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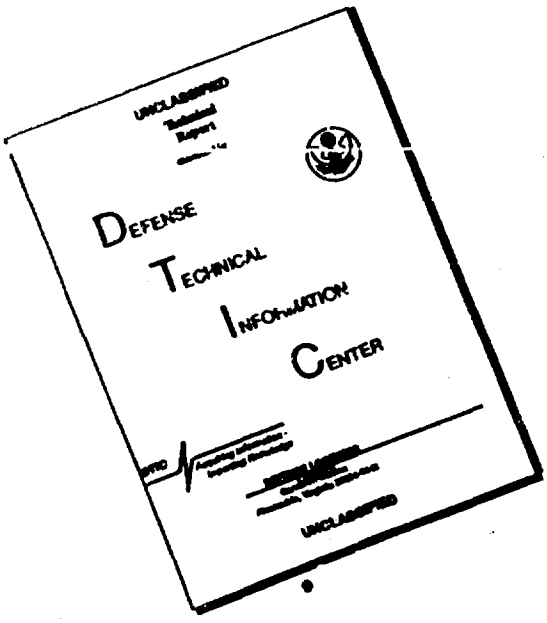

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EXPERIMENTS IN CHANGING THE NATURE OF WHEAT THROUGH VEGETATIVE HYBRIDIZATION

In this report we describe some of our experiments in vegetative hybridization of wheat conducted in the years 1940-1942. We concentrated on the transplantion of embryos of the seed of certain varieties upon the endosperm of other varieties and species of plants. Here are the results of the transplantation of embryos of wheat onto the endosperm of rice.

The choice of the embryo seed for a scion was based, first of all, on the fact that the embryo--the younger phase of plant life--is more easily influenced by external factors. It has been established that the embryo seed can develop not only on its own endosperm but also on a strange one.

The seed of wheat of Erytrospermum 0841 and Melianopus 069 were selected for the experimental work. The seed of rice of the Karatal'skii 8679 variety was selected for the stock (endosperm). After causing a slight swelling in all experimental seed, their embryos were cut off together with a small part of the endosperm (to avoid injuring the embryo). The wheat embryos were pasted with wheat dough to the emdosperm of rice on which the small area obtained after removing the embbryo expanded a little. The embryos grew firmly onto the rice endosrerm. The total number of grafts made was 100.

The grain of wheat thus prepared were planted at the end of April in paper cups filled with sand and a slight admixture of soil. In growing the plants by the method described, the wheat embryos enjoyed the nutrients derived from the substances of the rice endosperm.

Almost all of them germinated, but from thence their fates differed.

Most of the sprouts perished early; some of them succeeded in developing one or two regular leaves and then perished, and only a few specimens developed to the point of the formation of generative organs. Some sprouts may have perished as a result of insufficient nutrition due to the loss of contact between the embryo and endosperm.

Up to the phase of heading there were left 16 specimens of wheat. A few of them formed branches, but most of them produced only one stem. Many stems formed spikes which fluctuated in length from 1 to 10 cm. (begin p. 49) The spikelets of all spikes had scales of spikelets and buds, but the stamen and the pistils were absent from most of the bud. Although in fourteen out of sixteen plants the spikelet bud scales were well formed, they began early to turn brown and to fall off, so that nothing but the core was left of the spike. Only one plant of the Erythrospermum variety (fig. 1) and one plant of the Melianopus variety produced one spike with kernels each. Fifteen kernels were found in the spike of the first plant and in the spike of the second plant--8 kernels. The grains in both spikes were, gendrally very small and shrivelled, sometimes a little larger, but there was not a simple normal, fully developed grain. The grains in the grafted Erythrospermum were considerably whiter as compared with the original form. The only Erythrospermum spike which produced grains was distinguished bu a strong pubescene of the spike and flower scall, by porosity, by a large number of flowers in the spike--up to 11, counting the poorly developped and sterile flowers. Another spike of the same specimen disintegrated completely.

The fruit-bearing specimen of Melianopus (fig. 2) produced 3 spikes.

Fig. 1- Left -- Original form of Erythrospermum 0841.
Right-- Grafted plant (Photo of 1940).

Fig. 2 - Grafted plant of wheat, Melianopus 069 onto the endosperm of rice.

One grain-bearing spike had abnormally curved awns and a more porous structure than is normal. (Begin p. 50) The number of flowers in thespike came to 9, but only 6 were fertile. Another spike, also abnormally porous, had no awns, was sterile and soon disintegrated; a third spike -- compact, somewhat club-shaped, without awns and sterile.

Such were the hybrid plants of the wheat obtained in 1940.

To demonstrate the diversity of the plants grown form the seed obtained by vegetative hybridization, I shall describe the results of the crop from the seed harvested in 1940. As indicated above, only 2 spikes of two plants produced seed; the plant of Melianopus wheat yielded 8 grains, and the plant of Erythrospermum wheat -- 15 grains.

