A CYTOGENETICAL ANALYSIS OF SOME INDUCED ERECTOIDES MUTATIONS IN MONTCALM BARLEY

A Thesis Submitted to
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by

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ABSTRACT

Eight erectoid mutations were selected from an irradiation programme in Montcalm barley. Crosses were made amongst the erectoides, and the F_1's were examined cytologically. One of the erectoides was found to be associated with a translocation which involved chromosomes a and d. All the F_1 plants had lax heads. The F_2 of crosses between Montcalm and erectoides segregated in a 3:1 ratio lax:dense. The F_2 of crosses between different erectoides segregated in a 9:6:1 ratio lax:dense:very dense. Thus erectoidy is due to simply inherited, recessive genes at different loci. Four loci have been definitely established, but it is quite possible that each of the eight erectoides is governed by a gene at a different locus. More crosses are being investigated to test this. Two lines from one erectoid gave a significantly higher yield than Montcalm. Only one erectoid gave a lower yield. Further tests for agronomic adaptation will be made.

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I INTRODUCTION

Interest in induced mutation work in agricultural plants has greatly increased in recent years, and the mutagenic effect of irradiation is being studied in a wide variety of plants. It now seems that a certain amount of control of the mutation process is possible (1), and thus studies of mutations will take an increasingly important role in plant breeding.

As a result of reports from Sweden that beneficial mutations could be induced in barley at will by irradiation treatment, an induced mutation programme was initiated by Shebeski and Lawrence in 1950 (18), in Montcalm, the leading malting barley of Western Canada. Amongst the wide variety of mutants obtained were eight erectoids. These are viable morphological mutants characterised by compact heads and stiff straw, and with potentially good agronomic qualities. This report is concerned with the cytological, genetical, and agronomic analyses of these erectoides.

The chief objectives of this study were as follows:

1) To search for any major cytological disturbances in the erectoides caused by the X-ray treatment.
2) To compare the morphology of the erectoides with Montcalm.
3) To study the inheritance of the erectoides by means of

F_1 and F_2 analyses of progeny from crosses between the mutants and Montcalm, and between the different mutants.

4) To make preliminary agronomic tests of the erectoides by means of a yield trial.

II LITERATURE REVIEW

Induced mutation work in agricultural plants was initiated by Nilsson-Ehle and Gustafsson in 1928 in the hope of improving agricultural varieties (2,3,4). Until recently most of the work has been carried out in Sweden at the Swedish Seed Association in Svalöf.

The most extensively studied plant, with regard to induced mutations, is barley. Many different viable mutations have been produced. One of the commonest viable morphological mutants is the dense-headed type known as erectoides.

Barley erectoides and dense-headed mutants have been reported by a number of workers (2,3,5,7,8,9,10,12,13,14,15,16,17,18,20,22). About 100 such mutants have been reported from Svalöf (8, *), 65 of which have been more or less analysed. The Swedish erectoid material, all from two-row barley varieties, is described in detail by Gustafsson (2). The different mutants vary considerably in the compactness of the ear. The character is associated with pronounced pleiotropy, which is shown by differences in yield, straw strength and length, 1,000 kernel weight, and other more complex characters.

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*Personal communications with Hagberg.

Genetical studies of these erectoides are reported by Hagberg _et al_. (9). To date mutations at nineteen different loci have been found to influence ear density.*

The symbol "ert" was suggested to denote the erectoid factor (11). This is followed by a letter for the particular ert locus, and a number which is the original number given to the erectoid on discovery. These letters are in no way related to the letters that Dr. Burnham of Minnesota has assigned to the different chromosomes in his translocation stocks (8). A series of mutations at the "a" locus as described by Hagberg (7) illustrates this system, e.g., ert a 6; ert a 11; ert a 13; ert a 29; or at the "b" locus: ert b 2; ert b 4; ert b 5, etc. Eleven erectoides have been found for the "a" locus which appears to be more mutable than the others.

The question arises as to whether the mutations at a single locus are identical, or whether they represent different alleles. Hagberg _et al_. (9) studied this by measuring the ear density. They found that different ert mutations at one locus produced significantly different head densities, and thus concluded that they were allelic rather than identical. To date no two mutations have proven to be

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*Personal communications with Hagberg.

absolutely identical, except possibly ert b 2, ert b 4, and ert b 5 (7). In all cases so far studied the normal allele is dominant or partially dominant to the ert factor (8).

Linkage studies with some ert mutations in Gull (Golden) barley (8) have shown that loci b and d are not linked inter se, or with any other ert locus in this variety. Further linkage studies which are still in progress will make it possible to place the different loci on genetical chromosome maps.

Cytological studies have shown that ert c 1 and ert d 7 are closely associated with reciprocal translocations (Tr_1 and Tr_7). Here the "mutation" responsible for erectoidy may be due to either a chemical change in the gene caused by the disturbance of the chromatin, or else an alteration in the gene environment---i.e., a position effect (21). However, as Hagberg (7) pointed out, there are other ert mutations at the d locus which are not associated with a translocation, therefore mutations at this locus cannot be solely due to a position effect. Other ert mutations appeared with translocations, but in these cases the two were found to be inherited separately. The translocations are readily observable, as they cause partial sterility in the F_1, and their presence can be confirmed by a cytological study of the pollen mother cells.

Most of the cytological studies have been reported by Hagberg (8), Hagberg and Tjio (10,11), and Tjio and Hagberg (21). They attempted to locate the chromosomes involved in the erectoid translocations. They established the standard karyotype in the normal type Gull, and compared this with that of the homozygous translocation stocks. Where chromosomes of the latter deviate from the standard this indicates that these chromosomes are involved in the translocation. For example, they concluded that Tr_7 probably involves chromosomes b and a of the standard karyotype.

