INHERITANCE OF FERTILITY IN THE LATERAL SPIKELETS OF BARLEY[1]

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INTRODUCTION

A STUDY was made of the inheritance of fertility in the lateral spikelets of the cultivated barley species in an attempt to explain some of the differences in fertility known to exist in certain crosses between species.

Four species of cultivated barley have been recognized by HARLAN (1918) on the basis of the fertility of the lateral spikelets, these being *Hordeum vulgare*, *H. intermedium*, *H. distichon*, and *H. deficiens*. *H. vulgare* and *H. intermedium* are so-called 6-rowed species with all spikelets at a rachis joint at least partially fertile, the latter species being different from the former in that the lateral spikelets are only partially fertile or, when fully fertile, without awns or hoods. *H. distichon* and *H. deficiens* are so-called 2-rowed species with no fertility of the lateral spikelets. The side spikelets consist of glumes, lemma, palea, rachilla, and usually the rudiments of the sexual organs in *H. distichon;* but they are reduced in *H. deficiens* to only the glumes and rachilla with rarely more than one flowering bract (lemma or palea) and never the rudiments of sexual organs.

It has been observed that some crosses give intermediums[2] which have fertile lateral spikelets, while others give only segregates with infertile lateral spikelets. There is a possibility that some factor or factors other than those for non-6-row versus 6-row (*Vv*) and for intermedium versus non-intermedium (*Ii*) are necessary to explain the difference in behavior between fertile and infertile intermediums.

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[1] This material was taken from a thesis presented to the faculty of the Graduate School of the UNIVERSITY OF MINNESOTA in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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[2] Both intermediums and intermediates may have partial lateral spikelet fertility. Intermediums (*VVII*) are distinguishable phenotypically by the rounded lemmas of the lateral florets which are never awn-pointed. Fertile intermediums are genetically *VV* with partial fertility of the lateral spikelets. Infertile intermediums (*VVII*) are designated as forms with rounded lemmas with less than two per cent of the lateral spikelets fertile. Ordinarily, there is no fertility of the lateral spikelets.

LITERATURE REVIEW

Previous research in barley genetics has been reviewed rather extensively by several investigators: GRIFFEE (1925), HAYES and GARBER (1927), ROBERTSON (1929), BUCKLEY (1930), KUCKUCK (1930a), and DAANE (1931). In addition, a bibliography on genetic factors has been compiled by ROBERTSON, WIEBE and IMMER (1941). Consequently the work reviewed here will be that which pertains particularly to the inheritance of fertility of the lateral spikelets.

A single-factor difference has been found between crosses of *Hordeum vulgare* and *H. distichon*, *H. vulgare* and *H. deficiens*, and *H. distichon* and *H. deficiens*. They have been considered as an allelic series by ENGLEDOW (1924) and by HOR (1924). The intermedium versus non-intermedium (*Ii*) factor pair was found by HARLAN and HAYES (1920) and by ROBERTSON (1929, 1933) to be independent of the non-6-row versus 6-row (*Vv*) factor pair.

Two distinct types of inheritance have been obtained from crossing varieties of *H. distichon* and *H. deficiens*, both 2-rowed species, with varieties of *H. vulgare*. These types of inheritance will be described in some detail.

Many workers (ROBERTSON, et al. 1941) have obtained three classes from crosses of *H. vulgare* and *H. distichon* varieties. An intermediate[3] condition was found to exist in the F_1 generation with the lateral spikelets awned (or hooded) and high in fertility. The F_2 segregation has been readily explained as a single-factor difference with a 1:2:1 ratio of 6-rowed intermediate, and 2-rowed forms.

That more than three classes for fertility and rows could be separated in F_2 generations of 6-row × 2-row crosses was pointed out by ENGLEDOW (1920), followed shortly afterwards by a complete genetical analysis by HARLAN and HAYES (1920). The latter gave their results for a cross between Manchuria, a 6-rowed barley, and Svanhals, a 2-rowed *H. distichon* variety. They obtained an F_1 with lateral spikelets slightly fruitful and with intermediate awns. The F_2 genotypes were classified into seven classes on the basis of their F_3 behavior. GRIFFEE (1925) found a similar condition in a Svanhals × Lion cross. ROBERTSON (1933) obtained similar results in a cross between Colsess and *H. deficiens nudideficiens*. The data have been explained on a two-factor basis—that is, intermediums versus non-intermediums (*Ii*) and non-6-row versus 6-row (*Vv*), with the intermedium factor pair (*Ii*) hypostatic to that for rows (*Vv*). The F_2 genotypes as determined by F_3 behavior are as follows:

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[3] The term "intermediate" is used throughout this paper to designate the heterozygous condition of the non-6-row versus 6-row (*Vv*) factor pair. An intermediate may carry the genes *II*, *Ii*, *ii*, or any allele of this series.

