter IV tend to support many of the findings of previous workers as given in the review of literature. The points of comparison and contrast will be presented at this time.

Comparison of parental mean internode lengths, as given in Table 5 for the two years, 1947 and 1948, supports the findings of Harlan (4), 1914, and Wexelsen (16, 17), 1933 and 1934, in that density may vary significantly in different seasons.

Data from Table 17 support Neatby's (10), 1929, and Wexelsen's (16), 1933, findings in that one or more factors controlling inheritance of rachis internode length is located in linkage group I. Data from Table 18 also supports Wexelsen (16), 1933, where he found indications that another factor controlling inheritance of rachis internode length was located in linkage group V.

Data presented in Table 6 do not completely support any one of the three types of F_1 behavior reported by earlier workers. Crosses of Colsess I, Colsess V and Minnesota 90-5 X Accordian Rachis in both 1947 and 1948 plus crosses of Coast III X Accordian Rachis in 1948 show partial dominance for short rachis internode over long rachis internode. Such a condition cannot be classified in any one of the three types of F_1 behavior found by earlier workers which were as follows: 1. lax dominant over dense; 2. dense dominant over lax; and 3. intermediate between the two parents. Results from crosses of Nigrinudum I and Coast III X Accordian Rachis in 1947 agree with results reported by Hayes and Harlan (5), 1920, where they reported a case of almost complete dominance of short rachis internode over long rachis internode. The other four crosses gave mean rachis internode lengths in the F_1 generation which show partial dominance for short rachis internode over long rachis internode--a situation not reported by any previous worker.

Since study and proof of number of factors involved in inheritance of rachis internode length must await F_3 data, this paper will not discuss the available data in view of findings of previous workers. However, it is worthwhile noting that while Wexelsen (16, 17), 1933 and 1934, believes that as many as five factors were concerned with inheritance of rachis internode length, the linkage data from this paper indicate that three different factors are involved even though the number of factor pairs included in any one of the three different groups cannot be determined from the data available at the present time.

Statistical analysis of F_2 data from all five F_2 segregations support the findings of Wexelsen (17), 1934, and Neatby (10), 1929, where they found evidence of the occurrence of transgressive segregation.

Suggestions for further study

Theoretically, the best method would be to select random samples of each F_2 measurement class as given in Tables 7, 10, 12, 14, and 16 and plant them in the field in the spring of 1949 in conjunction with all six parents. Measurements of individual F_3 plants would be made as in previous years and the data would be analyzed to ascertain the breeding behavior of each F_2 measurement class. Knowledge of F_3 breeding behavior should make possible the formulation of conclusions concerning linkage of factors controlling the qualitative characters with factors controlling rachis internode length as well as the number of factors by which Accordian Rachis differs from the other parental varieties in respect to rachis internode length.

Such a procedure as outlined above would, however, be impossible to carry out due to lack of time and money. Therefore, in order to use the above method the field planting would probably be limited to one entire family--the choice as to which family to plant being dependent upon which would give the most information as determined by thorough study of F_2 data from all five of the crosses.

Chapter VI

SUMMARY

Five crosses were made using Accordian Rachis (a long rachis internode barley variety) as one parent, while the other parent was one of five short rachis internode varieties as follows: Coast III, Colsess I, Colsess V, Minnesota 90-5 and Nigrinudum I. These five short rachis internode varieties were used, since through their use it was possible to check for indications of linkage in all of the seven linkage groups in barley.

The individual F_1 plants from the five crosses were measured in respect to rachis internode length. Short rachis internode was completely dominant over long rachis internode in crosses of Nigrinudum I X Accordian Rachis. In crosses of Coast III X Accordian Rachis, data obtained in 1947 indicated that short rachis internode was completely dominant over long rachis internode. However, 1948 data showed that the dominance of short rachis internode was not complete. Crosses of Colsess I, Colsess V, and Minnesota 90-5 X Accordian Rachis indicated a partial dominance of short over long rachis internode. This was indicated by the fact that the mean of the F_1

fell somewhere between the two parents and statistical tests show that the mean rachis internode lengths of these three crosses lies considerably closer to the mean of the short rachis internode parents (Colsess I, Colsess V, and Minnesota 90-5) than to the mean of the long rachis internode parent.

The individual F_2 plants from the five crosses was classified into various qualitative phenotypic classes after which a rachis internode measurement was obtained for each plant. The data were then organized into a frequency distribution and treated statistically to check for possible linkages of qualitative and quantitative characters while at the same time trying to ascertain the number of factors differentiating the long and short rachis internode parents of the five different crosses. Indications of linkage in Coast III, Colsess I, and Colsess V X Accordian Rachis crosses were found in linkage group I between the factors controlling number of rows and factors controlling rachis internode length. Data for Nigrinudum I X Accordian Rachis crosses indicated linkage was occurring between factors controlling intermedium versus non-intermedium located in linkage group IV and factors controlling rachis internode length. Indications of linkage were found in crosses of Minnesota 90-5 X Accordian Rachis between factors controlling intermedium versus non-intermedium located in linkage group IV, and factors controlling long versus short haired rachilla located in linkage group V in respect to factors controlling rachis internode length in these crosses. Independent inheritance was found between the factor pairs for short versus long internode and black versus white floral bracts (group II), covered versus naked caryopsis (group III), hooded versus awned lemma (group IV), rough versus smooth awns (group V), and green versus chlorina plants (group VII).

Measurement class totals for the Nigrinudum I and Minnesota 90-5 X Accordian Rachis crosses indicated a difference of six pairs of factors while the Colsess I and Colsess V X Accordian Rachis crosses indicated a difference of three pairs of factors and the Coast III X Accordian Rachis crosses indicated a difference of five pairs of factors as the best assumption upon which to base further study in respect to rachis internode length.

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