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Genetical studies of branched spikes in soft wheat

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Introduction

As to the spike shape of wheat the so-called branched spikes rarely appear as an abnormality. This may be brought about by conditions in cultivation or at times it may be clearly attributed to heritability of this character. CANDOLLE¹⁾ has already mentioned the existence of branched wheat of the *Triticum turgidum* in A. D. 23-79. This was based on Plinius's mentioning the cultivation of a "Miracle wheat" in the same era.

In species other than *T. turgidum* numerous reports on branched wheat are seen after 1885 (*T. dicoccum*, KÖRNIKE and WERNER²⁾; *T. polonicum* and *T. spelta*, PENZIG³⁾; *T. dicoccum*, BONVICINI⁴⁾; *T. vulgare*, TUMANIAN⁵⁾, JACUBZINER⁶⁾). The appearance of branched ears by crossing reported by BIFFEN⁷⁾ (in *T. polonicum* × *T. vulgare*), KEZER and BOYACK⁸⁾ (in *T. vulgare* × *T. dicoccum*), MEUNISSER⁹⁾ (*T. turgidum* × *T. durum* and *T. turgidum* × *T. polonicum*). According to MEUNISSER, the branching tendency of *T. turgidum* was seen recessive, and in F₂ generations was divided into a ratio of 3:1.

Further in regard to the various types of branched spikes, NILSSON-LEISSNER¹⁰⁾ reported that in crossing experiments with *T. vulgare* × *T. spelta*, the branched spikes could be divided as follows, 1) short ramification, 2) bifurcated rachis, 3) long ramification. They pointed out that the branched spike is an appearance of character by hereditary factors. In contrast to the above, PERCIVAL¹¹⁾ while admitting hereditary influence, pointed out that the character is susceptible to environmental factors. SHARMAN¹²⁾ conjectured that the branching in *T. turgidum* is caused by a recessive *bh* gene, and that this factor causes branched spikes under normal conditions, while the appearance is inhibited by longer daylength or high temperature.

As mentioned above numerous reports have been made on branched wheat and considerable genetical studies have been made. Cultivation of branched wheat, however, has been limited as a localized variety, while it

may be cultivated as novelty. The main reason for this may be that the yield of branched wheat is not so high.

It is pointed out here that the revaluation of the agronomical and genetical significance of the character of branched wheat, especially that of *T. vulgare*, was made by Soviet genetic researchers. In 1949 the SOVIET NEWS¹³⁾ reported the high productivity of branched wheat. This was followed by a series of numerous Soviet workers reports (*T. turgidum*, JAKUBTSINER^{14,15)}; MEDVEDEVA and BAZAVLUK¹⁶⁾; BUJANOV¹⁷⁾; LEVITSKI and RUSZKOVSKI¹⁸⁾; *T. durum*, JAKUBTSINER¹⁹⁾; *T. vulgare*, LONSKII²⁰⁾, RYZEI^{21,22,23)}, MUHIN²⁴⁾, VASIN²⁵⁾ and VIGOROV²⁶⁾).

In addition, another wheat spike abnormality, the so-called additional spikelet, is known. Numerous reports have also been made on the appearance of this character. According to NILSSON-LEISSNER, there are two types of additional spikelets. When additional spikelets appear on the side of normal spikelets they are called right angle type, and when the additional spikelets appear at the base of normal spikelets they are called parallel type. These two types are considered as different genetically. As examples of the former type, reports by KÖRNIKE and WERNER, PERCIVAL, PENZIG, KAJANUS and NILSSON-LEISSNER may be referred to, while as examples of the latter MAYER-GMELIN²⁷⁾ and VAVILOV²⁸⁾ may be cited. Especially KAJANUS indicated that additional spikelets are the results of recessive gene and suggested the presence of multiple gene owing to the complexity of the division. NILSSON-LEISSNER also pointed out the presence of a recessive gene.

Until comparatively recent years, however, no mention has been made on the possible correlation between the appearance of additional spikelets and that of branched spikes. The Soviet genetic workers were the first to grasp the relationship of the two phenomena as a developmental course of character. In respect to this YOSHIOKA^{29,30)}. YOSHIOKA and TAKASHIMA³¹⁾ and YOSHIDA (unpublished) in Japan have clarified the relationship.

It has been reported that it is possible to lead to the eventual development of branched spikes by using additional spikelets of natural appearance from normal ears without resorting to crossing and by selectioning techniques. This was reported by LONSKII, RYZER, MUHIN, VASIN, VIGOROV, JACOMETTI³²⁾, YOSHIOKA, YOSHIOKA and TAKASHIMA. These developments are considered to be the result of interaction between plants and their environmental conditions. In time with this, RYZEI, MUHIN and VIGOROV have indicated that the main influencing factors on the plant are the nutritional conditions, while FEDOROV³³⁾ states that the length of day is the main factor.

As yet the course of development in branched spikes is not obvious, especially the relationship between parallel type and right angle type of additional spikelet is entirely not clear. Thus, in the present report author has conducted experimental work on several varieties of *T. vulgare* in order to investigate the following points;

- 1, How does long term selection affect branched spikes?
- 2, What course of development does it take?
- 3, What is the nature of the character acquired from a genetical and morphological point of view?

Material and method

The material used in the present experiment was a special wheat variety obtained by a previous crossing of Martin's amber and Red genealogical which was designated as MR strain by the author. This variety is belonging to winter soft wheat (*T. vulgare*) and generally does not show branching tendencies. During harvesting in 1955, however, several spikes accompanied with additional spikelets which were considered to be the initial form of branched spikes were observed. The seeds of these spikes were used as



Fig. 1. Spikes of MR 1 strain. A, short ramification; B, normal type; C, long ramification.

material in the present experiment. As control, several varieties were sown in autumn (Norin 8, Akasabishirazu 1 and Dowson 1).