CLASS	CLASSES WHICH SEGREGATE IN F_3	F_2 GENOTYPE	RATIO
1	6-row	*vvII* *vvIi* *vvii*	4
2	6-row, intermediate, and intermedium	*VvII*	2
3	6-row, intermediate, intermedium and 2-row	*VvIi*	4
4	6-row, intermediate, and 2-row	*Vvii*	2
5	Intermedium	*VVII*	1
6	Intermedium and 2-row	*VVIi*	2
7	2-row	*VVii*	1

That fertility of the lateral spikelets might be further influenced by minor modifying factors has been suggested by NEATBY (1929) and by HARLAN and HAYES (1920). GILLIS (1926) believes that a third factor pair (*Dd*) also is involved in fertility, being *D* in the intermediate forms and *d* in the *H. deficiens* types.

There is a possibility that some 2-rowed varieties of *H. distichon* really belong to the *H. intermedium* group genetically. This has long been suspected by HARLAN and MARTINI (1935) on the basis of extensive observations. They found occasional fertile lateral spikelets in 44 out of 408 supposedly normal 2-rowed varieties, or a total of 11 percent. Fertile lateral spikelets were especially plentiful in hybrid varieties and were much more common among dense-eared than among lax-eared barleys. These workers feel that different levels of fertility are correlated with a vigor of plant growth that may be significant. ENGLEDOW (1924) is also of the opinion that environment may influence fertility somewhat. In *H. intermedium haxtoni*, lateral floret fertility was influenced by time of planting, being much higher when planted early.

LINKAGE GROUPS IN BARLEY

Seven linkage groups have been established in barley. The literature on these groups has been reviewed by KUCKUCK (1930a, 1930b), DAANE (1931), ROBERTSON (1933, 1937, 1939), ROBERTSON, DEMING, and KOONCE (1932), and by ROBERTSON, WIEBE, and IMMER (1941). Since there are seven haploid chromosomes in cultivated barley, all linkage groups are thought to be found. As will be shown later, the factors concerned in this study are probably located in group IV. The factor pair for hoods versus awns (*Kk*) is located in this group. ROBERTSON (1933) found the factor pair for intermedium versus non-intermedium (*Ii*) to be linked with hoods versus awns (*Kk*) with 15.12 ±0.065 percent recombination.

MATERIALS AND METHODS

This study on the inheritance of fertility of the lateral spikelets of barley was made at the COLORADO EXPERIMENT STATION during the years 1931 to 1940, inclusive.

Symbols for genetic characters

The special fertility condition found in Mortoni involves the factor pair for non-6-row versus 6-row (*Vv*), but it must also be discussed in relation to the factor pair for intermedium versus non-intermedium (*Ii*). The genetic characters used in various crosses, together with their symbols, are listed below. The standard nomenclature suggested by ROBERTSON, WIEBE, and IMMER (1941) has been followed.

LINKAGE GROUP	CHARACTER PAIR	SYMBOLS
I	2-row versus non-2-row	*Vv*
	Green versus chlorina seedling color	*Ff*
II	Black versus white floral bracts	*Bb*
III	Covered versus naked caryopsis	*Nn*
IV	Hoods versus awns	*Kk*
	Intermedium versus non-intermedium (or 2-row)	*Ii*
V	Long versus short-haired rachillas	*Ss*
VI	Green versus xantha seedling color	*Xsxs*

Description of varieties used in experiments

The strains used in this experiment were as follows: Nudihaxtoni, Mortoni, Coast II, Smyrna I, Minnesota 84-7, Nilsson-Ehle No. 2, Nudideficiens, Nigrinudum, and Sublaxum. These varieties were made available by either the COLORADO EXPERIMENT STATION or the U. S. DEPARTMENT OF AGRICULTURE. Minnesota 84-7 came from the MINNESOTA AGRICULTURAL EXPERIMENT STATION.

H. intermedium nudihaxtoni (C.I. No. 2231) is an intermedium variety with complete fertility of the lateral spikelets. It is a naked barley with white kernels and floral bracts. The lemmas of the central spikelets are long-awned while those of the lateral spikelets are awnless.

H. intermedium mortoni (C.I. No. 2210) is a black, awned, covered variety with short-haired rachillas and purple plant color. It is a fertile intermedium with partial fertility of the lateral spikelets on practically every spike. (See fig. 1.) A count of the fertile and infertile lateral spikelets was made on the heads of seven parent plants used in crosses. From 32.2 to 51.2 percent of the lateral spikelets were fertile, the average being 40.7 percent.

The other varieties used in crosses generally were genetic testers. Except for Sublaxum, these strains have been described by previous workers (ROBERTSON 1929, 1933, 1937; ROBERTSON, DEMING, and KOONCE 1932). The factorial composition of the various parent lines is listed in table 1.

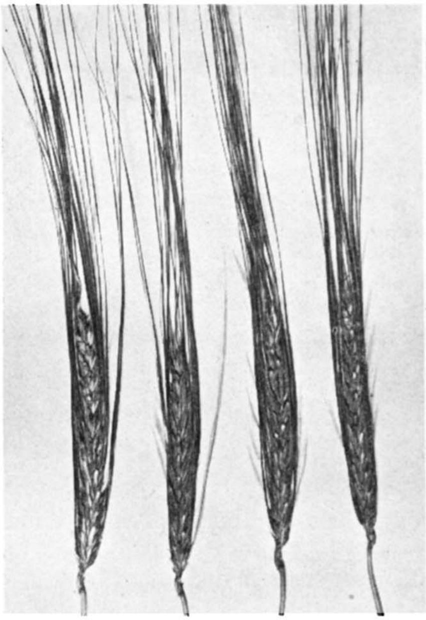

FIGURE 1 (left).—Heads of the Mortoni Parent. The partial fertility of the lateral spikelets is evident.

