M. Fellman

Reprinted from CROP SCIENCE
Vol. 3:261–264. 1963.

Inheritance of an Incompletely Dominant Character in Common Wheat Simulating *Triticum sphaerococcum*[1]

John W. Schmidt,[2] Dale E. Weibel,[2] and Virgil A. Johnson[3]

MANY investigators have reported the appearance in common wheat (*Triticum aestivum* L.) of speltoid types simulating *Triticum spelta* L. Generally these are due to the loss of the incompletely dominant gene *Q* on chromosome 5A (formerly chromosome IX) by aneuploidy (7) or by irradiation (3). Compactoid types ascribed to the action of the same gene, *Q,* but having some similarity to *T. compactum* Host were obtained in the same irradiation experiments from common wheat by Mac Key (3). Earlier, Unrau (9) located the gene governing *compactum* on chromosome 2D (formerly chromosme XX).

This paper reports the occurrence of a mutation in common wheat simulating a lesser-known wheat species, *T. sphaerococcum* Perc., and the inheritance of this mutant character.

REVIEW OF LITERATURE

Little is known concerning the origin of *Triticum sphaerococcum* itself. According to Ellerton (1), Percival was the first to describe the species although earlier references appear in the literature. Ellerton called it the common dwarf wheat of the Punjab and indicated that its center of origin was somewhat different from that of the other hexaploid wheats. He described the species as a drought-resistant, short-statured, heavily tillering wheat growing with a tufted appearance. The straw is stiff and erect. The head, which is never long awned, carries a short kernel enclosed by practically hemispherical glumes. The common name "shot wheat" is derived from the extremely short kernel.

Webster,[4] studying the F_2 and F_3 of a cross of Baart (common) × *T. sphaerococcum,* concluded that in this material kernel size was controlled by more than one factor or at the minimum by one major factor plus a number of modifying factors. F_2 and F_3 kernel-length, kernel-weight, and awn-length distributions appeared to vary significantly from the bimodal distribution expected from single-factor segregation. However, Webster reported that kernel length, kernel weight, spike length, and awn length were correlated.

In crosses of common Chinese white wheat with *T. sphaerococcum* var. *rubiginosum,* Ellerton could distinguish the heterozygote from either homozygote. Thus the character was neither completely dominant nor completely recessive. Further, since no tall, long-awned shot wheat types were obtained, he concluded that the *sphaerococcum* effect was due to a block of genes transmitted as a unit. While reciprocal translocations were present, Ellerton concluded that the gene block was not associated with translocations. Therefore, he suggested that a chromosomal deletion in common wheat gave rise to a new species, *T. sphaerococcum.*

Sears in 1947 (6) identified the *sphaerococcum* effect as the expression of a hemizygous ineffective recessive gene located on chromosome 3D (chromsome XVI). Since a Chinese Spring wheat nullisomic for 3D did not show the *sphaerococcum* effect, Ellerton's suggestion that *T. sphaerococcum* arose as a result of a deletion from common wheat was invalidated. The converse, that common wheat arose from a deficiency in *T. sphaerococcum* and that the normal allele is a null allele, is highly improbable. Later Sears (7) suggested that the normal (common) allele is in effect a gene covered by duplicate genes at other loci and that the *sphaerococcum* effect is due to a radical mutation. Sears (8) concluded that the *sphaerococcum* effect is due to one gene and that it appeared following the synthesis of the hexaploid group.

Ellerton (1) used *S* and *s* to designate the normal gene and the *sphaerococcum* gene, respectively. More recently (5), *S* was used for spelt and *sp* for *sphaerococcum.* Accordingly, in this paper *sp* will be used to designate the *sphaerococcum* gene.

MATERIALS AND METHODS

The mutant character simulating the *sphaerococcum* effect occurred in the hard red winter wheat backcross [(Comanche-Mediterranean-Hope) × Pawnee] F_1 × Pawnee at Manhattan, Kansas, in 1953. Four of 17 backcross plants were mutant. Seed from these four plants was grown to check for segregation of the mutant character and mutant plants were backcrossed again to Pawnee wheat for further studies. A mutant F_2 plant from this

[1] Contribution from the Department of Agronomy in cooperation with the Crops Research Division, ARS, USDA. Published with the approval of the Director as paper no. 1230, Journal Series, Nebraska Agricultural Experiment Station, Lincoln, Nebraska. Received Nov. 23, 1962.

[2] Professors, University of Nebraska and Oklahoma State University, respectively.

[3] Research Agronomist, Crops Research Division, ARS, USDA, Lincoln, Nebraska.

[4] Webster, G. T. Segregation of some quantitative characters in a Baart × shot *(Triticum sphaerococcum)* wheat cross. M.S. thesis, University of Nebraska. 1937.