As to the method of experiments, observations were conducted to determine, whether the characters of additional spikelets and branched spikes were hereditary, or whether they were merely coincidental characters brought about by nutritional conditions. At the same time, morphological studies were made in order to follow the course of development from additional spikelets to branched spikes. Further, since there is a suspicion that the character of branched spikes may be influenced by environmental conditions with special reference to soil and fertilizer conditions, a comparative study was made by planting grains under different conditions from the same spikes which were genetically considered the same.

Experimental results

In 1955, five spikes with additional spikelets were observed among MR strain planting under cultivation in the field at the Faculty of Science, Hokkaido University. These abnormal spikes were composed of 3 spikes with 3 additional spikelets, 1 spike with 2 additional spikelets and 1 spike with 1 additional spikelet. Further, the spikelet position at which the additional spikelets appeared was from 6th to 10th from the bottom on the rachis. With the exception of these five spikes, the spikes of the remaining MR strain were completely normal and in the control varieties no additional spikelets were observed either. The seed grains obtained from these spikes were designated as MR1 strain. Next in order to determine whether the appearance of the additional spikelets in question was mutations or merely accidental changes, the seed grains from each spikes were planted in 1956 (A, B, C, D and E strains).

The harvested results for 1956 were as follows (Table 1). The percentage of appearance of additional spikelets with at least one spike per plant was 16.7~82.4 (average of 52.9) % of the entire number of individual plants. Insofar as A~D strains were concerned, it seemed that among these strains no essential difference was seen. Further, the E strain as compared with the other four strains, showed an appearance of character of a lower degree and as a result in the ensuing selective experiments it was excluded owing to the lack of planting field space.

Additional spikelets which appeared for the first time in that year in the control were collected and the seed grains obtained from these spikes were designated as F strain. It is worthy of note that no significant difference was seen in the character appearance between A~E strains and F

TABLE 1. Spike abnormality in some strains of MR1 wheat (1955 and 1956)

Strain	No. of spikes	No. of abnormal spikes	%	No. of plants	No. of plants with one more abnormal spike	%	Position of abnormal spikelets on the spike	Highest grain number in one spikelet	Highest number of abnormal spikelets per spike	Mean number of seeds setting per spike
A	105	9	8.6	21	4	19.1	4-10	7	4	45.3
B	68	24	35.3	17	14	82.4	5- 8	6	4	38.6
C	81	34	42.0	26	20	76.9	5-10	11	4	40.7
D	100	30	30.0	20	13	65.0	5-10	9	4	42.5
E	85	4	4.7	18	3	16.7	2- 7	7	4	37.0
Total	439	101	25.3	102	54	52.9				40.7
Control	518	20	3.9	107	16	15.0		4		39.7
F							5-11	11	5	40.7
1955							6-10	6	3	47.8

TABLE 2. Spike abnormality in some strains of MR1 wheat (1957 and 1958)

Year	Strain	No. of plants	No. of normal plants	No. of spikes	No. of abnormal spike							Total	%
					Additional spikelet		Short ramification		Long ramification	Short ramification + Additional spikelet	Long ramification + Additional spikelet		
					A	B	A	B					
1957	A	56	3	699	202	84	93	0	4	68	451	64.5 ± 13.0	
	B	44	3	562	160	40	92	0	5	40	337	60.0 ± 12.0	
	C	112	13	1072	248	56	201	0	17	40	562	52.4 ± 9.7	
	D	128	5	1431	375	77	240	8	23	78	801	56.0 ± 13.9	
	F	45	5	368	84	13	61	0	8	14	180	48.9 ± 7.0	
	Total	385	28	4132	1069	270	687	8	57	240	2331	56.4	
	Control	33	28	156	2	0	6	0	0	0	8	5.1	
1958	A	249	2	1679	324	146	330	229	0	87	137	1253	74.6 ± 11.1
	B	252	6	1532	222	54	336	222	0	24	86	990	64.6 ± 8.7
	C	393	3	2135	243	69	470	465	0	34	322	1603	75.1 ± 6.7
	D	123	1	685	109	22	152	88	0	7	45	424	61.9 ± 8.2
	F	56	0	373	70	26	70	51	0	68	48	293	78.6 ± 5.6
	Total	1073	12	6404	968	317	1538	1055	0	220	638	4563	71.3
	Control	44	35	360	13	0	10	0	0	0	23	6.4	

strain. In each spike the position at which the additional spikelets appeared was from 4th to 11th in A~D strains with the exception of E strain. In that strain the position of additional spikelets was from 2nd to 7th. Also in regard to the number of grains per spikelet both categories showed 11 grains as the highest. As regards the largest number of additional spikelets per spike, the former showed 4 while the latter had 5. Thus, the number of additional spikelets was higher in the control than expected. As regards remarkable differences the only point worthy of note is that the frequency of occurrence of additional spikelets in B, C, D strains was high.

Even under the same cultivation conditions during the same year, no appearance of additional spikelets were seen among the other varieties, namely Norin 8 and Akasabishirazu 1. In contrast additional spikelets appeared as in the previous year in the MR strain even in the control group. This seems to indicate that certain varieties are more prone to produce additional spikelets than others.

Another point worthy of note is that highest number of grains in the previous year was 6 grains per spikelet, whereas in 1956 the count, including F strain, went up to 11 grains. It seems to author to indicate the possibility of a shift from additional spikelets to branched spikes. These phenomenon became apparent in MR1 strain. In the 1957 harvest, the character appearance was investigated by dividing spikes into several degrees in the same way as in 1956. As a result it was shown that there are two types in the shift from additional spikelets to branched spikes (Table 2).

In the first type, the rachilla was short with 5~10 florets per spikelet, in the other the rachilla had lengthened and it appeared just like a normal rachis with spikelets on both sides instead of florets, namely it seems to belong to exactly branched axis. The former was designated as "short ramification" and the latter was designated as "long ramification" by the author. Further, the present investigations were conducted in accordance with the following divisions (Fig. 1, 2).

- Additional spikelet A A single additional spikelet.
- Additional spikelet B Two or more additional spikelets.
- Short ramification A Those with the lower appearance of short branched rachis.
- Short ramification B Those with the higher appearance of short branched rachis.
- Long ramification..... Those with long branched rachis.
- Short ramification + Additional spikelet Short ramification with additional spikelets.