FIGURE 2 (right).—Classes in the F_2 generation of a Mortoni × Nigrinudum cross. The two heads on the left are infertile intermediums, the third head is a fertile intermedium, while the fourth is the type with inflated lateral spikelets classified as fertile.

Experimental methods

The experimental methods used were similar to those followed by ROBERTSON (1929). Particular attention has been given to the nature of fertility in the lateral spikelets. Three reciprocal crosses were made in each instance with the progeny carried to the F_3 generation. In the F_2 generation the plants were separated for the various character pairs being analyzed. Because of the difficulty in the separation of some of the classes, it was necessary in many cases to carry a random sample of the F_2 plants to the F_3 generation to determine the F_2 genotypes. A few heads were threshed from each F_2 plant, the seed of which was planted in individual 8-foot rows for the F_3 segregation.

The observed data were compared to calculated theoretical ratios and tested for goodness of fit by the use of χ^2 where two or more phenotypic

TABLE 1

List of the factor pairs found in the different parents.

	SYMBOLS FOR CHARACTERS							
VARIETY	*Vv*	*Ff*	*Bb*	*Nn*	*Kk*	*Ii*	*Ss*	*Xsxs*
Coast II*	*vv*	*FF*	*bb*	*NN*	*kk*	*II*	*ss*	*XsXs*
Minnesota 84-7	*vv*	*ff*	*bb*	*NN*	*kk*	—	*SS*	*XsXs*
Nilsson-Ehle No. 2†	*VV*	*FF*	*bb*	—	*kk*	*ii*	—	*XsXs*
Smyrna I	*VV*	*FF*	*bb*	—	*kk*	*ii*	—	*XsXs*
Nudihaxtoni	*vv*	*FF*	*bb*	*nn*	*kk*	*II*	*SS*	*XsXs*
Mortoni	*VV*	*FF*	*BB*	*NN*	*kk*	—	*ss*	*XsXs*
Sublaxum	*VV*	*FF*	*bb*	*nn*	*KK*	*ii*	—	*XsXs*
Nudideficiens	*VV*	*FF*	*bb*	*nn*	*kk*	*ii*	*SS*	*XsXs*
Nigrinudum	*VV*	*FF*	*BB*	*nn*	*kk*	*II*	*ss*	*XsXs*

* Coast II is heterozygous for green versus white seedlings (*Ac2 ac2*).

† Nilsson-Ehle No. 2 is heterozygous for albino seedlings (*A2a2*). These factor pairs segregated for 3:1 ratio in each case. Since they were not used in linkage relations, they will not be discussed further.

classes were involved. The interpretation of the significance of χ^2 values was the same as that used by FISHER (1934). The formula applied for the computation of χ^2 for a 3:1 ratio was as follows: $\chi^2 = (A-3a)^2/3N$ where A = the observed number in the dominant class, a = the observed number in the recessive class, and N = the total number of individuals. The probability value for one degree of freedom was determined by reference to a normal probability integral table.

The linkage determinations from F_2 data were made by the use of the product formula. The recombination percentages, as well as their standard errors, were determined from tables prepared by IMMER (1930). The F_2 and F_3 data were combined for the determination of the recombination value by the method suggested by IMMER (1934) as modified by ROBERTSON and COLEMAN (1940) for particular cases.

EXPERIMENTAL RESULTS

The experimental results will be presented in three parts—namely, (1) determination of the constitution of the parent material for non-6-row versus 6-row (*Vv*) and for intermedium versus non-intermedium (*Ii*), (2) inheritance of the fertile intermedium condition in Mortoni, and (3) the interrelationships of the factors concerned with lateral spikelet fertility with other factor pairs located in known linkage groups.

Row and intermedium constitution of parental material

It was first necessary to determine the genetic constitution of the parent material for the non-6-row versus 6-row (*Vv*) and intermedium versus non-intermedium factor pairs. The various lines studied were crossed on others of known constitution as determined by ROBERTSON (1929, 1937). These testers were: Nigrinudum (*VVII*), Nudideficiens (*VVii*), and Coast II (*vvII*). Nigrinudum is genotypically an infertile intermedium. From crosses with these testers, the factorial compositions of the parental lines were established as follows: Nudihaxtoni, *vvII;* Sublaxum, *VVii;* and Mortoni, *VV*. It was apparent that Mortoni, morphologically a *H. intermedium* variety, has the same composition for the 2-row (*VV*) condition as do some *H. distichon* varieties. It differs from the latter in that it is homozygous for partial fertility of the lateral spikelets. The intermedium versus non-intermedium (*Ii*) condition in Mortoni may not be the same as that in the other lines mentioned.

When the various known factorial constitutions for the row (*Vv*) and intermedium (*Ii*) factor pairs are summarized in the light of their F_1 phenotypic behavior, several facts are immediately apparent. Partial fertility of the lateral spikelets in the F_1 is due to the homozygous dominant intermedium, *II*, factorial condition in the presence of a heterozygous condition for rows, *Vv*. Non-fertility of the lateral spikelets in the F_1 is due to the presence of the heterozygous condition of the intermedium versus non-intermedium (*Ii*) factor pair in the presence of either *VV* or *Vv*. This is indicated in table 2.