Further work on the location of translocations has been done by Hagberg (8). He used known translocation stocks, and his results agree with those obtained by the cytological methods described above. Once the cytological position of the translocations is known it will be possible to map the already well known linkage groups cytologically.

The most important agronomic character associated with all erectoid mutations is increased straw-stiffness. In addition, some mutants show increased earliness as compared with the mother lines (2). Especially noticeable is ert 16 which is up to 7 days earlier than Maja. A few erectoides equal or surpass the mother lines in yield, under some conditions, but extensive trials have not shown any one mutant to be sufficiently superior to warrant its being named as a commercial variety.

Erectoides also form useful material for theoretical studies, such as those published by Hagberg on pleiotropism and heterosis (7), and by Gustafsson (4) on theories of species formation.

III MATERIALS AND METHODS

Montcalm and the eight erectoides mutants shown in fig. 1 were used in this study. The erectoides result from mutation work initiated at Saskatoon and continued at both the Universities of Saskatchewan and Alberta (13,14,18).

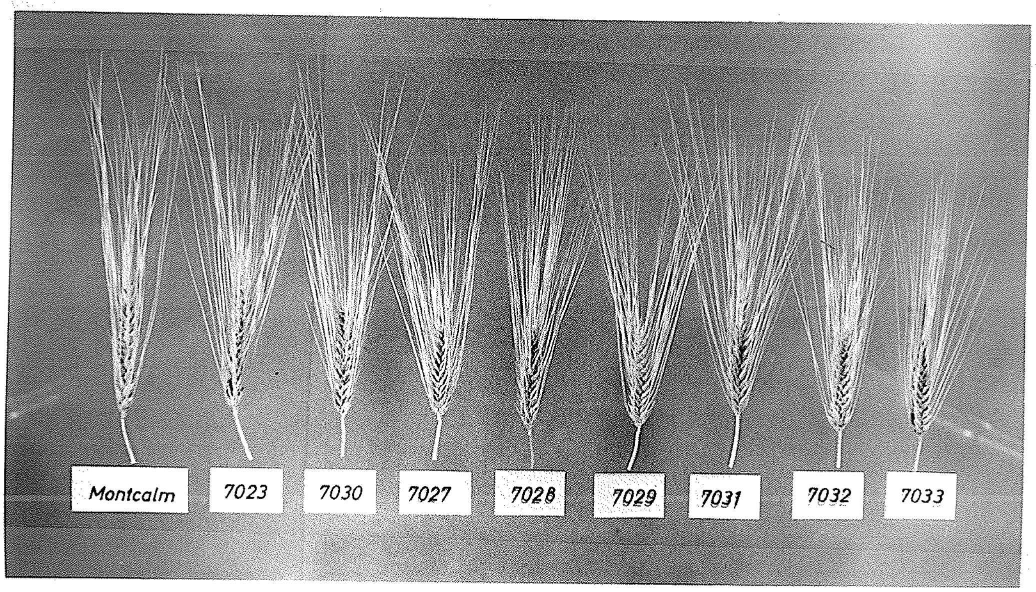


Fig. 1. Typical heads of Montcalm barley and the eight erectoides in order of density.

Montcalm is a six-rowed, smooth-awned barley with nodding heads. The erectoid character is due to shortened internodes of the head and often the culm, giving a shorter straw than usual. The erectoides are distinguished by their compact heads, often with projecting kernels and awns, especially at the base. There is also a tendency for the lateral florets to form two distinct vertical rows on the spike, so that the six rows are clearly delimited right to the tip. Table I lists the eight erectoides with the source of irradiation, and remarks on some more obvious characteristics.

Table I: The erectoides used in the study, with source of irradiation and notes on some characteristics.

Plant no. in crossing block	Saskatoon number	Source of irradiation	Remarks
7023	5203	P^{32}	Quite lax, difficult to distinguish from Montcalm
7027	5301	Betatron	
7028	5302	X-ray	High degree of sterility
7029	5303	X-ray	
7030	5304	X-ray	
7031	5305	Co^{60}	Showed sterility at the tip of the spike. Entirely erect.
7032		X-ray	
7033	5220	Radium-beryllium	Very dense and very short strawed. Entirely erect. Showed much sterility in field

A programme of diallel crosses was planned in the summer of 1954. Crosses were made between normal Montcalm and the eight erectoides and also amongst the different erectoides. Seed was obtained from 21 of the possible total of 36 crosses. Line 7028 was rather sterile, and produced only two seeds in the cross with Montcalm. Better results were obtained when it was used as a <u>female</u> parent in crosses with other erectoides in the fall of 1955. This suggests that the pollen is sterile.

The parental identity was maintained throughout the experiment. The crosses with the amount of seed obtained are shown in Table II. The methods and results are discussed under four headings.

Table II: Crosses made between erectoides and Montcalm and number of F_1 seeds obtained.

	Montcalm	7023	7027	7028	7029	7030	7031	7032	7033
7033	-	13	8	-	5	3	-	2	
7032	14	A5 B18	10	-	11	3	-		
7031	14	-	11	-	15	8			
7030	A14 B7	-	-	-	15				
7029	7	-	-	-					
7028	2	-	-						
7027	15	5							
7023	10								

(1) Cytology

The F_1's were grown in the greenhouse in the fall along with the parents. Young heads were collected and stored in Carnoy's 6:3:1 for cytological examination. They were taken from the first tillers of three F_1 plants where possible, and from three plants of each parent. Meiosis was studied in aceto-carmine squash preparations. The method is described in detail by Luther Smith (19). The metaphase plates of the F_1's were examined for major cytological disturbances, especially any rings of chromosomes, indicating heterozygosity for a reciprocal translocation. The parents were also checked.