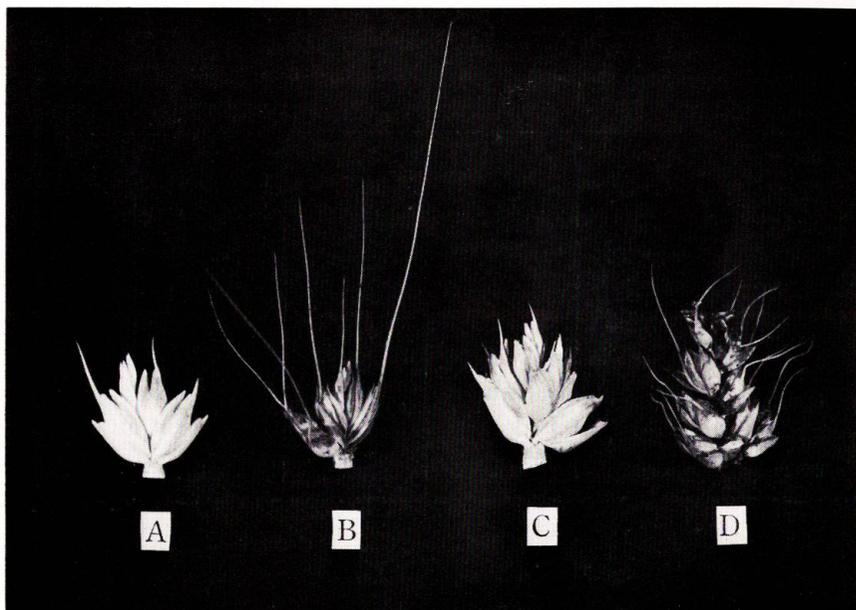


Fig. 2. Spikelets of MR1 strain. A, normal; B, additional spikelet; C, short ramification; D, long ramification.

When the frequency of appearance of character of abnormal types were compared with that of the previous year, it was found that the frequency of appearance of abnormal type considerably increased. In addition when studies were made spike by spike it was shown that the frequency of appearance of this abnormal type increased quantitatively and qualitatively.

The various strains of A~F which were subjected to selection two or three times showed a minimal 61.9% frequency of appearance of abnormal types with a maximum of 78.6%, which when compared the 48.9 and 64.5% of the previous year showed a higher degree of appearance. The frequency of appearance of abnormal types in the progeny of "short" and "long" ramification groups is shown in Table 3. The frequency of appearance of short ramification in both groups are respectively 41.6 and 41.5% which can be said to be identical frequency of appearance. In contrast the rate of appearance of the long ramification in later generation of long ramification was 10.0%, while in the later generation of short ramification the value was 5.3%, nearly half of the former. Further in the total of abnormal types including additional spikelets the value of the former was 71.1%, while that of the latter was 80.9% showing a slightly higher frequency of

TABLE 3. Comparison of the spike type between the progeny of long ramification (A-F) and short ramification type

Parent	Total number of spikes	Additional spikelet	Short ramification	Short ramification + Additional spikelets	Total of short ramification	Long ramification	Short / Total	Long / Total	Per cent of abnormal spikes
Long	6404	1285	2413	220	2633	638	41.1	10.0	71.1
Short	1556	276	291	44	335	82	41.5	5.3	80.9

appearance in the latter. As may be seen in these results in regard to the appearance of long ramifications, the long ramification type showed higher values and while in the case of short ramification both showed absolutely no difference between each other. In other words, there was no reason for dividing short and long ramification genetically.

From the above results it is clear that additional spikelet changes into branched spike by continuous selection and then branching phenomenon is fixed as inherent character. At the same time an gradual increase in frequency of appearance is seen. Whether the abnormal type will become long or short ramification type is not hereditary. It is conjectured herein that during the time of development the spikes in question are influenced by environmental conditions.

TABLE 4. Comparison of the spike abnormality in MR1 wheat (1958)

Strain	Number of spikes	Normal	Additional spikelet	Short ramification	Long ramification + Short ramification	Total number of abnormal spikes	%
Short	297	180	44	35	20	99	35.5
Long A	246	154	42	44	6	92	37.4
Long B	162	152	16	3	1	20	12.3

Table 4 shows the results of experiments in other field conducted in order to follow the course of selection. Both long A and long B indicate long ramification spikes of the previous year. The former is a group selected from samples with a higher degree of branching as compared with the latter. When long A and long B were planted in order to compare the results against short ramification, it was shown that a remarkable difference was present. In the long B group as a whole abnormal types were low and at the same time an exceptionally low frequency of appearance of short ramification was noted. The above seems to indicate that in the course of the shift from additional spikelet to the branched spike type, it has passed through a series of changes in order to bring about an appearance of character from a genetical point of view. And at the same time selection plays an important role in this course.

In order to investigate the cause of this character appearance the time of flowering was analysed by spike types. The results are as shown in Table 5. As may be seen 60 individual plants were selected at random from MR1 strain in the field. Each individual flowering time was inves-

TABLE 5. Relationship between the flowering periods and the occurrence of abnormal spikes obtained from 60 plants of MR1 wheat

Flowering period	No. of spikes	No. of normal spikes	No. of abnormal spikes					Short Long
			Total	Long ramification	%	Short ramification	%	
20-30/VI	128	38	90	13	10.2	77	60.2	5.92
1-10/VII	405	84	327	243	60.0	76	18.8	0.31
11-20/VII	243	90	153	143	58.0	10	4.1	0.07
Total	776	212	570	399	51.7	163	20.0	0.41

tigated day by day and grouped as follows; 20-30/VI, 1-10/VII, 11-20/VII. As a result, it was shown that the appearance of short ramification was mainly in the early flowering group, while it shows the lowest values in the latest flowering group. In contrast to the above in the case of long ramification the values were low in the first group with approximately identical values in the middle and late group. This relationship becomes apparent by calculating short: long ratio. Namely the value in the early flowering group is 5.9, while in the late group it is a mere 0.07.