TABLE 2

Fertility of the lateral spikelets in the F_1 generation for various genotypes for rows and intermediums in various crosses.

CROSS	FERTILITY CONDITION IN F_1 PLANTS	
	GENOTYPE	PHENOTYPE
Nudihaxtoni (*vvII*)×Nigrinudum (*VVII*)	*VvII*	Partial fertility
Coast II (*vvII*)×Nigrinudum (*VVII*)	*VvII*	Partial fertility
Coast II (*vvII*)×Nudideficiens (*VVii*)	*VvIi*	No fertility
Coast II (*vvII*)×Sublaxum (*VVii*)	*VvIi*	No fertility
Sublaxum (*VVii*)×Nigrinudum (*VVII*)	*VVIi*	No fertility

It is obvious that this fertile intermedium condition involves a heterozygous condition for the non-6-row versus 6-row (*Vv*) factor pair and the presence of the homozygous dominant intermedium (*II*) factor. The inheritance of the partially fertile intermedium as a homozygous condition is still to be considered.

The fertile intermedium condition in Mortoni

The factor pair for non-6-row versus 6-row (*Vv*) was studied in a cross between Mortoni and Nudihaxtoni. The F_1 plants were fertile intermediums. The lateral spikelets were 75 to 90 percent fertile, but with no awns or tip-awns on any of the lemmas. Three classes were separable in the F_2 generation—namely, 2-row, partially fertile intermediums, and 6-row. The observed F_2 data were calculated on the basis of a 1:2:1 ratio on the hypothesis that the observed classes could be explained by the non-6-row versus 6-row (*Vv*) factor pair. The data appear in table 3. The observed data afforded a poor fit to the calculated 1:2:1 ratio for non-6-row versus 6-row (*Vv*).

TABLE 3

Segregation in the F_2 generation for 2-row versus intermediates versus 6-row (Vv) in a cross between Mortoni and Nudihaxtoni.

ITEM	NUMBER OF PLANTS WITH CHARACTERS INDICATED			
	2-ROW	INTERMEDIATES	6-ROW	TOTAL
Observed counts	117	390	195	702
Calculated 1:2:1 ratio	175.50	351.00	175.50	702

$\chi^2 = 26.000$ $P = 0.000002$

The observed F_2 data were then calculated on a two-factor basis for the non-6-row versus 6-row (*Vv*) and for the intermedium versus non-intermedium (*Ii*) factor pairs. The data indicate two levels of fertility for intermedium—namely, partially fertile intermedium like the Mortoni parent and infertile intermedium as found in many 2-row sorts. The observed F_2 data, calculated on a two-factor basis with the intermedium condition hypostatic to the 6-row (*vv*) factor, are given in table 4. The observed data afforded a good fit to the calculated 3:9:4 ratio for a two-factor difference.

TABLE 4

Segregation in the F_2 generation for non-6-row versus 6-row and for infertile versus fertile intermedium in a Mortoni×Nudihaxtoni cross.

ITEM	NUMBER OF PLANTS WITH CHARACTERS INDICATED			
	INTERMEDIUM		6-ROW	
	INFERTILE	FERTILE		TOTAL
Observed counts	117	390	195	702
Calculated 3:9:4 ratio	131.62	394.88	175.50	702

$\chi^2 = 3.8510$ $P = 0.1484$

The F_2 data for the fertility of the lateral spikelets can be explained tentatively on the basis of the factor pair for non-6-row versus 6-row (*Vv*) and on the assumption of a single-factor difference for infertile versus fertile intermedium. It appears that an allelic series exists for intermedium. The intermedium condition, reported by ROBERTSON (1929), has non-fertile lateral spikelets and has been designated as II, while the non-intermedium allele has been designated as ii. Varieties with either factor pair in the homozygous condition are morphologically 2-rowed sorts in that they have only one fertile spikelet per rachis joint. Another allele found in the Mortoni parent, which breeds true for fertility on many lateral spikelets, will be designated as fertile intermedium (I^hI^h). This allele appears to be similar to the BB factorial condition found in the homozygous intermedium, Haxtoni ($aaBB$), reported by HARLAN and HAYES (1920). The infertile intermedium condition is dominant over partial fertility. All intermediums are genotypically VV. The cross, Mortoni (VVI^hI^h)×Nudihaxtoni ($vvII$), would be expected to segregate as follows in the F_2 and F_3 generations:

GENOTYPE	FREQUENCY	F_2 PHENOTYPES	RATIO	BEHAVIOR IN F_3 GENERATION
$VVII$	1	Infertile intermedium	3	Infertile intermedium
$VVII^h$	2	Infertile intermedium		Segregates 3:1 for infertile vs. fertility
$VvII$	2	Fertile intermediate	9	Segregates 1:2:1 for infertile, partial fertility and 6-row
$VvII^h$	4	Fertile intermediate		Segregates 3:9:4 same as F_2
VVI^hI^h	1	Fertile intermedium		Fertile intermedium
VvI^hI^h	2	Fertile intermediate		Segregates 3:1 for fertile intermedium vs. 6-row
$vvII$	1	6-row	4	6-row full fertility
$vvII^h$	2	6-row		6-row full fertility
vvI^hI^h	1	6-row		6-row full fertility