These grains were sown in a greenhouse on April 21, 1941. In the case of Melianopus all eight grains germinated, in the case of Erythrospermum only ten. On April 30 the plants were transplanted in the field. On the Melianopus plants 2 specimens reached the stage of seed formation, of the Erythrospermum plants -- 7 specimens.

The rest of the plants dried up and perished at certain stages of their development, or they produced sterile spikes. Harvesting of the plants was carried out on July 31, which means that vegetative period lasted exactly 102 days.

I shall describe briefly some of the vegetative hybrids derived from Erythrospermum and rice. Plan No. 1, first generation (fig. 3). Height of the plant 88 cm, length of spike -- 15 cm. Two spikelets are perched side by side at the bottom of the second, third and fourth rachises each; in addition to these three twin spikelets there are also 19 single spikelets. The total number of spikelets in the spike is 25 (including the three pairs of twins); grains -- 106. Qualitatively all grains are satisfactory, they are white of pibment and barrel-shaped in form.

Plant No. 2 (fig.4) reached the height of 82 cm including the spike. The spike contained 22 rachises. There were two spikelets on each -- the first, second, fourth, fifth, sixth, seventh and eighth rachises; on the remaining fifteen rachises there was one on each.. The number of grains in the twin spikelet ranged from one to five, in the upper six -- none.
(several words deleted) The 77 grains found in the spiked described were poorly developed, thin and of white pigment.

Plant no. 3 had especially large leave; the blades of the upper left -- 30 cm long and 1.8 cm wide (at the part where the width is broadest). The blade of the leaf is thick and has sharply protuding veins. In the one and only spike, twin sterile spikelets were found underneath the second and fourth rachises.

The first and third single spikelet are likewise sterile. In the rest of the spikelets; four grains each (1 spikelet), 3 grains each (3 spikelets), 2 grains each (6 spikelets) and one grain each (8 spikelets); total number of grains in the spike -- 33. The grains were full, large grains, but there were also small and poorly developed grains. Color and the form were the same as in the preceding ones.

A new characteristic which appeared in this generation is the distribution of twin spikelets on some of the rachises in a number of spikes. This characteristic was found in the progeny in the same incidence through the year 1946.

In 1941 new grafts were made. The embryos of wheat were grafted onto the endosperm of Karatal'sk rice; Tsezium 0111, Erythrospermum 0341, Melianopus 169 and Gordeiforme 0189. Altogether there were 400 graftings. The seeding was carried out on April 29.

On May 14, some plants with two leaves each were removed from the soil for inspection. Acyme could be clearly observed in the wheat embryo while it was in the ground. The part of its own endosperm which adjoins the cyme, left there when the operation was performed was completely absorbed; (begin p. 51) it had left on the cyme cavities and depressions containing reserves of nutrients. Nothing was left of the rice endosperm except the membrane; the wheat embryo had used up all the substances of the rice endosperm.

Fig. 3 -- First generation of hybrid wheat Erythrospermum grafted onto rice.

Fig. 4 -- First generation of hybrid wheat Erythrospermum grafted onto rice

Only 16 plants reached the phase of fruiting, and, in addition, three plants developed with sterile spikes. Partly sterile spikes were found in fertile specimens; for instance; a spike of Erythrospermum 0341 had a total of 14 spikelets, yet only 5 of these yielded 6 grains.

In hybrid plants of wheat emerged properties which are absent in the ordinary plants of the original varieties. These new properties are unequally distributed not only among separate specimens, but also within the bounds of a single branch and even a single spike. I shall cite examples of certain variations.

For instance, in one specimen of Gordeiforme the upper internode bearing the spike is 8 cm long; it ends with a spike 4.5 in length; both, the internode and the spike were confined in a strong sheath 18 cm long. The spike, markedly bent,, partly crumbled and sterile, emerged together with the internode that bears it not through the opening of the sheath apex, but through an opening in the side wall of the sheath. In another specimen of the Gordeiforme the spike came out only halfways and was sterile. There are perfectly shaped spikes which look normal, but are sterile.

Alongside of the plants that yielded 6, 11 and 20 grains, there are spikes which produced 75 grains in 15 spikelets, 78 grains in 18 spikelets etc. At times, the kernels were very fine, thin and poorly developed, at times -- large and well filled out.

The kernels in the wheat referred to above as Erythrospermum 0341, were distributed in the spike as follows: in the first, fourth, eighth and ninth spikelets --

one grain each, in the seventh -- two grains, the the remaining nine spikelets no grains whatever. Spikelets with a varying number of flowers, up to eleven were found in some hybrids. The number of grains in the spikelets was just as varied -- from zero to seven.