Figure 1—Effect on common wheat spikes and flag leaves produced by a mutation simulating *Triticum sphaerococcum.* A. Mutant segregates. B. Normal segregates.

backcross was crossed to *T. sphaerococcum* var. *globosum*[5] to check for allelism. The F_2 generation of the cross mutant × Pawnee was grown in the greenhouse at Lincoln, Neb., in 1955–56. The F_3 generation was grown in the field at Lincoln and at Denton, Texas. The F_2 of the cross to *T. sphaerococcum* was grown in a plastic greenhouse at Lincoln in 1958–59.

RESULTS

Progeny grown from the four original mutant *sphaerococcum*-like plants all segregated for the mutant character. This was interpreted to mean that this new *sphaerococcum*-like effect was due to a dominant or partially dominant gene in contrast to the recessive gene in *T. sphaerococcum.* Head and grain characteristics of the heterozygous mutant and a normal segregate are shown in Figures 1 and 2. The pleiotropic effect of the mutant gene is similar to that reported for the true *sphaerococcum* gene—awns shortened, spike more dense, glumes nearly hemispherical, and kernels very short. This similarity is evident in the photograph of the two types shown in Figure 3.

Plants were grown from the original seed of both parents of the original backcross population in which the mutant appeared and from additional crosses between the two parents. No mutants appeared. The mutant, therefore, occurred in one of the anthers of the male parent used in the crosses or as a sector in the head of the female used in this particular cross.

[5] Seed obtained from E. R. Sears.

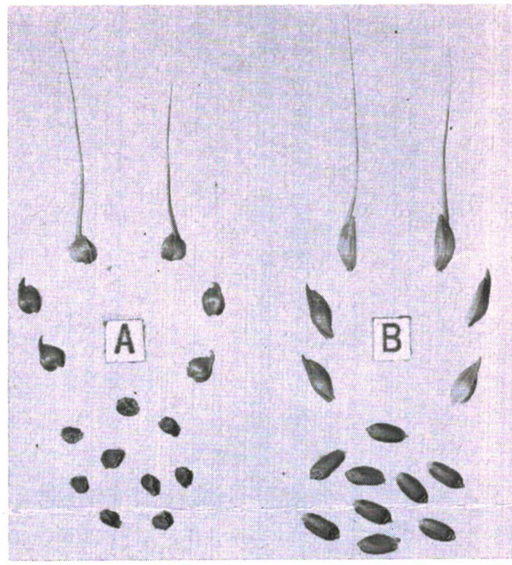

Figure 2—Effect on common wheat spikelets and grain produced by a mutation simulating *Triticum sphaerococcum.* A. Mutant segregate. B. Normal segregate.

Figure 3—Effect of the *sphaerococcum* gene on spike characters in spike A is very similar to that produced by a mutant gene in wheat spike B. In each case, awns are shortened, the spikes become more dense, and the glumes nearly hemispherical.

F_1 plants of the cross of mutant × Pawnee were mutant or normal. Progeny of the mutant F_1 plants were used for determining the inheritance pattern of the mutant character. In the F_2 there were 41 homozygous mutant, 70 heterozygous, and 30 normal progeny. The P value for goodness of fit to a 1:2:1 ratio was .5–.3. According to these data, the mutant *sphaerococcum*-like character was inherited as

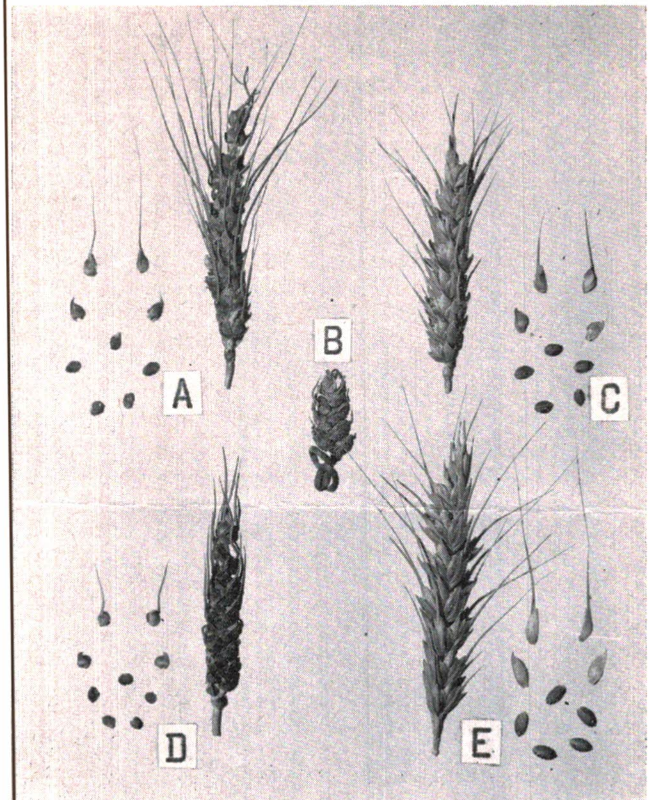

Figure 4—Five spike classes were recognizable in the segregates from a cross of ***T. sphaerococcum*** var. ***globosum*** with a common wheat mutant simulating the ***sphaerococcum*** effect. A. Heterozygous mutant. B. Homozygous mutant, sterile. C. Typical ***T. sphaerococcum.*** D. Heterozygous mutant and homozygous ***sphaerococcum.*** E. Normal common wheat.