The F_2 plants were grown in the F_3 generation to determine their genotypes. The $VvII$ and $VvII^h$ classes, being very difficult to separate in the field, were grouped together. As predicted from the F_2 data, the homozygous partially fertile intermedium (VVI^hI^h) plants had been grouped with the intermediate class for rows (Vv). The observed data presented in table 5 afforded a good fit to the calculated 1:2:1:6:2:4 ratio for independent inheritance of the non-6-row versus 6-row (Vv) and infertile versus fertile intermedium (II^h) factor pairs. An allelic series for the intermedium condition is indicated.

To verify the assumption that an allelic series for intermedium is involved, the three intermedium conditions, II, I^hI^h, and ii, were tested in crosses which involved all possible combinations of these factors.

The inheritance of non-intermedium (ii) versus fertile intermedium (I^hI^h) was studied in crosses between Mortoni (VVI^hI^h) and other varieties which were $VVii$ in constitution. The F_1 plants were non-intermedium with no fertility of the lateral spikelets—that is, the non-intermedium condition was dominant. The F_2 plants were classified as non-intermedium ($VVii$ and

TABLE 5

Observed and calculated F_2 genotypes for non-6-row versus 6-row and infertile versus fertile intermedium as determined by the F_3 segregation in a Mortoni×Nudihaxtoni cross.

ITEM	NUMBER OF INDICATED GENOTYPE						
	$VVII$	$VVII^h$	VVI^hI^h	$VvII$ & $VvII^h$	VvI^hI^h	6-ROW*	TOTAL
Obsvd. count	43	79	36	289	82	173	702
Calc. ratio†	43.88	87.75	43.87	263.25	87.75	175.50	702

* 6-row includes $vvII$, $vvII^h$, and vvI^hI^h.

† Compared with a calculated 1:2:1:6:2:4 ratio. $\chi^2=5.2331$. P=0.3903.

$VVII^h$) and fertile intermedium (VVI^hI^h). On account of the difficulty in separation of the F_2 classes, seed from the individual F_2 plants was grown in the F_3 generation to obtain the F_2 genotypes, the data for which are given in table 6. The data indicate that non-intermedium (ii) versus fertile intermedium (I^hI^h) is the result of the segregation of a simple Mendelian factor pair.

TABLE 6

Observed and calculated F_2 genotypes for non-intermedium (or 2-row) versus fertile intermedium as determined by the F_3 segregation in crosses between Mortoni and other varieties.

CROSS	NUMBER OF INDICATED GENOTYPE*					
	NON-INTER-MEDIUM (ii)	HETERO-ZYGOTES (I^hi)	FERTILE INTER-MEDIUM (I^hI^h)	TOTAL	χ^2	P
Nudideficiens×Mortoni	266	475	227	968	3.4774	0.1812
Nilsson-Ehle No. 2×Mortoni	126	256	118	500	0.5440	V. large
Sublaxum×Mortoni	201	429	197	827	1.2007	0.5586
Mortoni×Smyrna I	24	35	23	82	1.7805	0.4203
Minnesota 84-7×Mortoni	129	225	101	455	3.5011	0.1791

* Compared with a calculated 1:2:1 ratio.

A Sublaxum ($VVii$)×Nigrinudum ($VVII$) cross was used to study the inheritance of infertile intermedium versus non-intermedium (Ii). The F_2 data, presented in table 7, indicate a single-factor difference, although the fit of the total observed data to the calculated 3:1 ratio was not good. The discrepancy appears to be due to the II-32-149 cross in which the non-intermedium forms were consistently high. This is possibly due to the difficulty of separation of the two classes in the F_2 generation.

Nigrinudum ($VVII$) was crossed with Mortoni (VVI^hI^h), the F_3 data for which are presented in table 8. The F_2 data were classified so as to include a few plants with inflated but non-fertile lateral spikelets in the fertile intermedium class. (See fig. 2.) This appeared to be justified, since occasional plants of the Mortoni parent fail to show any fertility of the lateral spikelets. The observed data afford a good fit to the calculated 1:2:1 ratio for a monohybrid segregation.

TABLE 7

Segregation in the F_2 generation for intermedium and non-intermedium in a Sublaxum×Nigrinudum cross.

CROSS NO.	OBSERVED NUMBERS*			χ^2	P
	INTERMEDIUM	NON-INTERMEDIUM	TOTAL		
II-32- 55	262	90	352	0.0606	0.8026
-147	195	81	276	2.7826	0.0949
-148	230	89	319	1.4305	0.2301
-149	239	108	347	6.9404	0.0085
-150	223	87	310	1.5527	0.2113
Totals	1149	455	1604	9.6958	0.0019

* Compared with a calculated 3:1 ratio.

Since a monohybrid segregation was obtained in crosses with the infertile intermedium (II), non-intermedium (ii), and fertile intermedium (I^hI^h) factors taken in all possible combinations, a multiple allelic series is definitely indicated.