Awns are subject to strong variation. In some Gordeiforme spikes the awns are very long (up to 23 cm), curved, and, at the top, strongly diverge in different directions -- the space between the tips of the awns measures 22 cm. In other Gordeiforme plants the awns project straight upward and rise above the spike only 5 cm. Finally, there was a plant with practically no awns on the spike; only in two spikelets the flowers had awns up to 4 cm in length, but in the rest of the flowers the scales taper off either with awns up to 1mm, or into a sharp point. The awns in experimental plants of Melianopus wheat are also extremely varied as to length and pigment (from black color to white), they are of a different length and color even in one and the same spike, and even the same awn is differently colored in different parts.

An interesting phenomonon is the branching out of the stem. Branching was observed in experimental plants of two varieties: Melianopus and Gordeiforme. For instance, in Melianopus 069 (fig. 5) a side shoot emerges from the axil of the third leaf; the stem is 4 cm long; it has at ist tip a spike 2.3 cm long, and including the awns -- 13 cm long. The spike boars a spikelet with eleven sterile flowers. On the same plant, a sedentary spike, 2 cm long and 1.8 cm wide at the upper and broadest part, emerged from the axil of the fourth leaf. The single spikelet had 7 flowers with awns up to 7.5 cm; the spikelet yielded two good and one sickly grain. The top spike of this plant (length 5 cm, and with awn -- 13.5 cm) is found on the upper internode, 4 cm long. The awns are yellow-green at the base, yet at the central and upper parts they are slightly gray-brown to brown and even entirely black (different awns are differently colored). Long awns are found only in the lower flowers, the rest have either none or some that do not exceed 7 mm. A spike that has 19 spikelets; one of them had seven flowers and yielded 5 grains. The rest of the spikelets were sterile.

Out of ten plants, Gordeiforme produced three plants with ramose stems. One of these plants is constructed as follows: from the axil of the third loaf emerges a stem with two internodes: the first -- 3 cm long, and the second -- 1.77cm. The latter ends with a spike 3 cm long, with the awns 10 cm. The spike produced 8 small but full grains. From the leaf axil of this axillary shoot another stem grew out -- 2 mm long -- and ended with a spike 1.8 cm long and with the awns 5 cm long. This spike produced six grains. The top spike yielded 11 shrivelled poor grains. From three spikes of one stem a total of 25 kernels were harvested.

In another plant of Gordeiforme 0189 (fig.6), the lower spikelet of the top spike lags 3 cm behind the others; the length of the rest of the spike is 6 cm.

The longest awns are those at the top, up to 4.0 cm; in the middle part they are considerably shorter, and the lower spikes have no awns. The spikes yielded 19 grains. From the leaf axil a stem grew out ending with a 6 cm long spike. The spike had 15 spikelets which contained 48 grains. The largest number of grain in a spikelet was five; the length of the grains fluctuated from 4.5 to 8 mm. The longest awns were in the middle part of the soike; the spikelets at the top and at the bottom had no awns whatever.

Fig. 5 -- Plant of the Melianopus 069 variety grafted onto the endosperm of rice.

Fig. 6 -- Plant of the Gordeiforme 0189 variety grafted onto the endosperm of rice.

Among plants with non-ramose stems were found spikes which contained more than 70 kernels. Many spikelets of the same plants contained an increased number of flowers and grains.

All seed of the 1941 crop were sown in the field on May 11, 1942. The sowing was carried out with a spacing of 65 x 35 cm. The plants were harvested on August 29.

An analysis of the first generation of wheat plants, spikes and spikelets of Erythrospermum 0841 produced a great variety. Regardless of the fact that Erythrospermum has long awns, all the hybrid plants of 1942 were nearly awnless; awns were found only in five-six upper spikelets, yet not in all of them and their length dis not exceed 1.5 cm. The number of spikelets in the spikes fluctuated sharply; from eight to twenty-five. The same in the preceding year, twin spikelets were found on some spikes, i.e. not one, as is customary; but two and sometimes even three spikelets were located on one rachis. The number of these twins fluctuated between one and eleven (there was one spike on which 11 twins and 4 single spikelets were perched on fifteen rachises). More often than not thes twin spikelets were sterile. The spikelet and flower scales were strongly depressed.

The number of flowers in the spikelet also varied. There were spikelets with three flowers, yet spikelets with eight flowers were also encountered. There were sterile spikes with but tow-three grains, yet there were also spikes containing more than fifty grains (the largest number was 85 grains, and in a spikelet -- 7 grains).

The progency of wheat grafted in 1941 was marked by the absence of ramose forms. Productive bushiness was varied; the number of stems with reproducing spikes fluctuated in individual plants between 1 ans six; yet concomitantly, entirely sterile spikes were found in the very same shrubs. There were also plants which has sterile spikes only.