(2) Morphology

The only morphological character studied in detail was the head density. As an index of this, the length in millimetres of ten internodes was measured from the fifth node in the ear to the fifteenth (8). This index is actually a measurement of laxity, as high values indicate a lax ear, and low values a dense one. The averages of measurements of ten heads from the F_1 of each cross, and also from twenty heads of the parents from both the greenhouse and the field were taken where possible, and standard errors were determined.

The F_2 seed from each cross was then bulked separately and stored until the spring. The seed from the parent lines was also bulked and stored.

(3) Genetics

In the spring of 1955 the F_2 seed was space sown (2 inches between seeds) in the field with a V-belt seeder in 12 foot rows, 1 foot apart, and with parental check rows beside each F_2 population. The amount of F_2 seed varied considerably; there being from one to seven rows per cross.

The material was ready for harvesting in early August. The F_2 plants of each cross were pulled separately, and then grouped on the basis of head density, using the parents for comparison. Within each cross the number of plants per group was recorded, and deviations from the expected ratio were measured by a standard chi-square test.

(4) Yield trial

In the fall of 1954 single plant selections were made from the erectoides listed earlier. Seed of these was increased during the winter in California (by the courtesy of the Canada Department of Agriculture). In order to check for heterogeneity within a given erectoid, in some cases more than one line was used to represent the erectoid in the yield test. Montcalm and U.M. 570, an unnamed variety developed at the University of Manitoba, were used as checks. Montcalm is a weak-strawed, high-yielding variety. U.M. 570 was included because it has stronger straw than most commercial varieties. The following lines were tested:-

Checks:- Montcalm and U.M. 570.

Erectoides:- 7023; 7027 lines A and B; 7029; 7030 lines A, B and C; 7031 lines A and B; 7032; 7033.

The yield test was set up in a six replicate randomized block design. Each replicate contained 13 plots. The individual plots of the yield trial consisted of four 12 foot rows, spaced 1 foot apart. The trial was seeded with a power-seeder at a rate of one gram of seed per foot of row. The erectoid 7023 was used for guard rows. Notes were taken on the degree of lodging and on days to heading. The central two rows of each plot were then harvested by hand, leaving 1 foot at either end. The grain was threshed and weighed, and the results were analysed.

IV EXPERIMENTAL RESULTS

(1) Cytological analysis of F_1

In each of the crosses examined cytologically the meiosis configuration showed either normal pairing with seven bivalents (Fig. 2 and 3), or else five bivalents and a ring of four chromosomes (5 II and 1 IV) (Fig. 4). The results are shown in Table III.

Table III: Meiosis configurations in F_1 plants from crosses between erectoides.

	Mont-calm	7023	7027	7028	7029	7030	7031	7032	7033
7033	-	7 II	7 II	-	7 II	7 II	-	-	
7032	7 II	-	7 II	-	7 II	7 II	-		
7031	5 II 1 IV	-	5 II 1 IV	-	5 II 1 IV	5 II 1 IV			
7030	7 II	-	-	-	7 II				
7029	7 II	-	-	-					
7028	-	-	-						
7027	7 II	-							
7023	7 II								

All four crosses involving 7031 showed five bivalents and a ring of four chromosomes at metaphase. As at least

Fig. 2. Late diakinesis in a normal pollen mother cell with seven bivalents. (c.x 1,200)

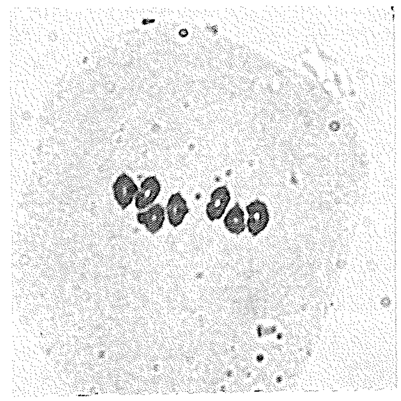


Fig. 3. Seven bivalents on the metaphase plate. (c.x 1,000)

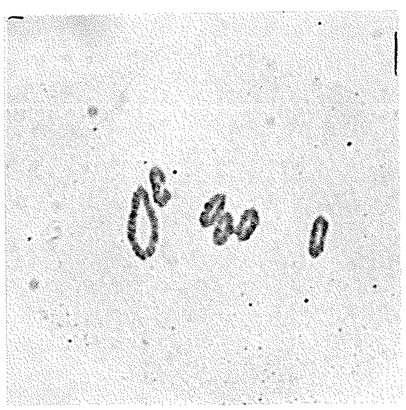


Fig. 4. One ring of four and five bivalents at metaphase from F_1 of cross between 7031 and normal line. (c.x 1,000)

Fig. 5. One ring of four and five bivalents at late diakinesis, showing some pairing in the arms of the ring. (c.x 1,200)

three heads were examined from each cross this is a strong indication that the parent 7031, which is homozygous for the erectoid character is also homozygous for the translocation, and that the translocation is associated with the ert locus. The translocation involved a fairly large part of the chromosomes, as the quadrivalent always formed a closed ring, and no open chains were found. A few clear slides of diakinesis showed some pairing in the arms of the ring (Fig. 5), which confirmed this assumption.

Micro-nuclei were found in a few of the quartets, indicating that one chromosome of the ring had lagged at anaphase, and had been excluded at the second division to form a micro-nucleus.

All the crosses in which 7029 was a parent, had a higher than average number of open bivalents. There may have been some minor chromosomal aberration associated with this erectoid, which reduced the homology between the two chromosomes of the pair, causing formation of open bivalents. Number 7027 may also have a minor chromosomal aberration.

Identification of the translocation 7031

The chromosomes involved in 7031 were identified by examination of F_1 meiosis configurations from crosses between 7031 and tester translocation stocks. The testers are homozygous translocation stocks in Mars barley which were obtained from Dr. Burnham, and a series of these, which included translocations involving each chromosome, was crossed with the erectoid translocation stock 7031 in the summer of 1955 in the field. Seed was obtained from only four of the ten crosses. The F_1 plants were grown in the greenhouse in the fall, under artificial lighting and young heads were collected for cytological examination. Fortunately these four hybrids proved sufficient to identify the chromosomes involved in the translocation 7031. The results of the analysis are given in Table IV.