The order of flowering in an individual plant coincides with the ear-

TABLE 6. Result of the field test in 1959. In each block, selected branched strains of MR1 wheat are randomized. Within parentheses, the number of prominent branched spike more than 2.0 g grain weight are given

Row	Block			
	1	2	3	4
0	35-c (0)	35-s (6)	50-c (0)	50-s (3)
1	60-8 (1)	57-5 (0)	1-41 (1)	24-70 (0)
2	51-37 (2)	13-50 (0)	47-26 (0)	44-16 (5)
3	40-1 (0)	2-75 (0)	11-1 (0)	3-28 (0)
4	38-49 (2)	10-21 (0)	29-17 (0)	28-45 (0)
5	20-65 (0)	63-2 (0)	55-2 (0)	1-40 (0)
6	24-2 (2)	51-12 (0)	24-73 (0)	20-2 (0)
7	27-6 (0)	50-5 (0)	5-11 (0)	48-2 (0)
8	50-27 (1)	40-3 (0)	37-21 (0)	10-20 (0)
9	8-31 (1)	16-42 (0)	4-04 (0)	50-2 (0)
10	24-1 (0)	55-1 (0)	24-72 (0)	15-27 (0)
11	63-1 (4)	25-14 (0)	48-1 (0)	20-66 (0)

liness or lateness of spike primordia formation. It is also conjectured that it is related to the order of tillering of the stem. Therefore, the spikes of the early flowering group in which short ramifications were predominant, may have had an early development of spike formation. The spikes in which flowering occurred during the middle and the late period may be considered as individuals in which spike primordia formation was later than above. While the author does not have sufficient data to determine what influence the time difference of spike primordia formation act on the determination of spike type. At least it may be said that the cause is not mainly due to genetical difference between long and short ramification.

From data obtained within the present experiments, the degree of appearance of branching and the changes in type of branching seem to be influenced by environmental conditions. Thus in the 1959 investigation special considerations were made on the growth conditions in the field, namely branched spikes of the highest quality among the various strains were selected (Table 6).

With respect to the above, comparative study was made in order to determine the pattern of growth in the field. With the exception of the first row at both ends of the field, the 10 rows of wheat subjected to identical conditions were divided into 4 groups. The pattern of appearance of branched spikes in the 4 blocks and 10 rows was studied. In each block seeds from the one spike were planted and at the same time special care was taken so that various strains would be planted in a random fashion.

First in Table 7-1 the average of the 10 rows, in the 1st and 4th block which are the opposite end of the rows, shows respective values of 6.0 and 7.7, while in the 2nd and 3rd block the respective values are 3.9 and 4.2. The average value by rows ranges from 2.5 to 10.2. As may be seen in the variance analysis in Table 7-2, whereas among the average values between blocks a significant difference was seen. Thus it may be accepted that in regard to the appearance of branched spikes the rate is higher at both ends of the rows.

From the above results, it would seem that the difference may be due to the position in the field, whether the location of the plants were in the center or at the end of the field, rather than caused by the difference in individual heredity. In other words, it would seem that the frequency of appearance is subjected to the environmental conditions in which the plants grow. One of the factors influencing the above may be space condition or may possibly be nutritional and light conditions of the plants.

Further the numbers in the brackets in Table 6 express the spike count

TABLE 7-1. Frequency of branched spikes of MR1 Wheat in a randomized experiment (1959)

	Block				Total	Mean
	1	2	3	4		
1	12.5	9.3	10.6	8.5	40.9	10.2
2	4.0	4.5	1.8	5.5	15.8	4.0
3	3.0	5.0	7.0	12.4	27.4	6.9
4	10.7	8.3	1.3	3.9	24.2	6.1
5	2.4	2.6	6.8	2.8	14.6	3.7
6	11.0	6.7	4.6	12.7	35.0	8.8
7	7.7	0.9	1.4	9.4	19.4	4.9
8	2.9	0.8	1.5	11.8	17.0	4.3
9	1.9	0.5	3.3	4.3	10.0	2.5
10	3.7	0.0	3.3	6.1	13.1	3.3
Total	59.8	38.6	41.6	77.4	217.4	
Mean	6.0	3.9	4.2	7.7		5.5

TABLE 7-2. Analysis of variance

Source of variation	Degree of freedom	Sum of squares	Mean square	F
Total	39	56349		
Rows	9	9716	1079.56	1.22
Block	3	22693	7564.33**	8.53
Error	27	23940	886.67	

with grain weight per spike over 2g. The spikes with heavier grain weight were invariably found in spikes which showed branching. It was also apparent that the location of these spikes with heavy grain weight was limited to the outer fringes of the field. It can be said that heavy grain weight means a generally healthy growth of the spikes. It follows that the outer fringes of the field were closer to the ideal condition than the center of the field.

Further as an additional experiment intravarietal crossing was conducted in order to determine whether the branched character or its frequency of appearance would be influenced by crossing. Crosses seeds from two spikes from the previous year and control were compared. Group 35-c and 50-c are both strains resulting from branched spike intravarietal crossing and

35-s and 50-s are both self pollinated controls.

Appearance of abnormalities in 35-c and 50-c respectively were 75.4 and 65.5%, and in contrast 35-s and 50-s showed values of 66.8 and 75.4%. As regards the degree of branching no special difference was seen. It would be impossible to present a strong argument on the strength of the above two experiments, but it may be said that branched spike crossing does not necessarily raise the tendency to increase branching.