TABLE 8

Observed and calculated F_2 genotypes for infertile versus fertile intermedium as determined by the F_3 segregation in a Mortoni×Nigrinudum cross.

ITEM	NUMBER OF INDICATED GENOTYPE			TOTAL
	INFERTILE INTERMEDIUM (II)	HETEROZYGOTES (II^h)	FERTILE INTERMEDIUM (I^hI^h)	
Observed count	101	202	81	384
Calc. 1:2:1 ratio	96	192	96	384

$\chi^2=3.1250$ P=0.2122

The data for one Coast II×Mortoni cross indicate that some Coast II plants carry the fertile intermedium allele (I^hI^h). The F_1 plants in this particular case had fully fertile lateral spikelets with tip awns less than one-half the length of the awns on the central spikelets. The F_2 plants were classified as fertile intermediums, intermediates, and 6-row. All intermediums showed some fertility of the lateral spikelets. The F_2 plants grown in the F_3 generation showed all intermedium genotypes to have fertile lateral spikelets. The infertile intermedium form was not recovered.

Since the intermedium allelic series is hypostatic to the 6-row (*vv*) condition, it is necessary to determine the intermedium constitution of 6-rowed varieties used in crosses where fertility is being studied genetically. The value of known testers is obvious. An infertile intermedium 2-rowed variety such as Nigrinudum ($VVII$) could be used to test the constitution of unknown 6-rowed and 2-rowed varieties for the intermedium allelic series as follows:

(a) Unknown 6-row (vv—)×$VVII$ gives non-fertile lateral spikelets in F_1 when the 6-rowed variety is $vvii$. Non-intermedium forms are recovered in F_2 and F_3

(b) Unknown 6-row (vv—)×$VVII$ gives partial lateral spikelet fertility in the F_1 when the 6-rowed variety is either $vvII$ or vvI^hI^h. In case it is $vvII$ the F_2 will segregate into three classes in a 1:2:1 ratio—namely, infertile intermediums, fertile intermediates, and 6-row. This segregation may be verified in the F_3 generation. When the unknown 6-rowed variety is vvI^hI^h, the F_2 will give infertile intermediums, fertile intermediums and fertile intermediates (indistinguishable), and 6-row. The F_3 segregation will give infertile intermediums and fertile intermediums among the seven phenotypic classes.

(c) The *H. distichon* and H. *deficiens* varieties—that is, morphological 2-rowed varieties, may be crossed with Nigrinudum to determine their constitution for II or ii.

Factor interrelationships

Mortoni, classified as *H. intermedium* by HARLAN (1918), appears to be genetically VVI^hI^h. The interrelationships of the partial lateral spikelet fertility factor with others in known linkage groups were studied with the view that the fertility condition was due to another allele, (I^hI^h). Two-row non-intermedium ($VVii$) testers were used in the study of interrelationships with the non-intermedium versus fertile intermedium (I^hi) factor pair.

Characters inherited independently

The various characters inherited independently of the non-intermedium versus fertile intermedium (I^hi) factor pair in Mortoni crosses are given in table 9. The F_1 plants in all cases were characterized by infertile lateral spikelets. The F_2 plants were classified for non-intermediums, fertile intermediums, and the other factor pairs studied in particular crosses. Because of the difficulty in classification, the selfed F_2 plants were grown in the F_3 generation to determine the F_2 genotypes.

The segregations in the F_3 generation indicate a good agreement between

TABLE 9

Observed F_2 genotypes for non-intermedium versus fertile intermedium and factors inherited independently as determined by F_3 segregations in crosses of Mortoni with other varieties.

MORTONI CROSSED WITH:	GENO-TYPE STUDIED	LINK-AGE GROUP	GENOTYPES*									TOTAL	χ^2	P
			AABB	AABb	AAbb	AaBB	AaBb	Aabb	aaBB	aaBb	aabb			
Minn. 84-7	I^hiFf	I	41	62	26	63	106	56	25	55	21	455	9.8431	0.2772
Nudideficiens	I^hiBb	II	62	127	77	119	232	124	45	117	65	968	9.7934	0.2810
N. Ehle No. 2	I^hiBb	II	31	65	30	55	130	71	26	60	32	500	3.4080	0.9028
Nudideficiens	I^hiNn	III	58	138	70	116	245	114	61	108	58	968	6.1363	0.6322
Nudideficiens	I^hiSs	V	47	60	24	60	135	72	22	59	33	512	14.4610	0.0713
Smyrna I	I^hiXsxs	VI	9	15	—	9	26	—	7	16	—	82	2.8802	0.7179

* Compared with calculated 1:2:1:2: 4:2:1:2:1 ratio in all cases except Mortoni×Smyrna I cross which was compared with calculated 1:2:2:4:1:2 ratio.

the observed data and the calculated ratios for independent inheritance. It appears that the factor pair for non-intermedium versus fertile intermedium (I^hi) is inherited independently of factor pairs as follows: Green versus chlorina (Ff) located in linkage group I, black versus white (Bb) floral bracts known to be in group II, covered versus naked seeds (Nn) located in group III, long versus short-haired rachillas (Ss) previously placed in group V, and green versus xantha seedling color ($XsXs$) known to be in group VI. The non-intermedium versus fertile intermedium (I^hi) factor pair was not tested with factors located in group VII.