Table IV: Meiosis configurations in F_1 hybrids from crosses between 7031 and Burnham's tester stocks.

Tester parent	Chromosomes in tester translocation	Cytological configuration	Chromosomes in 7031 translocation	No. of F_1 plants examined
C1420	e - f	2 IV 3 II	not e or f	2
C1315	b - g	2 IV 3 II	not b or g	3
C1363	b - d	1 VI 4 II	either b or d	1
C1384	a - b	1 VI 4 II	either a or b	2

The translocation does not involve chromosomes b, e, f or g. As chromosome b is excluded it must therefore involve a and d.

(2) Morphological analysis

The different erectoides showed variation in head density which was readily observed, although it was impossible to group the types on the basis of visual observation alone. Measurements were therefore made of internode length. Ten primary tillers of field-grown plants were used from each erectoid.

Similar measurements had also been made on material grown in the greenhouse, but these were found to vary rather widely from the field measurements, probably due to the variable light conditions in the greenhouse, and the fact that many secondary tillers were measured, as primary tillers had been taken for cytological study. The coefficient of variation was higher in the greenhouse material, being over 2%, and under 1% in all field-grown material. Differences in head density between the various erectoides and Montcalm were determined by the unpaired comparison "t" test. Results of measurements are presented in Table V, where the erectoides are grouped according to head density.

Montcalm and 7023 gave a "t" value which was highly significant at the 1% level. Both these are, however, far more lax than the other erectoides. When first selected 7023 was considered a physiologically stiff-strawed mutant, but these measurements showed that it could be included with the erectoides.

There was no significant difference between 7027, 7028, 7031, and 7029; neither was there a significant difference between 7032 and 7033.

Table V: Analysis of ten measurements of ten internodes of erectoides and Montcalm grown in the field, and their grouping.

Plant number	Average length of ten internodes in mm.	Group
Montcalm	37.7 ± .21	
7023	34.9 ± .15	1
7030	28.4 ± .15	2
7027	25.7 ± .16	3
7028	25.5 ± .13	3
7031	25.0 ± .19	3
7029	24.9 ± .14	3
7032	23.2 ± .19	4
7033	23.0 ± .11	4

Four groups are thus distinguishable on the basis of these head measurements. However, it has already been mentioned that head density varies considerably with conditions, and therefore these values would not suffice for the recognition of the different erectoides. If there is a characteristic value for head density in the Montcalm erectoides, as Hagberg (8) has shown for the Swedish two-row varieties, it can only be obtained by taking an average of values from plants grown under a wide variety of conditions.

(3) Genetical analysis

F_1 analysis

Measurements of head density were used to compare the phenotypes of F_1 with those of the parents. The head measurements of the F_1's were compared with those of the check parents grown in the greenhouse at the same time. Although these measurements are less reliable than the field ones, it was considered to be a sounder basis for comparison to take plants grown under the same conditions, than to compare the greenhouse-grown F_1 with the field-grown parents.

Where possible ten well-formed heads from different plants of the F_1's were taken for measurement and 20 from the erectoides and Montcalm. Where there were under ten plants the largest heads were chosen from tillers of a lower order. This is undoubtedly a further cause for less reliable results. Because of inconsistencies in the greenhouse material these results can only give a general comparison. However they are in agreement with the conclusions deduced from the F_2 ratios, and are included here for interest. The results are shown in Table VI, and they are also summarised graphically in the form of a histogram (Fig. 6). To facilitate discussion the results have been divided into two sections: the crosses between the mutations and normal, and the crosses between the different mutations.

Segregation for types with lax heads was found in the progeny of 7032 when it was grown as a check with the F_2 of the cross 7032 x 7030. The F_2 ratio of this cross gave a poor fit to expected (chi-square of 0.05-0.02), and it was assumed that the segregation in this 7032 parent was due to heterozygosity rather than later contamination of the seed. The results of this cross were therefore discarded.

I. Crosses between erectoides and Montcalm: In all crosses between an erectoid and Montcalm the F_1 head was as lax, or nearly as lax, as Montcalm, showing that the normal allele is at least partially dominant to the mutated allele. The degree of dominance appears to vary with the different erectoides. Typical heads of the parents and F_1, from the cross 7031 x Montcalm are shown in fig. 7. This illustrates the lax and semi-sterile F_1, which is heterozygous for the translocation.

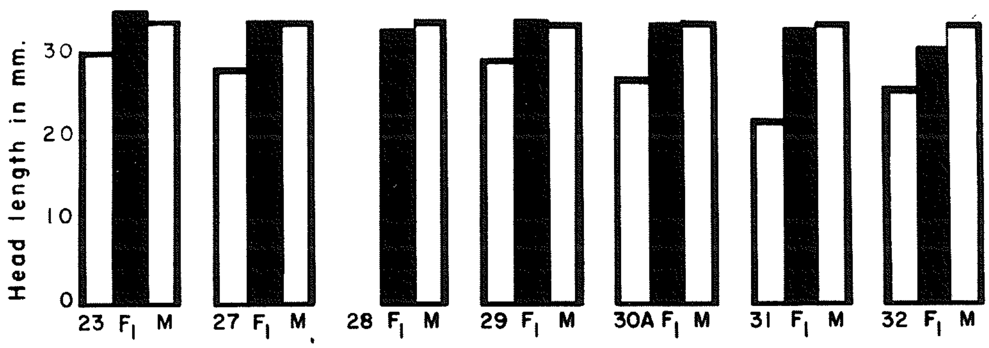
Comparison by means of a "t" test showed that there was little or no significant difference between the head density of Montcalm and of the F_1 in these crosses.