a single factor, incompletely dominant with a dosage effect. All three classes were clearly recognizable. The homozygous mutant plants were sterile dwarfs and often did not head. F_3 progeny rows of each F_2 plant classified as heterozygous mutant were field grown at Lincoln, Nebr., and Denton, Texas. In only a few instances when the number of F_3 plants was too small did the expected 1:2:1 segregation fail to occur.

The heterozygous-mutant F_3 plants were bulk harvested. Grain characteristics of the mutant bulk were compared with those from the bulk-harvested normal F_3 segregates. Grain from mutant plants was lower in bushel weight (53 vs. 56 pounds) and 1000-kernel weight (19.24 vs. 31.63 g.) but higher in protein content (18.9 vs. 14.9%, dry weight basis).

Table 1—Segregation* for an incompletely dominant mutant character in wheat simulating the ***sphaerococcum*** effect and for the ***sphaerococcum*** effect itself in the F_2 of the cross ***T. sphaerococcum*** var. ***globosum*** × [(Comanche × Mediterranean-Hope) × Pawnee[3]].

Phenotypes and ratios					P values for goodness of fit
Homozygous mutant	Heterozygous mutant: non-sphaerococcum	Heterozygous mutant: Homozygous sphaerococcum	Non-mutant, homozygous sphaerococcum	Normal	
(26)†	(38)	(16)	(4)	(14)	
4	6	2	1	3	.5-.3
← 13 →				3	.3-.2
← 12 →			1	3	.5-.3

* Segregation data are from the progeny of mutant F_1 plants only.
† Number of plants in each phenotype.

Figure 5—Plant types associated with the 5 classes of segregates of the cross ***T. sphaerococcum*** with a common wheat mutant simulating the ***sphaerococcum*** effect. A. Normal common wheat. B. Heterozygous mutant. C. Typical ***T. sphaerococcum.*** D. Heterozygous mutant but homozygous ***sphaerococcum.*** E. Homozygous mutant.

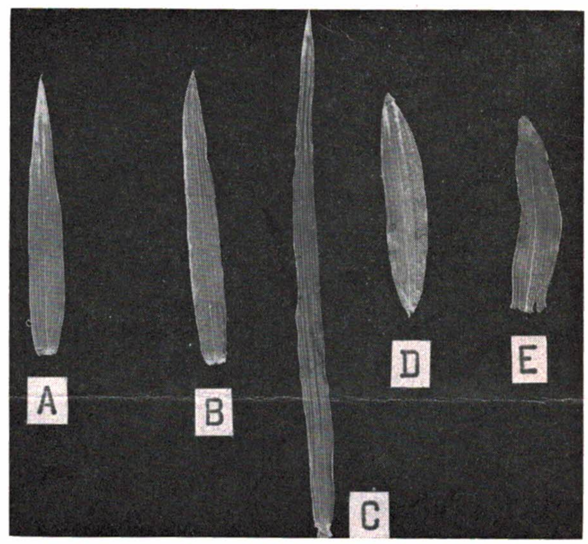

Figure 6—Leaf types associated with the 5 classes of segregates of the cross of ***T. sphaerococcum*** with a common wheat mutant simulating the ***sphaerococcum*** effect. A. Typical ***T. sphaerococcum.*** B. Heterozygous mutant. C. Normal common wheat. D. Heterozygous mutant and homozygous ***sphaerococcum.*** E. Homozygous mutant.

A two-factor segregation (Table 1) was obtained from progeny of mutant F_1 plants obtained from the crossing of *T. sphaerococcum* var. *globosum* with the heterozygus mutant. Allelism of the mutant gene with the *sphaerococcum* gene is ruled out. Since as many as 5 classes could be recognized, 3 different ratios could be fitted satisfactorily to the data obtained. All are based on the assumption that

Table 2—Mean plant height and mean tiller number in wheat associated with 5 F_2 phenotypes from the cross of *T. sphaerococcum* × *sphaerococcum*-simulator mutant (greenhouse data).