The number of kernels in different spikes is also quite varied; variations were observed also in the dimensions ans in other properties of the kernels. Much variation was observed in the awns.

It should be noted that culture of the seed of Erythrospermum 0841, first obtained in 1940 by growing its embryo on the rice endosperm, was continued annually through 1946. Many variations survived seven generations. Figure 7 shows the multiformity of spikes obtained in the sixth generation (1946).

First of all, one notes the conspicuous absence of awns which, in the original form of Erythrospermum 0841, were twice as long as the spike. The spikes of hybrids are considerably longer than the spikes of the original form grown, for comparative reasons, under identical external conditions. Thus, the spikes of the original form are most frequently 8-9 cm long, yet the average length of the spike of a vegetative hybrid is 11-13 cm. In structure the spikes are dissimilar; there are spiles with twin spikelets, i.e. two spikelets (occasionally even three spikelets) are perched on one rachis. At times the spikelets are multiflorous and yield but 2-3 grains; seen from the face, the first are considerably wider than the latter.

The spikelet and flower scales are thckly furred, this characteristic is less pronounced in the flowers at the top of the spikelet. The kernels are closely

encased in the flower scales and do not spill.

Big differences are observed in the kernels. In the original form they are red, comparatively thin and long. Hybrid kernels are white with a slight yellowish hue, shortened and thicker (fig. 8). Equal amounts of the largest kernels of both forms were used for dimensional comparison; the length of kernels from the original form equalled 8.3 mm, and the width-- 3.3 mm; In the hybrid form the corresponding sizes were: 7.3 mm and 3.8 mm. The maximum length of the kernels of the original form -- 9 mm, maximum width -- 3.5 mm; the corresponding sizes in the hybrid form; 8 mm and 4.5 mm. Therefore the weight of the selected largest seeds of both forms of wheat is fairly close: 1000 grains of the original form weigh 51 grams, of the hybrid -- 55 grams.

Fig. 7 -- Variation in the form of spikes of the vegetative hybrid Erythrospermum 0841 x rice in the sixth generation (1946)

If the form and structure of the spike do not as yet represent stable characteristics (multiflorous and multi-grain spikelets, the presence of twin spikelets on the rachis), then the form of the endosperm, are extremely varied and extend to the generative organs as well as to the vegetative ones, while they become fixed in the seed offspring.

Among hybrid plants are found superior, economically valuable forms. For instance, plants, the grain of which have the absolute weight of 47 g, arouse considerable interest. The specimens which yield 5-6 reproductive spikes etc. are also valuable. It is our task to secure in the following generations these superior traits of altered plants.

On the basis of observation of the hybrids obtained, it is possible to draw certain preliminary conclusions as to whether those valuable properties which would be desirable not only to preserve, but also to strengthen in the new forms, are tapering out, or are progressing while the generations are in the process of development.

The overwhelming majority of agricultural characteristics, such as spike formation, high quality of grain (fulness, dimensions), productivity per plant among the better specimens produce in the offspring higher indicators in comparison with the parent forms. The amount of grain in the spikelets increases, but the number spikelets in the spike decreases somewhat, hence here is a decrease in the amountof grain per spike; but this does not occur in all plants.

It was mentioned above that culture of the progeny of a plant grafted in 1940 continued through the year 1946, and that if firmly retained many positive indicators.

Among the hybrid plants obtained are found quite a few shortcomings (sterility etc.), but there are also many valuable properties. Yet of the highest importance is the fact that by practicing vegetative hybridization it is possible to obtain offspring of the kind of plants in which sexual hybridization is impossible (rice and wheat). The practice of directed culture and selection of the best plants for vegetative hybrids will produce economically highly valuable forms with properties that will sharply differ from those in the initial material.

Fig. 8-- Top row --
Kernels of the original form of Erythrospermum 0841; Bottom row
Kernels of the hybrid form of Erythrospermum.

CONCLUSIONS

1. Introduction into the tissues of an embryo, that is beginning to develop, nutritive substances unadapted to its nature, diverts the course of the developmental processes from the normal and, as a result, new properties are formed in the plant cells; these properties appear in the form of distinguishing morphological and physiological plant characteristics.

2. Various new characteristics do not appear immediately in the year the grafting is performed, but they continue to form and develop in subsequent generations.

3. The instability of characteristics, the disappearance of former ones, appearance of new ones, indicate a mutability, an inconstancy of the inherited nature of vegetative hybrid plants.

4. Cells and tissues, the generative as well as the somatic, consist of multiple properties within the limits of a single plant, a single spike, spikelet, bud.

5. In our experiments in addition to the general disturbance of the hereditary properties of wheat, the hybrid plants were fed some of the properties of rice. We refer to the change in the color of grain from red to white, the compactness of flower scales, reduction of dimensions and color of awns, appearance of pubescence on the scales of spikelets and flowers, and some others.