COMPARATIVE GENE ANALYSIS OF COMMON WHEAT AND ITS ANCESTRAL SPECIES. III. GLUME HAIRINESS[1]

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FOR the study of origin and differentiation of common wheat, a new method of "comparative gene analysis" has been proposed (TSUNEWAKI and KIHARA 1962). According to this method, gene analysis is carried out in common wheat and in parallel in its relatives against the same genetic background. From the results obtained, the origin of genes which are found in common wheat can be traced, and its coming into existence can be based on the origin of those genes. TSUNEWAKI and KIHARA (1962) and TSUNEWAKI (1966) carried out some investigations along this line on four characters of wheat, i.e., necrosis, waxiness, growth habit and awnedness. From these results TSUNEWAKI (1966) proposed that Northern Iran is the most probable birthplace of common wheat. In the present article, results of an investigation conducted on glume hairiness will be reported.

Inheritance of glume hairiness in common wheat has been already studied by many workers, all but HOWARD and HOWARD (1915) reporting 3:1 segregation of hairy and non-hairy plants in the F_2 of crosses hairy × non-hairy. This result indicates that glume hairiness is controlled by a single, dominant gene. HOWARD and HOWARD (1915), on the other hand, observed 15:1 segregation of the hairy and non-hairy plants. SEARS (1954) was the first to locate the gene, *Hg*, for glume hairiness on chromosome 1A (formerly XIV). His result was later confirmed by KUSPIRA and UNRAU (1960) and TSUNEWAKI (1961).

In emmer wheat the same mode of inheritance was reported by MALINOWSKI (1914) and many later workers. However, which chromosome of emmer wheat is the carrier of this gene has not so far been determined.

MATERIALS AND METHODS

Various species belonging to three groups of wheat—common wheat ($2n = 42$), emmer wheat ($2n = 28$) and einkorn wheat ($2n = 14$)—were involved in this investigation. For common wheat 1,047 varieties or strains of *Triticum aestivum* L., 63 of *T. compactum* Host, two of *T. macha* Dek. et Men., five of *T. spelta* L. and seven of *T. sphaerococcum* Perc. were employed. Of those 200 are Japanese local varieties, and 70 are from China, 19 from Tibet, 41 from Pakistan, 39 from Afghanistan, 143 from Iran, 24 from U.S.S.R., 62 from Sweden and Finland, 148 from

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Spain and Portugal, 287 from U.S.A. and 73 from Australia. The remaining 18 are of unknown sources. One hundred and four varieties of emmer wheat, belonging to nine different species, and 15 of einkorn wheat, either *T. monococcum* L. or *T. boeoticum* Boiss., were also included in this investigation. Most of them belong to the collections of the Kihara Laboratory, National Institute of Genetics, Japan, and the Samuel Rosner Chair in Agronomy, University of Manitoba, Canada. A hexaploid wheat that was synthesized by DR. E. R. SEARS from *T. durum* Desf. var. Golden Ball and *Aegilops squarrosa* L. var. *typica* Zhuk. was used in order to study the hairy-glume gene of emmer wheat on the hexaploid level.

The monosomic series of *T. aestivum* L. var. Chinese Spring was employed for monosomic analysis of common wheat and of the synthesized 6x strain.

For the comparative gene analysis, the following three investigations have been undertaken: (1) monosomic and conventional gene analyses of common wheat, (2) monosomic analysis of synthesized 6x wheat, and (3) survey of the distribution of the *Hg* gene. Details of the methods for each investigation will be described in the corresponding sections of the results.