Table VI: Average of measurements of ten internodes of erectoides and Montcalm, and F_1 hybrids from greenhouse grown material.

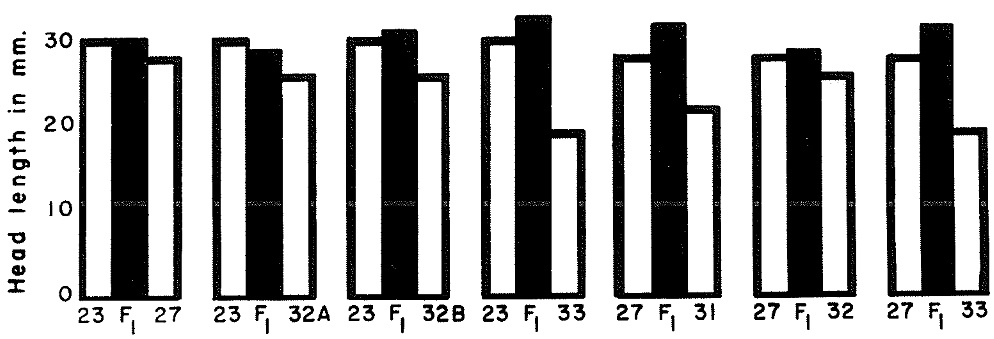
Parent 1	Head length in mm.	Parent 2	Head length in mm.	Head length of hybrid in mm.
I 7023	30.9 ± .64	Montcalm	34.4 ± .41	35.9 ± .81
7027	28.7 ± .81	"	34.4 ± .41	34.4 ± .24
7028	-	"	34.4 ± .41	33.4 ± 1.01
7029	29.8 ± .79	"	34.4 ± .41	34.6 ± .18
7030 A	27.6 ± .78	"	34.4 ± .41	34.2 ± .28
7030 B	" "	"	34.4 ± .41	31.8 ± .20
7031	22.7 ± .64	"	34.4 ± .41	33.8 ± .14
7032	26.5 ± 1.15	"	34.4 ± .41	31.4 ± .26
II 7023	30.9 ± .64	7027	28.7 ± .81	30.9 ± .37*
7023	30.9 ± .64	7032 A	26.5 ± 1.15	29.7 ± .29*
7023	30.9 ± .64	7032 B	26.5 ± 1.15	31.8 ± .14*
7023	30.9 ± .64	7033	19.8 ± .43	33.2 ± .14
7027	28.7 ± .81	7031	22.7 ± .64	32.5 ± .20
7027	28.7 ± .81	7032	26.5 ± 1.15	29.4 ± .16*
7027	28.7 ± .81	7033	19.8 ± .43	32.1 ± .20
7029	29.8 ± .79	7030	27.6 ± .78	31.8 ± .26*
7029	29.8 ± .79	7031	22.7 ± .64	32.5 ± .15
7029	29.8 ± .79	7032	26.5 ± 1.15	30.9 ± .23*
7029	29.8 ± .79	7033	19.8 ± .43	31.1 ± .15*
7030	27.6 ± .78	7031	22.7 ± .64	30.9 ± .17
7030	27.6 ± .78	7033	19.8 ± .43	32.2 ± .17
7032	26.5 ± 1.15	7033	19.8 ± .43	30.2 ± .28

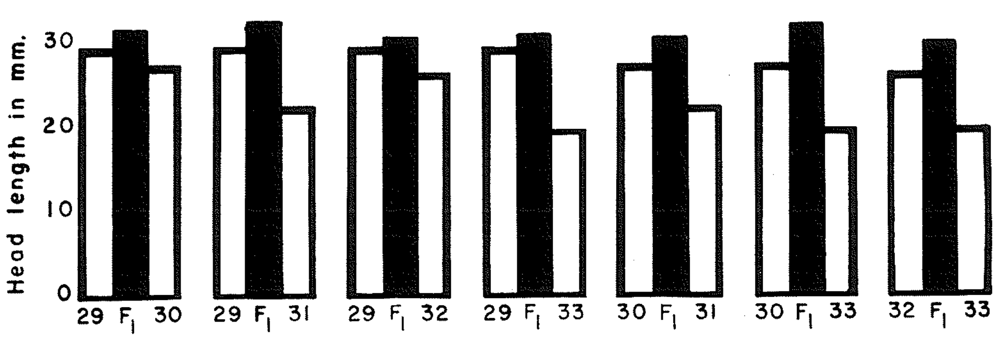
*F_1 not significantly different from the more lax parent.

FIGURE 6. HISTOGRAMS ILLUSTRATING THE RELATIONSHIP OF HEAD DENSITIES OF F_1'S AND PARENTS.



I Crosses involving erectoides and Montcalm.





II Crosses involving different erectoides.

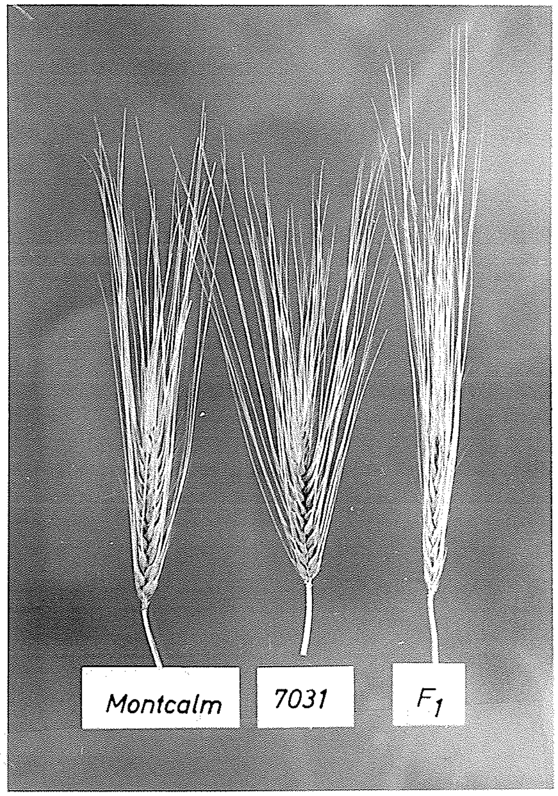


Fig. 7. Typical heads of Montcalm, 7031, and the F_1 of the cross between them.