Table 8 shows the results of an investigation made in order to determine the extent of nutritional influence on the appearance of branched spikes. In this investigation 12 individual plants with full tillering were

TABLE 8-1. Effect of fertilizer on the appearance of additional spikelets and branched spikes. Individual plant was divided into five stocks in order to receive the different fertilizer treatment

Plant	No. of abnormal spikes in each stock					Total	Mean
	No fertilizer	With fertilizer					
		N, P, K	P, K	N, K	N, P		
1	0	6	3	1	2	12	2.4
2	2	3	1	1	5	12	2.4
3	2	2	3	3	2	12	2.4
4	6	3	1	3	2	15	3.0
5	0	5	0	5	4	16	3.2
6	0	5	1	1	2	9	1.8
7	0	4	0	6	2	12	2.4
8	0	3	1	3	1	8	1.6
9	3	0	1	1	0	5	1.0
10	1	4	2	4	5	16	3.2
Total	16	35	13	28	25	117	
Mean	1.6	3.5	1.3	2.8	2.5		2.34

TABLE 8-2. Analysis of variance

Source of variation	Degree of freedom	Sum of squares	Mean square	F
Total	49	155		
Fertilizer	4	32	8.0**	2.9
Individuals	9	23	2.6	0.9
Error	36	100	2.8	

selected. In early spring, each individual plants was divided into five separate bodies and planted separately in pots. One of the pots was left unfertilized, while three pots were treated with two of the following three elements; nitrogen, phosphoric acid, potassium. And the remaining pot was given all three factors. The five separated bodies showed a slight difference in growth each other. In order to minimize this difference when the pots were divided into groups this was done in a random fashion. It may be said that the three-element group showed the highest frequency in appearance of abnormalities, while the non-fertilized group and the non-nitrogen group showed the lowest frequency in appearance of abnormalities. These results seems to indicate that a close correlation exists between the appearance of abnormalities and nitrogen administration. At the same time it would seem that branched spike formation is influenced by nutritional conditions during flower bud formation.

Since the appearance of branching seemed to be in many cases influenced by the growing conditions of the spike, as described above, a comparison in MR1 strain was carried out to determine the size of final leaves which is most intimately connected with the young spike formation in growing point. The results are seen in Table 9 and 10. Table 9 shows the total of single individuals showing branching in all spikes and the total of cases in which no branching was seen. When the branching type and normal type were compared by the lamina length of the final leaves, the former was 32.1 cm and the latter was 29.2 cm. In the lamina width the former was 19.1 mm and the latter was 15.7 mm. In both cases the former showed higher values. But when both were studies statistically a different

TABLE 9-1. Analysis of lamina length and lamina width of the final leaves in normal and branched type of MR1 A wheat

Group I (Branched type)			Group II (Normal)		
Plant	Lamina length (mm)	Lamina width (mm)	Plant	Lamina length (mm)	Lamina width (mm)
5-1	298	18.7	7-3	290	17.4
13-3	351	20.0	5-3	270	16.0
12-2	309	18.5	13-2	302	13.5
7-4	300	18.5	10-1	338	15.7
11-1	350	20.0			
Total	1608	95.7		1200	62.6
Mean	321	19.1		300	15.7

TABLE 9-2. Statistical analysis of lamina width in two groups

Group	Number of plants	Degrees of freedom	Mean lamina width	Sum of squares
I	5	4	191	250
II	4	3	157	782
		Sum = 7	Difference = 34	Sum = 1032

pooled variance $S^2 = 1032/7 = 147.43$

$S_x = \sqrt{147 \times 9/20} = 8.15$

$t = 34/8.15 = 4.17$

TABLE 9-3. Statistical analysis of lamina length in two groups

Group	Number of plants	Degrees of freedom	Mean lamina length	Sum of squares
I	5	4	321	3855
IIj	4	3	300	2448
		Sum = 7	Difference = 21	Sum = 5303

pooled variance $S^2 = 5303/7 = 757.57$

$S_x = \sqrt{758 \times 9/20} = 18.46$

$t = 21/18.46 = 1.14$

TABLE 10. Statical analysis of lamina width in two groups of MR1A wheat. In this case, all the plants have branched and normal spikes in different ratios

Spike	Number of plants	Degrees of freedom	Mean lamina width	Sum of squares
Branched	27	26	183	9163
Normal	33	32	162	11632
		Sum = 58	Difference = 21	Sum = 20795

pooled variance $S^2 = 20795/58 = 359$

$S_x = \sqrt{359 \times 60/891} = 4.91$

$t = 21/4.91 = 4.28$

result was obtained. In other words though in width a significant difference was seen, in the length on significant difference was seen. Table 10 shows

cases in which the same individual plant showed both branching and normal spikes. When these were divided into branching and normal types and totalled, similar results were obtained. Namely as regards the lamina length of the final leaves, that of branched types was 31.6 cm and that of normal types was 31.3 cm. And as regards the lamina width, the former was 18.3 mm and the latter was 16.2 mm, and at the same time the significant difference was seen between the two. In other words, the final leaves which formed on branched spikes showed a distinctly broader width even in the same individual plant than the final leaves formed on normal spikes. Since the spike primordia formation occurs slightly before or after the final leaf formation, it may be said that the nutritional conditions in this period exert on the final leaves to broaden, likewise exert their strength on branching of spikelets during the spike primordia formation period.

The morphology of branched spikes

As a result of selection in MR1 strain, it was shown that the branching tendency gradually increased quantitatively and qualitatively. Up to now, author has obtained several branched varieties. In these strains the frequency of branched spikes amounted to almost 100% (140 grains per ear).