Linkage of characters

The interrelationship of the character pairs for non-intermedium versus fertile intermedium (I^hi) and hoods versus awns (Kk) was tested in a cross between Sublaxum and Mortoni. The factor pair for hoods versus awns (Kk) is known to be located in group IV. The F_1 plants were 2-rowed, hooded, and with non-fertile lateral spikelets. The observed F_2 data for these characters are given in table 10.

The observed data afford a poor fit to the calculated 9:3:3:1 ratio for independent inheritance. It is noted that the non-intermedium awned and fertile intermedium hooded plants are fewer than expected for independent inheritance. These are recombination classes, since the Sublaxum parent was non-intermedium hooded and the Mortoni parent fertile intermedium awned. Linkage in the coupling phase is indicated. The recombination percentage, calculated by the product method, was found to be 13.12 ± 1.27. The fit of the observed data to the calculated segregation for 13.12 percent recombination is very good. A linkage of the factor pairs for non-intermedium versus fertile intermedium (I^hi) and hoods versus awns (Kk) is indicated. These data verify the hypothesis that an allelic series exists for intermedium—that is, I, I^h, and i.

TABLE 10

Segregation in the F_2 generation for non-intermedium versus fertile intermedium and hoods versus awns in a Sublaxum×Mortoni cross.

ITEM	NUMBER OF PLANTS WITH CHARACTERS INDICATED					χ^2	P
	NON-INTERMEDIUM		FERTILE INTERMEDIUM		TOTAL		
	HOODS	AWNS	HOODS	AWNS			
Observed count	588	49	50	144	831		
Calc. 9:3:3:1 segregation	467.44	155.81	155.81	51.94	831	339.3392	V. small
Calc. 13.12 percent recombination	572.31	50.94	50.94	156.81	831	1.5678	0.6713

The data for the F_2 phenotypes and F_2 genotypes from the 9:3:3 classes in F_2 were combined for the calculation of linkage by use of the formulae suggested by IMMER (1934). The formula for the calculation of linkage intensities for F_2 genotypes as determined from the segregation for the 9:3:3 F_2 phenotypic classes is as follows:[4,5]

$$\frac{2e+f+g+k+m}{p}-\frac{f+g+2j+k+2l+m}{1-p}+\frac{2(j+k+l+m)p}{1-p^2}-\frac{2(h+i)(1-2p)}{1-2p+2p^2}-\frac{2(e+f+g+h+i)p}{2+p^2}=0.$$

The information in F_3 for n plants is:

$$\frac{4n(6-10p+5p^2-4p^3+20p^4+2p^5+2p^6)}{p(1-p)(1+p)^2(2+p^2)^2(1-2p+2p^2)}.$$

The recombination value for the combined F_2 phenotypes and genotypes was found to be 14.32 ± 0.61 percent. The observed data for the F_2 genotypes as determined from the F_3 segregation are given in table 11.

The F_3 data gave a good fit to the calculated ratio with 14.32 percent recombination, which indicates that the non-intermedium versus fertile intermedium (I^hi) and hoods versus awns (Kk) factor pairs are in linkage group IV.

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[4] Modification for 9:3:3 class worked out by O. H. COLEMAN, COLORADO EXPERIMENT STATION.

[5] Symbols used to designate the observed frequency of occurrence of individuals in various genotypes:

	AA	Aa	aa
BB	e	f	l
Bb	g	h i	m
bb	j	k	n

TABLE II

Fit of F_2 genotypes in a Mortoni×Sublaxum cross to a calculated ratio with 14.32 percent recombination.

ITEM	NUMBER OF PLANTS OF INDICATED GENOTYPE								TOTAL
	$iiKK$	$iiKk$	$iikk$	I^hiKK	I^hiKk	I^hikk	I^hI^hKK	I^hI^hKk	
Observed count	153	44	2	57	331	43	6	46	682
Calc. 14.32 percent recombination	153.30	51.24	4.28	51.25	315.16	51.24	4.28	51.25	682

$\chi^2=6.2335$ $n^1=8$ P=0.5139

DISCUSSION OF RESULTS

The results of this study indicate that partially fertile intermediates obtained in the F_1 generation from 2-row and 6-row barley crosses are heterozygous for the non-6-row versus 6-row (Vv) factor pair and homozygous dominant for infertile intermedium (II). The complete lack of lateral spikelet fertility found in F_1 plants apparently results when the non-6-row condition (VV or Vv) is present with the infertile intermedium versus non-intermedium factor pair in the heterozygous condition (Ii).