RESULTS

1. *Critical analysis of the glume hairiness in common wheat. Monosomic analysis:* Jones Fife and Prelude, both with hairy glumes, were crossed as the male parent with the 21 monosomic lines of Chinese Spring, which has non-hairy

TABLE 1

Segregation of glume hairiness in the F_2 lines of Chinese Spring monosomics × Jones Fife and Prelude

F_2 lines	Jones Fife			Prelude		
	No. of plants		χ^2 (3:1)	No. of plants		χ^2 (3:1)
	Hairy	Non-hairy		Hairy	Non-hairy	
Mono-1A	62	3*	14.40**	58	3*	13.12**
1B	23	5	.76	125	48	.70
1D	74	32	1.52	157	48	.27
2A	37	5	3.84	48	17	.05
2B	60	17	.35	. .	. .	. .
2D	25	5	1.11	73	21	.35
3A	54	20	1.16	115	38	.00
3B	17	5	.06	13	4	.00
3D	62	26	.97	146	44	.34
4A	51	14	.42	129	53	1.65
4B	40	12	.10	54	22	.63
4D	69	34	3.52	69	26	.28
5A	42	12	.22	111	48	2.28
5B	44	12	.38	102	34	.00
5D	90	31	.02	139	48	.04
6A	62	22	.06	118	36	.22
6B	69	15	2.29	141	61	2.91
6D	60	17	.35	82	31	.36
7A	47	14	.14	31	7	.88
7B	59	17	.28	13	4	.00
7D	44	9	1.82	122	38	.13

* All plants were apparently nullisomic.
** Significant at the 1% level.

glumes. All F_1 plants derived from the crosses between those varieties and the Chinese Spring monosomic series had hairy glumes, confirming the fact that hairiness is dominant.

In all F_2 populations (Table 1), except that derived from F_1 plants monosomic for chromosome 1A, the segregation closely approached a 3:1 ratio of hairy to non-hairy-glumed plants. The segregation in F_2 populations derived from mono-1A F_1 plants deviated highly significantly from the 3:1 ratio in both cases. Three plants in each population possessed glabrous glumes and in all cases they appeared to be nullisomic.

These facts indicate that a single dominant gene on chromosome 1A of both Jones Fife and Prelude controls glume hairiness.

Conventional analysis: Eight varieties of common wheat, i.e., Jones Fife, Prelude, Chinese Spring, Elgin, Kharkov, Red Bobs, Red Egyptian and S-615, were crossed in diallel combinations. Among those, the first two varieties had hairy glumes, while the other six had non-hairy ones.

F_1 plants derived from crosses between non-hairy parents were all non-hairy. All crosses involving one or two hairy parents produced only hairy F_1 plants, indicating that hairiness is dominant. In the F_2 generation, crosses involving only hairy or only non-hairy parents produced no segregants. All crosses between hairy and non-hairy parents produced 3:1 F_2 ratios of hairy to non-hairy segregants, as shown in Table 2. These results indicate that a single dominant gene controls the expression of glume hairiness and that the two hairy varieties possess the same gene at the same locus.

Summary: The results of monosomic analysis indicated that a single dominant gene on chromosome 1A of both Jones Fife and Prelude controls glume hairiness. The conventional analysis fully supported this result, suggesting that the varieties carry the same gene at the same locus. SEARS (1954) has reported that chromo-

TABLE 2

The F_2 segregation of glume hairiness in hairy by non-hairy crosses

Cross combinations	No. of plants		χ^2 (3:1)
	Hairy	Non-hairy	
Jones Fife × Chinese Spring	590	181	.95
× Elgin	143	56	1.05
× Kharkov	167	62	.53
× Red Bobs	204	77	.86
× Red Egyptian	204	61	.55
× S-615	327	101	.45
Prelude × Chinese Spring	275	88	.11
× Elgin	289	91	.22
× Kharkov	35	15	.67
× Red Bobs	124	51	1.60
× Red Egyptian	69	32	2.41
× S-615	84	26	.11

TABLE 3

Segregation of glume hairiness in the F_2 generation of Chinese Spring monosomics × ABD-VI

F_2 lines	No. of plants		χ^2 (3:1)
	Hairy	Non-hairy	
Disomic	703	229	.09
Mono-1A	37	2†	8.21**
1B	55	18	.00
1D	32	12	.12
2A	40	17	.71
2B	53	18	.00
2D	12	11	6.39*
3A	59	11	3.22
3B	5	0	.60
3D	36	13	.06
4A	12	6	.30
4B	9	6	1.09
4D	58	20	.02
5A	21	11	1.50
5B	19	10	1.39
5D	54	18	.00
6A	9	1	.53
6B	22	7	.01
6D	13	4	.00
7A	31	16	2.05
7B	21	6	.11
7D	14	7	.78