Additional spikelet type. The additional spikelet obtained in MR1 strain attaches itself horizontally to the original spikelet and is of so-called

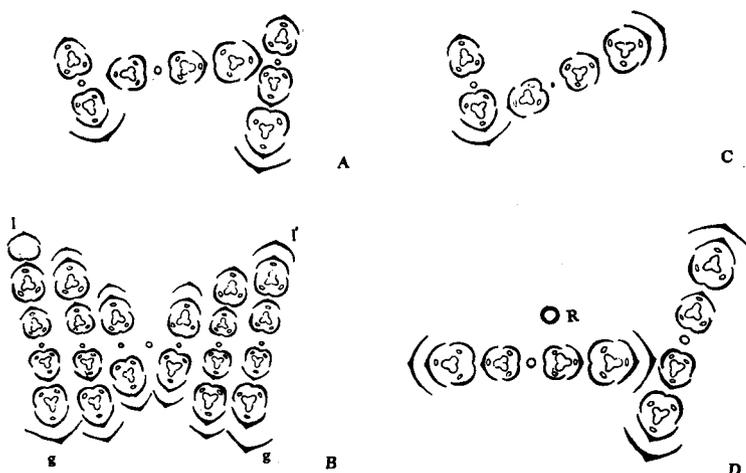


Fig. 3. Floral diagrams of spikelet of MR1 strain. A and B, long ramification; C and D, additional spikelet. R, rachis; g, empty glume; l, l' lemmas of the lowest floret transformed into empty glume.

right angle type. In the case of Vasin, YOSHIOKA and TAKASHIMA, it was reported that parallel type of additional spikelets were the basis, while in MR1 strain, with the exception of one case, no other examples were seen. In MR1 strain, the empty glumes are attached to both spikelets, with two pairs in each node of the rachis. This type, as a result of histological observations, seems to have transformed into a spikelet from the 1st floret (Fig. 3 C, D). It is observed that the lowest floret on the side which additional spikelets are attached becomes abortive and then it has transformed into empty glumes.

Short ramification. A morphological analysis was made and it was revealed that the short ramification in MR1 strain was identical to the Nilsson-Leissner's observation. In short ramifications, the spikelets in the lower region of spike have supernumerary florets and these spikelets have secondarily two small but complete empty glumes and two or more florets instead of one floret. And these secondary spikelet are generally developed

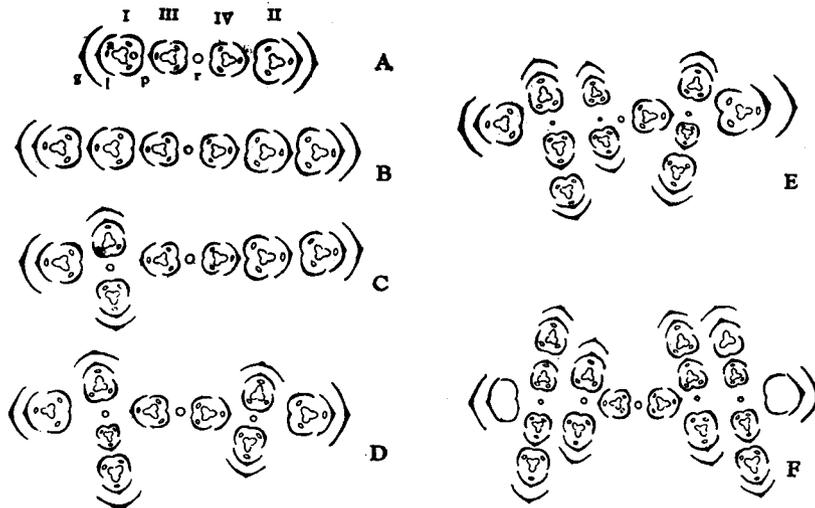


Fig. 4. Floral diagrams of normal and short ramification spikelet of MR1 wheat.

A, normal; B, supernumerary; C~F, short ramification.

I, first floret; II, second floret; III, third floret; IV, fourth

floret; g, glume; l, lemma; p, palea; r, rachilla; a, anther.

from the 3rd or 4th floret of the initial spikelet and have changed into complete spikelets (Fig. 4).

It was shown that while the 1st and 2nd floret in the spikelets showed

no change, the 3rd and 4th floret and those above changed into spikelets. While it is not known why a floret changes into spikelets, both the lemma and palea remaining as they are, sometimes show a transformation of stamen and pistil into a scaly form and also at times the internal organs show a transformation into infant spikelets though the degree is merely at a trace level. In other words it may be conjectured that the internal organs of a single floret have transformed into a spikelet.

Once a spikelet is formed, it is possible for the lemma and the palea to form a pair and play the role of an empty glume. The order of development would be as follows: First, the 3rd floret change into a spikelet, next in the order of the 4th and 5th floret and those above a transformation into spikelet occurs, and at the same time the rachilla shows a slight enlargement to such an extent that it can support the spikelets which change from florets; thus forming branched rachis; as described above in the short ramification type, the 3rd floret and those above transformed into spikelets while the 1st and 2nd floret remain unchanged. When this branching tendency is strengthened, contrary to expectations the 1st and 2nd floret atrophy, and a partial disappearance of these florets is seen. The original empty glumes, however, do not disappear and protect the spikelets which have changed into branched spikes.

Long ramification. Long ramification in MR1 strain was differentiated from others by designating those which showed remarkably extended branched rachis as compared with short ramification. The outstanding feature of the long ramification of MR1 strain was that the 1st and 2nd floret also transformed into spikelets which differed entirely from short ramification. Especially in long ramification of MR1 which is in the course of development, the morphological aspects which resemble those of light angle type of additional spikelets are characteristic. As described above the present branching type commences to transform into spikelets in an orderly fashion from the 1st floret. In the early stages of development, the empty glumes which are present from the beginning remain, and protect the original spikelets from both sides. Later on when the development of branching reaches a sufficient stage, these empty glumes become one of the pair in the empty glumes of spikelets which transformed from the 1st and 2nd floret. Thus, at the beginning stage of the spikelet which transformed from the 1st and 2nd floret, the spikelet only has half an empty glume with one missing. With the increase in floret numbers in these spikelets, then on the side which lacks the empty glume, the lowest floret loses the development of inner organs and the lemma alone remains. This lemma

eventually transforms into an empty glume. Only after the above described transformation, does the 1st and 2nd spikelet have a pair of empty glumes on both sides (Fig. 3 A, B).