Some varieties of barley classified as *Hordeum intermedium* have partial fertility of the lateral spikelets that breeds true. This was found to be true of Mortoni (C.I. 2210). The results of this investigation indicate Mortoni to be a fertile intermedium (VVI^hI^h) barley with 10 to 50 percent of the lateral spikelets generally fertile. The data obtained indicate that partial lateral spikelet fertility in Mortoni is due to another allele of the infertile intermedium versus non-intermedium (Ii) factor pair which has been designated as fertile intermedium (I^hI^h). The allelic series for intermedium has been established as I, I^h, and i. These three intermedium conditions (II, I^hI^h, and ii) were tested in crosses of parents that carry these factors in all possible combinations. A monohybrid segregation was obtained in each case, a condition necessary for multiple alleles. Non-fertility appeared to be dominant over fertility in every instance. The intermedium allelic series, together with the expected classes in crosses between 6-rowed and 2-rowed barley varieties, in the F_3 generation, may be summarized as follows:

While a single factor appeared to explain the fertility condition found in Mortoni, it was also observed that environmental conditions influence fertility to some extent. In crosses of Mortoni with some 6-rowed varieties, it was also evident that minor modifying factors possibly influence fertility of the lateral spikelets. Fertility of the lateral spikelets was more evident in space-planted F_2 rows than in drilled F_3 rows. Some plants genetically fertile failed to develop fertility in thick stands in the drilled rows. In studies of the intermedium series, it is recommended that the selfed F_2

CLASS	PHENOTYPIC CLASSES	F_2 GENOTYPES					
		Ii		II^h		I^hi	
				(From F_3 Segregation)			
1.	6-rowed*	$vvII$		$vvII$		vvI^hI^h	
		$vvIi$	4	vvI^hI	4	vvI^hi	4
		$vvii$		vvI^hI^h		$vvii$	
2.	6-rowed, intermediates, intermediums						
	(a) Fertile intermediums	—		VvI^hI^h		VvI^hI^h	2‡
	(b) Infertile intermediums	$VvII$	2	$VvII$	2	—	
	(c) Fertile and infertile intermediums	—		$VvII^h$	4	—	
3.	6-rowed, intermediates, intermediums, 2-rowed†						
	(a) Fertile intermediums	—		—		VvI^hi	4‡
	(b) Infertile intermediums	$VvIi$	4	—		—	
4.	6-rowed, intermediates, 2-rowed	$Vvii$	2	—		$Vvii$	2‡
5.	Intermediums						
	(a) Fertile intermediums	—		VVI^hI^h	1	VVI^hI^h	1
	(b) Infertile intermediums	$VVII$	1	$VVII$	1	—	
	(c) Fertile and infertile intermediums	—		VVI^hI	2	—	
6.	Intermediums and 2-rowed						
	(a) Fertile intermediums	—		—		VVI^hi	2
	(b) Infertile intermediums	$VVIi$	2	—		—	
7.	2-rowed	$VVii$	1	—		$VVii$	1

* The 6-row (*vv*) factor is epistatic to the intermedium alleles (I, I^h, and i). These genotypes are never observed.

† Two-rowed is considered here as *VVii*.

‡ Segregation not actually observed.

plants of the fertile intermedium class be space-planted in the F_3 generation to permit the most favorable environmental conditions for the development of fertility of the lateral spikelets. This is particularly desirable for crosses like Mortoni × Nigrinudum that involve segregation of the infertile versus fertile intermedium (II^h).factor pair. In this cross it was difficult to distinguish between the homozygous fertile intermedium (I^hI^h) rows and those heterozygous for the infertile and fertile condition (II^h).

The non-intermedium versus fertile intermedium (I^hi) factor pair appeared to be linked with that for hoods versus awns (*Kk*) located in group IV with a recombination value of 14.32 ±0.61 percent as determined from the combined F_2 phenotypes and genotypes. Such a linkage would be expected on the hypothesis of an allelic series for intermedium.

From the evidence available, it appears that there has been a change in the use of the term intermedium from its original form. HARLAN and HAYES

(1920) indicated that their homozygous intermedium barley, Haxtoni, designated by them as *aaBB*, had lateral spikelet fertility that averaged from 17.8 to 54.6 percent in different F_3 progeny lines. It seems reasonable to conclude that this is the intermedium described by students of barley classification. The intermedium factor (I^hI^h) defined in this paper appears to be similar to the *BB* factor reported by HARLAN and HAYES (1920). The fertile intermedium condition in Mortoni (VVI^hI^h) is probably identical with that described for the homozygous intermedium, Haxtoni. Homozygous fertile segregates were obtained in the F_3 generation for various crosses of Mortoni with both 2-rowed and 6-rowed varieties. The establishment of an allelic series for intermedium (I, I^h, and i) removes the confusion that has prevailed in the interpretation of the various intermedium conditions.

SUMMARY

A study was made to determine the inheritance of fertility in the lateral spikelets of the Mortoni variety of barley classified as *H. intermedium.*

The fertile intermedium condition found in the F_1 generation in crosses between some 2-row and 6-row barleys is due to the genetic constitution *VvII.*

Homozygous partial lateral spikelet fertility found in the Mortoni variety appeared to be due to a fertility allele of the infertile intermedium versus non-intermedium (Ii) factor pair. The allelic series for intermedium appears to be I, I^h, and i, with infertility dominant over fertility.

The non-intermedium versus fertile intermedium (I^hi) factor pair, from the combined F_2 and F_3 data, was found to be linked with that for hoods versus awns (Kk) with 14.32 ± 0.61 percent recombination. Hoods versus awns (Kk) is known to be located in group IV. The non-intermedium versus fertile intermedium (I^hi) factor pair was found to be inherited independently of factors known to be located in groups I, II, III, V, and VI. It was not tested with factors in group VII.

A method of testing barley varieties for intermedium constitution is suggested.

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