* and ** Significant at the 5% and 1% level, respectively.
† Both plants appeared to be nullisomic.

some 1A of the variety Indian possesses a gene *Hg* for glume hairiness. The present results confirm his finding and suggest the genotype *Hg Hg* for Jones Fife and Prelude and *hg hg* for the other six non-hairy varieties.

Since chromosome 1A belongs to the A genome (OKAMOTO 1962), the *Hg* locus should be present in both emmer and einkorn wheat.

2. *Monosomic analysis of glume hairiness in synthesized 6x wheat:* A hexaploid wheat called ABD-VI, which was synthesized from *T. durum* Golden Ball (hairy) and Sears' *Ae. squarrosa* (non-hairy), has hairy glumes, the gene for which was apparently derived from the emmer parent. In order to know the mode of inheritance of this character in the synthesized hexaploid, ABD-VI was crossed as the male parent with the Chinese Spring monosomic series.

In the F_1 generation all the disomic and 21 monosomic F_1's had hairy glumes, again indicating dominance of hairiness. In all F_2 populations (Table 3), except those derived from F_1 mono-1A and 2D, the segregation closely approached a 3:1 ratio of hairy to non-hairy plants. The segregation in the F_2 derived from F_1 mono-1A deviated highly significantly from a 3:1 ratio. Two plants of this population, both of which appeared to be nullisomic, possessed exceptionally glabrous glumes. The segregation in the F_2 of mono-2D also deviated significantly

from a 3:1 ratio. In this case, however, there was no correlation between chromosome number and hairiness of glume, and the deviation was in the opposite direction to that expected if chromosome 2D carried a gene for glume hairiness. These results indicate that a single, dominant gene located on chromosome 1A of ABD-VI controls glume hairiness. Since chromosome 1A belongs to the A genome, this gene is undoubtedly derived from the emmer component, Golden Ball. In fact SHEYBANI and JENKINS (1961) reported that glume hairiness of Golden Ball is controlled by a single, dominant gene.

The result of the present experiment suggests that the gene controlling glume hairiness of ABD-VI and, consequently, *T. durum* Golden Ball is the same as the *Hg* allele of common wheat.

3. *Survey of the distribution of the* Hg *gene in various wheat populations. Distribution in various wheat species:* In all cases so far reported, including those in the present report, the gene *Hg* expresses its effect in a single dose, and no epistatic inhibitor is yet known. Based on these facts, an investigation of glume hairiness in various wheat species has been undertaken in order to clarify the distribution and the origin of the *Hg* gene. The results (Table 4) clearly show that both *Hg* and *hg* are present in all three groups of wheat. However, there are some remarkable differences in the distribution pattern of *Hg*. In einkorn wheat, wild *T. boeoticum* possesses the gene *Hg*, while the cultivated species, *T. monococcum*, does not. In emmer wheat, both wild and cultivated species

TABLE 4

Frequencies of the varieties with hairy and non-hairy glumes in various species of wheat

Species	No. of varieties			Percent hairy
	Total	Hairy	Non-hairy	
Einkorn wheat				
T. boeoticum (wild)	4	3	1	75.0
T. monococcum (cult.)	11	0	11	0.0
Emmer wheat				
T. dicoccoides (wild)	8	5	3	62.5
T. dicoccum (cult.)	18	4	14	22.2
T. durum (cult.)	31	10	21	32.3
T. orientale (cult.)	3	3	0	
T. persicum (cult.)	9	3	6	
T. polonicum (cult.)	9	6	3	
T. pyramidale (cult.)	10	3	7	53.2
T. turgidum (cult.)	14	9	5	
T. abyssinicum (cult.)	2	1	1	
Total of cult. emmer species	96	39	57	40.6
Common wheat				
T. aestivum (cult.)	1,047	105	942	10.0
T. compactum (cult.)	63	2	61	3.2
T. macha (cult.)	2	0	2	
T. spelta (cult.)	5	2	3	14.3
T. sphaerococcum (cult.)	7	0	7	
Total	1,124	109	1,015	9.7