Super short ramification. While this branching type resembles short ramification, in this type the branched rachis is considerably shortened and was first obtained 1959. As a result of a morphological examination on

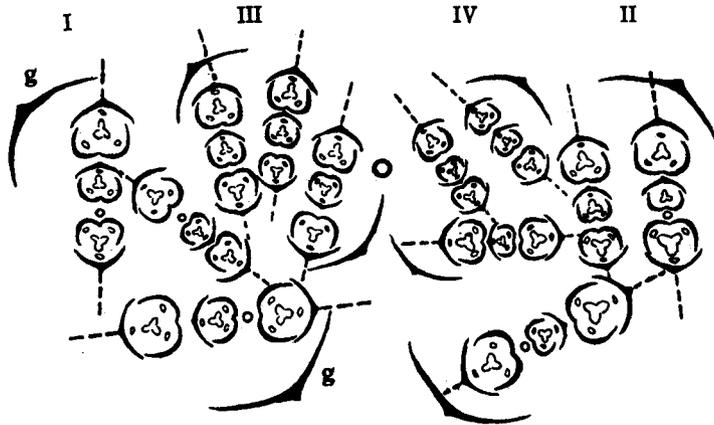


Fig. 5. Floral diagram of supershort ramification type from one original spikelet. I, II, III, IV, each spikelets group originated from 1st, 2nd, 3rd and 4th floret respectively; G, secondarily developed glumes. The broken line shows the plane of each spikelet.

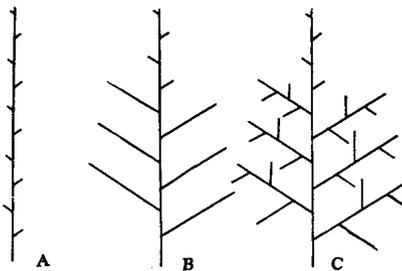


Fig. 6. Schematic diagram of branched and normal spikes in MR1 strain. A, normal; B, single branching; C, double branching (super short type).

the branching of this type, it was shown that this was an entirely complicated type. Namely, if the previous branching type is considered as the primary branching type, this type is a special type in which a secondary

branching appears. In other words after the initial transformation from the florets to spikelets, new transformation from the florets of the new spikelets occurs and the relationship is shown in Figures 5 and 6. Namely, the empty glumes coming from the initial transformation exist without disappearing, and clasp the various spikelets from secondary transformation. Therefore, between the one pair of these empty glumes, 2nd to 4th spikelets are protected. Hence, rather than being called super short ramifications, this type should possibly be called double branching type. In this type in one node of the original rachis from 30 to 40 florets are present, and since they are so closely packed the fruiting ability is low and they are characterized by small grains.

Crossing between branched spikes and normals spikes

As mentioned above, hitherto strains which showed branching tendencies were bred by selecting additional spikelets appearing among normal spikes. Now, in order to determine or otherwise clarify the heritability it becomes necessary to conduct crossing experiments. During the years 1960~63, MR1 strain with branching was crossed with an entirely different variety T-186 which had normal spikes. In F_1 the spikes were normal, however, in F_2 of 70 individual plants two were short ramification and another two showed additional spikelets; namely a total of four abnormal spikes were seen. Incidentally, since T-186 was awnless and the MR1 strain was slightly awned, the conditions of awns were analyzed. As a result, there were 22 awned against 48 awnless in F_2 generation. When compared with this segregation ratio, it can be said that the appearance of branched spikes is extremely low.

But again, during the years 1970~73, MR1 strain with branched spikes was crossed with variety Norin 35 which also had normal spikes. At F_1 a fairly high segregation of 16 normal against 25 branched spikes or additional spikelets were seen. But, this branching character was poor as compared with that of the parent branching form. In spite of the limited number of crossings, it is apparent from them that these ten years the branching tendencies have increased with years and fixed as hereditary characters. Some combinations make an appearance in F_1 , however, the other did not appear until F_2 , and since the segregation ratio is complex it would be impossible to assume the number of genetical factors, for instance polygene, and to give a satisfactory explanation.

Discussion

Since LYSENKO pointed out the importance of breeding branched wheat, even when limited to *T. vulgare*, a large number of reports have been made to date in the SOVIET Union and East European countries (LONSKII, LYZEI, MUHIN, VASIN, MJAKOV³⁴), VIGOROV, FEDOROV, STOLETOV³⁵), IVANOV et al³⁶), VISLOTSKA and ROZENGNALOVA³⁷). On the above, WISLOTSKA and ROZENGNALOVA reported that the frequency of branching did not increase and that branching is not a hereditary character and entered a doubt in regards to the effect of progressive selection. With the exception of the above, all other workers reported that branched wheat may be bred by selection.

It was shown that even in MR1 strain the branched spike character increases gradually with time and repetition, in spite of MENISSER and TSCHERMAK³⁸), who had it that this was a mutation of a single gene. According to Vasin, the order of the shift to branched spikes commences from the adventitious scales like needles which appear at the base of spikelets. This shows a gradual development and becomes an added spikelet, in other words a so-called parallel type of additional spikelet, which in turn advances to a right angle type and as the last step shows an appearance of branching spikes. In MR1 strain the branching tendency, commencing from additional spikelets, was increased by progressive selection. In regard to those with a higher degree, however, in our experiments hardly any observations were made on appearance of parallel type of additional spikelets. Thus while it was possible to follow the course of development from right angle type of additional spikelets to branched spikes, the course from scale-like process to parallel type was not seen in the MR1 strain.

As may be apparent in the experimental results shown in Table 7, the frequency of character appearance was high at the outer fringes of the field, and low in the central areas. In regard to this point it has been noted hitherto that in field cultivation the yield of the outer fringes is higher than the center parts (refer to HAYES and GARBER³⁹).

That the appearance of character of branched spikes is influenced by nutritional conditions was also confirmed by another point. In other words, in the relationship between spike shape and final leaf, while in the length of final leaves no significant difference was seen, in the leaf width a significant difference was present. This indicates that the final leaves of stems which produced branched spikes when compared with the final leaves of non-branching forms, generally had wider leaves. The formation period of

final leaves coincides with the formation period of spike primordium and the fact that a significant difference was seen in the width of final leaves when it can be assumed that these plants are genetically the same, clearly shows that this difference comes from the difference in nutritional conditions during the course of development of the individual plants. Thus it may be assumed that the broader final leaf appears when the nutritional conditions are favorable and in such a case they may also lead to the formation of branched spikes.