II. Crosses between different erectoides: Measurements confirmed the observation that heads of F_1 plants were more lax than either parent, although a statistical analysis showed that in seven out of the fourteen crosses, the F_1 was not significantly different from the more lax parent. The general tendency toward laxity in the F_1 indicated that two loci were involved in crosses between two erectoides. F_2

segregation ratios supported this. In these crosses the F_1 heads are more dense than in those involving Montcalm, averaging about 30 mm. instead of about 34 mm. The two erectoid loci must have an additive effect, reducing still further the partial dominance of the normal allele.

F_2 analysis

I. Crosses between erectoides and Montcalm: (a) The lax F_1 suggested that the normal type is dominant to the mutant gene controlling the erectoid character. The F_2 was therefore expected to segregate in a 3:1 ratio of lax to dense. The observed ratios were compared with the expected by chi-square, and the P value was high for all crosses. As shown in Table VII cross 7028 x Montcalm was an exception ($P = .05 - .02$), but here the population was very small.

(b) In the cross 7031 x Montcalm, three classes were distinguished, as plants heterozygous for the translocation were partially sterile. The three classes were:---1 homozygous lax (quite fertile): 2 heterozygous lax (partially sterile): 1 homozygous dense (quite fertile). Partial sterility was only found in the lax group. This indicates a close linkage between the translocation and the gene for erectoidy.

There is a small but fairly constant deficiency in the class of homozygous recessives. This agrees with reports from the Swedish workers (4,5).

Table VII: Chi-square analysis of F_2 ratios of crosses between erectoides and Montcalm on the basis of an expected 3:1 ratio.

Erectoid parent	F_2 Lax observed	Lax expected	Dense observed	Dense expected	X^2	P at .05
7023	194	181.5	48	60.5	1.12	.30-.20
7027	313	306.75	96	102.25	0.51	.50-.30
7028	41	34.5	5	11.5	4.90	.05-.02
7029	290	291.75	99	97.25	0.04	.98-.95
7030 A	337	328.5	101	109.5	0.88	.50-.30
7030 B	153	150.0	47	50.0	0.24	.70-.50
7032	326	321.0	102	107.0	0.31	.70-.50

Analysis of cross 7031 x Montcalm on the basis of an expected 1:2:1 ratio.

Erectoid parent	Fertile lax obs.	Fertile lax exp.	Semi-sterile lax obs.	Semi-sterile lax exp.	Fertile dense obs.	Fertile dense exp.	X^2	P at .05
7031	17	14.75	28	29.5	14	14.75	0.46	.80-.70

II. Crosses between different erectoides: (a) The lax F_1 suggested that the two recessive genes for erectoidy were at two different loci. The laxity was due to the two normal alleles at these loci. The expected F_2 ratio was therefore of the 9:7 type, which could be broken down further, depending on the ability to distinguish the different classes.

In all crosses at least three classes were recognised:-

1) lax: heads indistinguishable from Montcalm.

2) dense: heads similar to either parent.

3) very dense: heads considerably more dense than either parent. These are known as the zeochriton type.

The results are given in Table VIII, and figure 8 shows typical heads of parents and F_2 classes from one of these crosses.

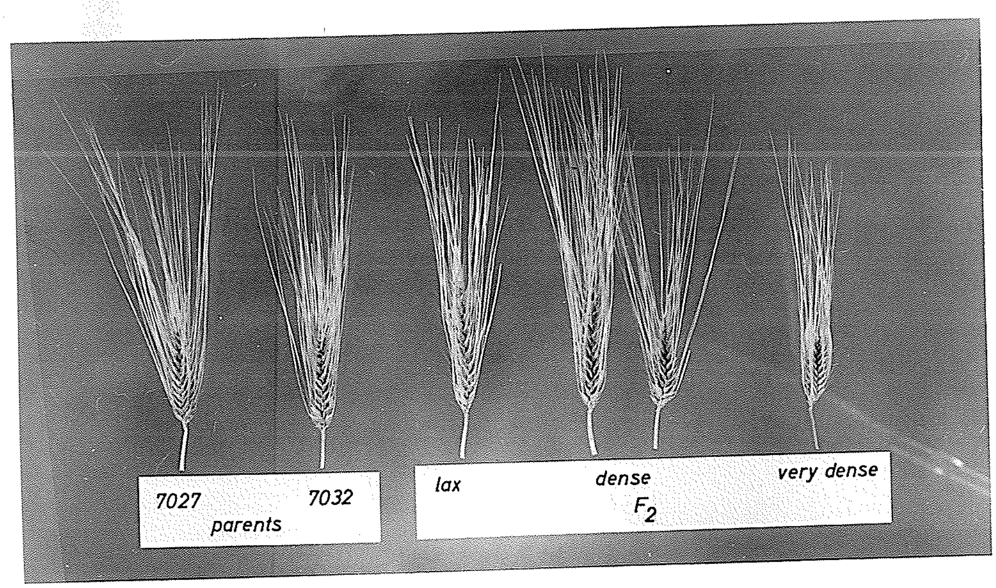


Fig. 8. Typical heads of 7027, 7032, and the F_2 classes from the cross between these.