TABLE 5

Frequencies of the Hg *gene in various geographical populations of common wheat*

Locality	No. varieties examined	No. varieties with *Hg*	Percent
Japan	200	1	0.5
China	70	0	0.0
Tibet	19	2	10.5
Pakistan	41	6	14.6
Afghanistan	39	22	56.4
Iran	143	48	33.6
Russia	24	4	16.7
Sweden and Finland	62	0	0.0
Spain and Portugal	148	8	5.4
U. S. A.	287	13	4.5
Australia	73	3	4.1

contain *Hg*, the frequencies being 62.5% and 40.6%, respectively. The frequency is relatively low in *T. dicoccum* (22.2%) and *T. durum* (32.3%). The *Hg* gene is most rare in common wheat, where its frequency amounts to only 9.7% among 1,124 varieties so far tested.

Distribution in various geographical populations of common wheat: The frequency of *Hg* in common-wheat varieties (Table 5; Figure 1) is high in three countries of Central Asia, where common wheat originated, gradually decreasing both east- and westwards along the routes of its dispersion. From this fact it is assumed that the frequency of *Hg* is higher in primitive than in advanced wheat populations. In order to test this assumption, 287 varieties of the U.S.A. were chronologically grouped according to their C.I. number, and the frequency of *Hg* in each group was estimated. The result is given in Table 6. The frequency is the highest among varieties with C.I. number up to 5,000, being lower among those with C.I. number of the next 3,000. No variety having the *Hg* gene was found among 127 varieties with C.I. number higher than 8,000.

DISCUSSION AND CONCLUSION

Monosomic and conventional analyses of eight common-wheat varieties indicated that glume hairiness is controlled by a single, dominant gene, *Hg* located

TABLE 6

Chronological change of the frequency of the Hg *gene in common wheats of the U. S. A.*

C. I. number*	No. varieties examined	No. varieties with *Hg*	Percent
1– 5,000	63	7	11.1
5,001– 8,000	97	6	6.2
8,001–13,000	62	0	0.0
13,001–13,701	65	0	0.0
Total	287	13	4.5

* Cereal investigation number.

on chromosome 1A belonging to the A genome. Genotypes of Jones Fife and Prelude and the other six varieties are *Hg Hg* and *hg hg* respectively. The similar analysis of ABD-VI revealed the glume hairiness of this synthetic is also controlled by a single dominant gene that is derived from *T. durum* Golden Ball and is located on chromosome 1A, indicating homology of the *Hg* gene of emmer to that of common wheat. According to SMITH (1936) a dominant gene controls glume hairiness of einkorn wheat. Since the *Hg* genes of both emmer and common wheats belong to the A genome, it is reasonable to assume that the *Hg* gene of einkorn wheat is homologous to the one in the polyploid species.

The result of a survey of the distribution of this gene in three groups of wheat strongly suggests that the following events might have occurred in the course of evolution of wheat:

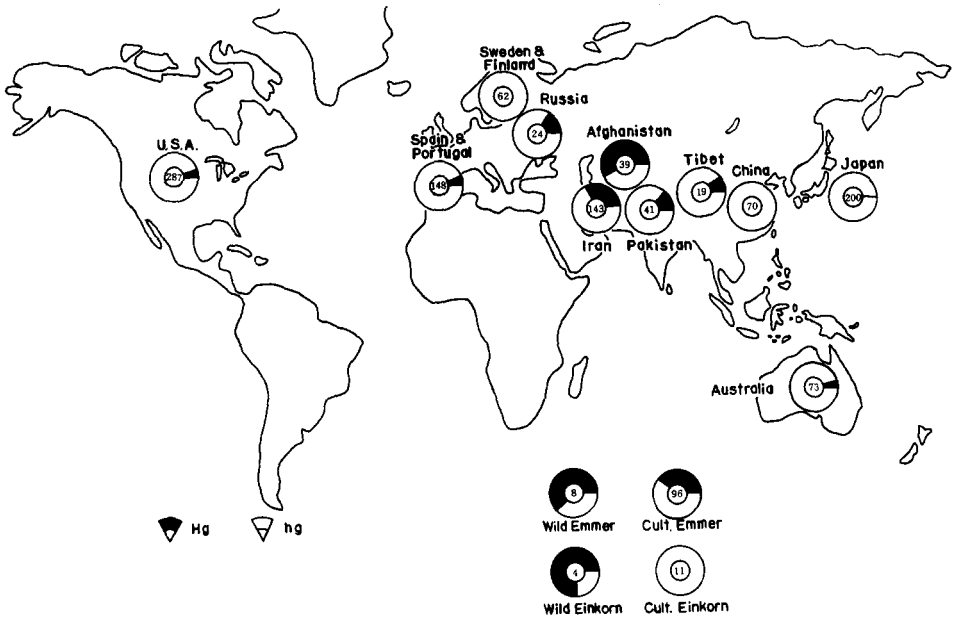

FIGURE 1.—Distribution of the *Hg* gene among various geographical populations of common wheat. Frequency of the same gene in einkorn and emmer wheats is also shown in the bottom. The Arabic numeral in each circle indicates the number of varieties or strains examined in a respective population.

(1) In common wheat both *Hg* and *hg* are present, but there is undoubtedly a significant difference between their frequencies in various parts of the world. Primitive populations, both geographically and chronologically, contain more varieties with *Hg* than advanced populations do. Apparently the *Hg* gene is selected against in common wheat and is gradually being eliminated.

(2) In emmer wheat *Hg* and *hg* are common in both wild and cultivated species. Therefore, *Hg* and *hg* found in common wheat seem to have been introduced from emmer wheat when the first 6x wheat was produced or, later,

through formation of pentaploid hybrids between the already existing hexaploid and emmer wheats.

(3) *T. boeoticum*, the wild species of einkorn wheat, has *Hg*, while its cultivated species contains only *hg*. Considering the fact that mutation of a recessive to the dominant allele occurs much more seldom than in the reverse direction, it is assumed that the gene *Hg* of emmer was derived from einkorn wheat when the first tetraploid wheat was produced. Since introgression of genes from einkorn to emmer wheat through the formation of triploid hybrids is very difficult, the origin of *hg* in emmer wheat can hardly be traced back to einkorn wheat. It is, on the other hand, more likely that *hg* originated on the tetraploid level by a recessive mutation of a preexisting *Hg* gene.

(4) Taking all these considerations into account, it can be proposed that *T. dicoccoides*, the wild emmer species, was produced from a cross between *T. boeoticum* with *Hg* and some species of Sitopsis (most likely *Ae. speltoides*), followed by amphidiploidization of the hybrid. In this way, *Hg* of wild einkorn wheat was introduced into the wild emmer wheat, in which mutation of *Hg* to *hg* took place. Both genes were transferred to cultivated emmer wheat at or after its differentiation from the wild form, and later incorporated into common wheat.

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SUMMARY

Comparative gene analysis of common wheat and its ancestors, emmer and einkorn wheats, has been carried out for glume hairiness. This character of common wheat, emmer wheat and, probably, einkorn wheat is controlled by the same dominant gene, *Hg*, located on chromosome 1A (XIV) in the A genome.

Ten percent of common-wheat varieties have *Hg*. Many more varieties of emmer wheat (42%), including both wild and cultivated species, have *Hg*. In einkorn wheat, *T. boeoticum* possesses it, while *T. monococcum* does not. From this fact it is concluded that the former species was one of the parents of emmer wheat. In common wheat primitive populations, both geographically and chronologically, contain more varieties with *Hg* than advanced populations do. This tendency is also apparent among different taxa of wheat.

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