From the above, it is conjectured that the appearance of branched spikes is strongly influenced by environmental conditions such as nutritional conditions and light length etc. But, it is clear that the influence is not limited to environmental conditions and is hereditary. This may be said because almost no branching is seen in other varieties under the same cultivation conditions, and it is also clear from the crossing experiment with varieties which showed no branching tendencies. Thus the branched spike character as seen in MR1 strain, may be considered as the result exerted by inheritance (internal conditions) and environmental conditions (external conditions). That environmental conditions play an important role in the appearance of branching character may readily be seen in VIGOROV's report, in which it is indicated that branched spikes were obtained in highly fertile soil and also in RYZEI's who after removing the majority of the spikelets gave abundant nutrition to the remaining spikelets and produced branched wheat.

Whereas, in the present experiment, in MR1 strain, the types of branched spike obtained may be divided into long ramification, short ramification and super short ramification. Genetically no qualitative difference was seen among the three. As may clearly be seen in morphological observations, short ramification is a type in which the 1st and 2nd floret show no change while the florets above the 3rd change into spikelets. In contrast, in long ramification type the 1st and 2nd floret also change into spikelets. Therefore, the difference between the two lies in whether the 1st and 2nd floret change into spikelets or not. When the 1st and 2nd floret do not change and the spikelets transform into branched spikes, the original empty glume remains intact. When the 1st and 2nd floret change into spikelets, the original empty glume forms a pair with the newly formed empty glume and protect the 1st and 2nd new spikelets.

According to ARBER⁴⁰⁾ and HITCHCOCK⁴¹⁾, the spikelet is a axillary bud, and the empty glume or lemma is homologous to the bract, while the palea is homologous to the prophyll. The difference between the empty glume

and lemma depends on whether florets are present beside them or not. In the course of development of long ramification type, where there was only one empty glume each at the 1st and 2nd new spikelet, a pair is formed and helps the complete development from rachilla to branched rachis. The difference between the growth of rachilla in long and short ramification may have something to do with this point but little is known.

Both of the above types have their basis in the single transformation from floret to spikelet, but as described before in the new super short ramification type, a second qualitative transformation took place which may be called double transformation type. While no actual reports are seen to date in regard to this type, TAKASHIMA's branched wheat obtained from Norin 16 and 52 is no doubt super short ramification.

According to FEDOROV^{42,43}) slowing up of differentiation of the growing point is brought about by using the long day treatments and at the same time branched spikes are formed by giving abundant nutrition to encourage growth, and as a result of delay in the differentiation of flower buds, the organ which should become florets shows an extra differentiation. And when the advancement of this extra differentiation results in the transformation of florets to spikelets, author finds that this is a hypermorphic phenomenon, namely, if the primordia which are to become the various organs of florets undergo a second differentiation and in turn form several primordia, the florets will transform into spikelets. Thus it may be said that the origin of branched spikes, from a histological point of view, has its basis in the transformation from floret to spikelet and in an orderly transformation.

According to VASIN, the formation of the parallel type of additional spikelets is a supplementary course, and then it transforming into right angle type. But the author could not find evidence of the relationship between parallel type and right angle type of additional spikelets. Namely the author is of the opinion that the parallel type and the right angle type are different in nature.

Whereas WADDINGTON⁴⁴) suggested his genetic assimilation theory from his experimental work in phenocopy, it is clear that his ideas are based on polygenics. In his elucidation of acquired character, he has it that selection is possibly only in the presence of genes and states that it is a result of cumulative polygenic factors. As regards the morphological aspects of branched spikes in MR1 strain, based on crossing experiments and others, it seemed unreasonable to consider a single gene. It would seem that in this character appearance various factors are concerned. Thus it was indicated that these factors are none other than several physiological factors

which have something to do with the metabolic system in the plant body. In environmental conditions in which the plant bodies can show a substantial growth, when such multiple factors are allowed sufficient influence, the appearance of the character of branching spikes would seem possible. But when the environmental conditions are such that the physiological influences are not completely satisfied, it would seem that branched spikes would fail to make appearance and normal spikes would appear. At all events insofar as the branched spikes in MR1 strain are concerned, it would seem that the appearance of branched spikes becomes possible only when the internal hereditary influences and the external environmental conditions at the same time exert their character.

Conclusion and summary

As a result of progressive selection in branched wheat, it was clearly demonstrated that the appearance of character by gradual selection is accumulated quantitatively and qualitatively. Whereas additional spikelets at a glance may seem as a supplementary phenomenon, it was shown that as intimate relationship with branched spikes was present. Namely, the additional spikelet type comes from the transformation of 1st floret to spikelet, while long ramification is the result of transformation of 1st and 2nd floret or more of florets to spikelets, and short ramification is the result of transformation of the 3rd floret or more of florets to spikelets. In MR1 strain, super short ramification was also seen. Among these four types no single gene difference was seen. In all types the transformation of florets to spikelets is the basis, and this phenomenon is considered as hypermorphosis of organ formation.

The factor which is concerned with the appearance of hypermorphosis is that relationship between growth and development of organisms as reported by LYSENKO⁴⁵⁾, which is under a strong influence of nutritional conditions. As mentioned above, while the transformation from floret to spikelet may be explained as a hypermorphotic phenomenon, it may be pointed out that the character which resulted from the influence of environmental conditions was definitely not in the nature of casual appearance, and that by progressive selection the character increased in intensity to the level of heredity. Thus, the cumulative results of changes with a definite direction may readily be explained as heredity of acquired character.

The branched spikes obtained in this experiments are the result of hypermorphotic expression in the initial stage of development in which several physiological factors are combined. As a result of selection, the

appearance of branched strains may be considered as the result of balance of growth and development in the plant. In this case, it may be considered that strains with rapid development, as compared with growth, were selected. Based on above views, assuming that these various physiological factors are polygenic, it would be seen entirely appropriate to recognize the inheritance of acquired character.

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