Table VIII: Chi-square analysis of F_2 ratios of crosses between different erectoides on the basis of an expected 9:6:1 ratio.

	F_2							
	Lax		Dense		Very dense			
Parents	obs.	exp.	obs.	exp.	obs.	exp.	X^2	P at .05
7023 x 7027	50	46.7	33	31.1	0	5.2	5.55	.10-.05
7023 x 7032	89	91.08	66	60.12	7	10.12	1.75	.50-.30
7027 x 7031	144	136.17	87	90.78	11	15.13	1.73	.50-.30
7027 x 7032	226	208.6	121	139.2	24	23.2	3.82	.20-.10
7027 x 7033	240	231.75	151	154.5	21	25.75	1.28	.70-.50
7029 x 7032	262	237.6	133	158.4	27	26.4	6.59	.05-.02
7029 x 7033	180	174.6	115	116.4	15	19.4	1.18	.70-.50
7030 x 7029	152	135.9	76	90.6	13	15.1	3.55	.20-.10
7030 x 7031	33	36.9	29	24.6	4	4.1	1.20	.70-.50
7031 x 7029	47	42.3	23	28.2	5	4.7	1.50	.50-.30
7032 x 7023	209	211.5	149	141.0	18	23.5	1.77	.50-.30
7032 x 7033	75	69.3	43	46.2	5	7.7	1.64	.50-.30
7033 x 7023	150	143.1	84	95.4	20	15.9	2.75	.30-.20
7033 x 7030	44	38.7	23	25.8	2	4.3	2.14	.50-.30

The only cross with a low P value was 7029 x 7032 (P = .05-.02), but the presence of the expected number in class 3 (double homozygous recessives, aabb) indicated that here, as in other crosses, two loci were involved. The poor fit was not due to linkage between the two loci as the second class (parental types) was deficient. Both parents segregated as expected in other crosses.

(b) In the three crosses between 7031 and other erectoides five classes were distinguished, on the basis of head density and semi-sterility.

The ability to distinguish the semi-sterile plants was tested by dividing the F_2's into two groups: fertiles and semi-steriles. The size of these two groups was near to the expected 1:1 ratio as shown by the chi-square test.

On the basis of semi-sterility therefore, the two major groups of the 9:6:1 ratio were further sub-divided to give a total of five classes, viz.,

9 lax	(3 fertile ((6 semi-sterile	6 medium dense	(4 fertile ((2 semi- (sterile	1 very dense - fertile

Thus using a 3:6:4:2:1 ratio, the chi-square test gives the following probabilities at the 5% level.

7027 x 7031	P =	.30-.20
7030 x 7031	P =	.95-.90
7031 x 7029	P =	.95-.90

This means that all plants heterozygous for the erectoid gene brought in by 7031 were also semi-sterile or heterozygous for the reciprocal translocation. This is therefore a further indication that the erectoid character is associated with the breakage point of the translocation. It is probable that there is a very close or complete association between the translocation point and the locus for erectoidy; but this has not been irrevocably proved.

Discussion

According to the Swedish work there are three possibilities for the genetical relationships of these eight erectoids:-

1) Any erectoid in one morphological group may be the same as another in that group.
2) Any erectoid may be allelic to any other one, or to several, forming a multiple allelic series.
3) Each erectoid may be due to a mutation at a different locus. (Mutations at different loci may or may not differ phenotypically from each other.)

Results have been obtained from 13 of the possible 28 combinations of the eight erectoides. These 13 crosses all involve two different unlinked loci for the erectoid character. From these results four separate loci can be deduced. Table IX shows all the crosses which have been analysed.

Table IX: Crosses used in the analysis of the gene loci.

	Montcalm	7023	7027	7028	7029	7030	7031	7032	7033
7033		x	x		x	x		x	
7032	x	x	x		x				
7031	x		x		x	x			
7030	x				x				
7029	x								
7028	x								
7027	x	x							
7023	x								
Montcalm									

Examination of the table shows the following facts about the loci:-

1) Erts 29, 32 and 33 all differ from each other, giving loci "1", "2" and "3".
2) Erts 23 and 27 differ from each other, and both differ from 32 and 33. Either one could be allelic to ert 29, but not both. Therefore there must be one other locus involved---number "4".
3) Ert 30 differs from 29, 31 and 33, but may be allelic to ert 32.
4) Ert 31 differs from 27, 29 and 30.
5) Ert 28 may be allelic to any other ert.

These facts are summarised in Table X.

Table X: The possible loci involved in the eight erectoides, deduced from analysis of only 13 crosses.

Ert.	Loci 1	Loci 2	Loci 3	Loci 4	Other loci
7033	33				
7032		32			
7031	31?	31 or ? 30		31 or ? 30	31 or ? 30
7030					
7029			29		
7028	28?	28?	28?	28?	28?
7027			27 or ? 23	27 or ? 23	27 or ? 23
7023					

These four loci are definitely established. To complete the series of 28 possible combinations of the eight erectoides more crosses were made in the greenhouse in the fall of 1955. No results were available at the time of writing however.

(4) Yield trial

The mean yields in bushels per acre are shown in Table XI with other agronomic characters. The lines have been placed in decreasing order of yield. Montcalm headed 49 days after seeding, this is indicated as 0 on the table, and the number of days later than Montcalm is given for other lines. The degree of lodging is arbitrarily marked 1 - 4; 1 indicates no lodging at all, and 4 indicates severe lodging.

Table XI: Yield, heading and lodging of eleven selected erectoid lines compared with Montcalm and U.M. 570.