Phenotype	Mean plant ht., in.	Mean tiller numbers
Normal	31.9	12.7
Heterozygous mutant, non-sphaerococcum	30.2	20.1
Non-mutant, homozygous sphaerococcum	27.0	18.8
Heterozygous mutant, homozygous sphaerococcum	23.4	23.3
Homozygous mutant*	8.8	21.3

* Separation into sphaerococcum and non-sphaerococcum impossible in this group.

Table 3—Chi-square values for independence of (1) phenotypes and glume discoloration and (2) phenotypes and leaf color in F_2 of *T. sphaerococcum* × *sphaerococcum*-simulator wheat mutant.

Attributes	Chi-square	DF	P
(1) Phenotypes and glume discoloration	26.1	3	.01
(2) Phenotypes and leaf color	116.7	9	.01

Pertinent associations for (1) Sphaerococcum simulator and a glume discoloration. (2) Sphaerococcum simulator and yellowish-green leaf color. Combined sphaerococcum effect and sphaerococcum simulator with dark green leaf color. Sphaerococcum effect and bluish-green leaf color. Normal plants with normal green leaf color.

one gene is dominant and the other recessive. The 5 classes are shown by head characteristics in Figure 4, as plants in Figure 5, and as leaf types in Figure 6. As with *T. sphaerococcum,* there is associated with this mutant a decrease in plant height and an increase in tiller number (Table 2).

Two additional associations were noted in this F_2 material. A significant association was recorded (Table 3) between the heterozygous mutant and a glume discoloration very similar to, if not identical with, the brown necrosis or pseudo-black chaff of Hope wheat and its derivatives. A second highly significant association existed between certain phenotypes and certain leaf colors. Mutant plants have leaves with a yellowish-green color while leaves of *sphaerococcum* plants are bluish-green. Both deviate from normal green leaf color.

DISCUSSION

The appearance in common wheat of a monogenically controlled mutant character simulating in every way the species *T. sphaerococcum* is of interest taxonomically and phylogenetically. Taxonomically this adds evidence to the suggestion by Mac Key (4) that the present hexaploid wheat species *T. compactum, T. vulgare* Vill., *T. spelta, T. macha* Dekap. and Menab. and *T. sphaerococcum* should be considered as subspecies of *Triticum aestivum* L. Single genes with pleiotropic effects or gene blocks acting as a unit are responsible for these so-called hexaploid wheat species. Thus, the present division into taxonomic units at the species level is questionable.

The appearance of this rare and drastic mutant in common wheat is not readily explained. Since the mutant gene is not allelic to the *sphaerococcum* gene, it could well be located on one of the other chromosomes of homoeologous group 3. Attempts to determine the chromosomal location of the mutant gene with the monosomic series were unsuccessful because of sterility caused by interactions of this mutant and the monosomic condition in 10 of the 21 chromosomes.

The association of this *sphaerococcum*-simulating mutant and a glume discoloration similar to Hope wheat brown necrosis or pseudo-black chaff is of considerable interest. According to Kuspira and Unrau (2), the Hope wheat gene for pseudo-black chaff (designated *pbc*) is located on chromosome 3B (III), one of the chromosomes of homoeologous group 3. However, they stated that it is present in the Hope variety as a recessive gene. If in this Hope wheat derivative the gene for the *sphaerococcum* simulator is closely linked with a gene for a glume discoloration having the appearance of pseudo-black chaff, the latter is being expressed in the heterozygous condition as is the *sphaerococcum*-simulator gene itself. However, the recessive *pbc* gene would not be expected to express itself in the heterozygous state. Therefore, if the glume discoloration in this instance was caused by the action of the *pbc* gene, a possible explanation is that chromosomal duplication may have been involved in the appearance of the *sphaerococcum*-simulator character and the expression of glume discoloration. Chromosomal duplication could have given dosage equivalent to dominance to otherwise recessive genes.

The symbol for the *sphaerococcum* gene should be changed from *sp* to sp_1 and the *sphaerococcum*-simulator gene designated Sp_2.

SUMMARY

The appearance of a spontaneous mutation in common wheat simulating *Triticum sphaerococcum* Perc. is reported. According to the data presented, this mutant character is under the control of a single gene or gene block incompletely dominant in effect. This gene or gene block is not allelic to the *sphaerococcum* gene or gene block located on chromosome 3D in *T. sphaerococcum* var. *globosum*, but it has similar pleiotropic effects. The heterozygous mutant is associated with a glume-discoloration character very similar to the brown necrosis seen in Hope wheat and its derivatives. The *sphaerococcum*-simulator mutant first appeared in a Hope wheat derivative. Attempts to locate the mutant gene chromosomally by monosomic analysis failed because of sterility interactions in 10 of the 21 monosomic lines including chromosomes 3A and 3B.

The symbol for the *sphaerococcum* gene should be changed from *sp* to sp_1 and the *sphaerococcum*-simulator gene designated Sp_2.

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