Lines	Mean yield in bu./acre	Heading: days after Montcalm	Lodging	bu./wt. lbs./bu.	1,000 kernel weight
7027A	48.9	0	3	43.0	25.0
7027B	47.0	0	4	44.3	27.0
7030B	46.3	1	2	45.8	27.5
7023	44.4	0	1	44.0	28.0
7030C	43.9	0	2	44.8	27.5
7031A	43.0	1	3	43.5	25.8
U.M. 570	42.8	0	2	43.5	24.5
7032	40.8	1	2	45.5	26.5
7031B	40.1	1	3	43.8	26.0
7030A	40.0	1	3	45.3	27.5
Montcalm	38.9	0	4	41.3	23.0
7029	35.4	4	1	47.8	33.5
7033	19.5	5-7	1	47.0	33.3

LSD = 7.6 bu./acre at 5% level
10.1 bu./acre at 1% level

The yields of both 7027A and B are significantly higher than Montcalm. The yield of 7029 is rather low, but it is not significantly lower than Montcalm. Line 7033 has a very low yield.

Montcalm and most of the erectoides headed about 49 days after seeding. Only the two lowest yielding types, 7029 and 7033 were considerably later than Montcalm.

Notes on lodging resistance were taken after a strong wind soon after heading, and also a week later, when there had been some recovery. Montcalm, 7027A and B, 7030A and 7031A and B, remained rather badly lodged throughout the ripening period. There was virtually no lodging in 7023, 7029 and 7033. The high resistance to lodging in 7023 is of particular interest as this is the most lax erectoid, originally selected on the basis of straw stiffness alone. It seems that straw stiffness is not necessarily correlated with head density.

Discussion

In this one year's yield trial both selections from erectoid 7027 had a considerably higher yield than Montcalm. The erratic and somewhat severe lodging may have masked any differential between 7027 and Montcalm in lodging resistance. They will be further tested for agronomic qualities along with other more promising lines. Lawrence (13) reported the results of a preliminary quality prediction test on some Montcalm erectoides which suggested that the erectoid may have a lower quality than Montcalm.

Between the two lines from 7027 and 7031, and the three from 7030 there is no significant difference in yield. But in 7030 two lines had an average yield close to Montcalm, and one was far lower. If this lower yield is consistent, it may indicate segregation for yield within the erectoid, perhaps due to other mutations at the time of irradiation.

Both 7029 and 7033 are late heading, very resistant to lodging, and low in yield. It would be interesting to make correlation studies on these characters.

V GENERAL DISCUSSION

These studies on the erectoides of Montcalm barley indicate that erectoidy in six row barleys is comparable in behaviour to that of the two row barley varieties.

Firstly, the erectoides show wide variation in head density and pleiotropic effects. Out of the eight studied there were at least four significantly different morphological head types. The erectoid habit was found to be simply inherited as a recessive gene. The character is controlled by genes at different loci, at least four having been found in Montcalm. The effect of these genes is additive, so that plants homozygous at two loci have very dense heads (7). It therefore seems that the name erectoid, which was assumed at the beginning of this study, is justified, in that these mutants behave genetically in a very similar way to the well known Swedish erectoides.

There have been many dense-headed mutants described in the past, especially in connection with linkage studies (15,16,17), and it is probable that these also are erectoides in the Swedish sense. It would be of great interest to collect seed of all known dense-headed types and examine their behaviour in crosses, to determine how many different loci are involved and also if there are some allelic series. Many theoretical studies would be possible on similar lines to the work being carried out by Hagberg *et al.* (8), and this would supplement their conclusions with data from six rowed varieties.

It is not known whether the loci discovered in this study are the same as any of the ert loci found by the Swedish workers. In order to test this it would be necessary to make intercrosses between representative erectoides from the 19 different Swedish ert loci and the erectoides described here. It would then be possible to designate a system of symbols to these erectoides so that the gene nomenclature could be correlated.

The only major cytological disturbance was found in line 7031, which contains a reciprocal translocation between chromosomes a and d. This appears to be closely associated with the ert locus, but not enough plants have been examined to be quite certain. This erectoid may be of use in helping to identify the exact position of the translocation in linkage studies.

Agronomic value

Only two of these erectoid mutations reduced the yield below that of the parent variety, and few were later than Montcalm. Otherwise all the characters yet tested showed an agronomic improvement or little significant change over Montcalm.

There appears to be an association between very dense head, resistance to lodging, lateness and low yield in 7029 and 7033. Presumably these only differ in two genes affecting head density. It would be interesting to investigate this further, especially as the agronomically desirable quality of high lodging resistance is here associated with a low yield, and in 7027 high yield is associated with a lower resistance to lodging.

Other relationships between different pleiotropic effects have not been sufficiently studied to draw any inferences. However, von Wettstein's findings (22) are of interest in this connection. He worked with an allelic series, and stated that every allele seemed to have an independent action on different organs.

Erectoid 7023, which was originally thought to be physiologically stiff-strawed has undergone fairly extensive yield trials, but was found not to be significantly better than Montcalm in yielding ability. However, the two lines of 7027 each yielded significantly more than Montcalm, and also well above U.M. 570 in this one year's test.

The tentative conclusion may be drawn, on the basis of only one year's trial, that the erectoides character is frequently associated with desirable agronomic qualities, one of the most important being increased straw-stiffness.

Although much genetic variation is still available to plant breeders through the classical methods of hybridization and selection, these results support the mounting body of evidence (6) in favour of using induced mutations in a breeding programme, either as an additional source of new gene material, or directly to improve crops --- in which case new varieties may be produced more quickly and cheaply.

D'Amato and Gustafsson (1) have shown that various chemical pretreatments can alter the proportion of different mutations. It thus appears likely that with further basic research, the direction of mutations will come more under the control of the geneticist. These authors also suggest that even without directing the mutation process, a methodical breeding programme could be set up to improve crops. For example, in barley the erectoides mutants are fairly common, and every tenth erectoid either equals or surpasses the mother strain. Thus a programme starting with large scale irradiation would rapidly establish a high yielding erectoides type, automatically possessing the required superior straw strength.

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