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# Genetics and Breeding in the Improvement of the Soybean

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UNIVERSITY OF ILLINOIS  
AGRICULTURAL EXPERIMENT STATION  
BULLETIN 384





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# Genetics and Breeding in the Improvement of the Soybean

By C. M. WOODWORTH, Chief in Plant Genetics

## INTRODUCTION

**A**NATIVE of the orient, the soybean has proved a valuable addition to American crop plants. Since its introduction into the United States it has spread over much of the territory east of the Mississippi river, becoming well established in the crop schemes of this area. It has many characteristics to recommend it to American agriculture. Being a legume it has the ability to utilize the free nitrogen of the air thru the symbiotic relationship with bacteria living on its roots, and is therefore of value from the soil fertility standpoint. The plant itself is high in nutritive value, the seeds especially so, making it particularly valuable as a livestock feed. The crop also has high commercial value, the seed furnishing oil and other products useful in industry.

Hundreds of varieties of soybeans have been brought into the United States thru the plant introduction service of the U. S. Department of Agriculture. Practically all as introduced were badly mixed and had to be purified before they could be multiplied for trial in different parts of the country. In this work single plant selection has been resorted to, for the most part, rather than the elimination of rogues or off-type plants. As a result of the work done by the U. S. Department of Agriculture and subsequent work by various state experiment stations, numerous types have been developed that differ in maturity, habit of growth, seed color, and special adaptation to varying soil and climatic conditions.

The work of developing this versatile plant to its full possibilities, however, is only in its beginning. The problem is complicated, and will take long and patient study. In this bulletin an attempt has been made to bring together the essential information on soybean genetics available at the present time; to discuss the principles of breeding that are applicable to soybean improvement; and to review the results of investigations made at this and other institutions with a view to improving the crop in certain special features.

## DESCRIPTION OF THE PLANT

The soybean belongs to the genus *Soja*, family *Leguminosae*. This genus contains about fifteen species that are native of Asia, Africa, and Australia. Only one species, *Soja max*, is of any economic importance. The wild soybean, *S. ussurriensis*, as grown at Urbana is very fine-stemmed, prostrate in habit of growth, and very late in maturing. It is probably the type from which our common varieties have descended.

The soybean plant is an erect, bushy, rather leafy annual and attains a height of several feet under favorable conditions. If given sufficient space in which to grow, it branches profusely from the lower nodes of the main stem, but if the plants are crowded, very little branching occurs. In general, the soybean may be said to be indeterminate as to habit of growth. Types are known, however, that differ greatly from the typical indeterminate habit, resembling plants showing the determinate type in that there is a terminal inflorescence. In some indeterminate varieties the stems are so fine and small at the tip that they show a tendency to twine about one another.

Like the clovers, the soybean plant has trifoliolate leaves; that is, each compound leaf is made up of three leaflets. Occasionally compound leaves with four and five leaflets have been observed. The first leaves to appear above the cotyledons in the seedling are simple, and these are opposite, one on each side of the stem. The compound leaves originate at the nodes and are alternate. The shape of the leaflet is ovate-lanceolate (Piper and Morse<sup>35\*</sup>) but a few types are known in which the leaflets are narrowly lanceolate or almost linear. The leaves, as well as the stems, are covered with numerous fine hairs, the pubescence, except of course in glabrous varieties. As the time of maturity approaches, the leaves of yellow cotyledon varieties turn yellow and finally drop off, but in green cotyledon varieties the leaves do not turn yellow—they remain green until they finally drop off, leaving the stems bare except for the pods.

The flowers are borne in axillary racemes or peduncles at the nodes. Considerable variation exists in the average number of flowers per raceme in different varieties. Flowers appear first at the base of the main stem, then progressively toward the tip, and this order of blooming is followed on the branches also. The period of flowering in the soybean is usually not over three weeks. Hence the pods come to maturity at almost the same time. This is of considerable importance from the standpoints of harvesting and subsequent handling of the crop.

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\*These numbers refer to literature citations on pages 402 to 404.

Soybean pods are small, containing one to four seeds. The proportion of 1-, 2-, 3-, and 4-seeded pods varies greatly in different varieties as well as in different plants of the same variety. Soybean pods are straight or slightly curved like a scythe. In size they show a relation to the size of the seeds they contain. Varieties with large seeds bear large pods, and those with small seeds, small pods. In all but the glabrous varieties the pods are covered with numerous fine hairs, the pubescence. Soybean pods are two-valved. The shattering or bursting apart of the valves or halves of the pods is an objectionable feature because the seeds are scattered over the ground and lost. The tendency to shatter is, to some extent, a varietal characteristic. Pods of some varieties shatter badly, others only slightly.

The seed of the soybean is pea-like, containing an embryo, two cotyledons, two seed coats, but no endosperm. Practically all the food material in the seed is contained in the cotyledons. The seeds of different varieties vary in shape from round to elliptical and from small to large in size. The hilum, or seed scar, is the place of attachment of the seed to the pod. Usually the seed separates from the pod cleanly, leaving the hilum with a smooth, straight surface, but in the Soysota variety, as noted by Owen,<sup>32\*</sup> the seed separates from the pod in such a way as to leave the hilum with a characteristically rough surface. The seeds are attached to one side of the pod only. This is readily seen when the two halves of the pod are broken apart. Also in multi-seeded pods the seeds are attached first to one side of the pod, then to the other side, and so on, giving a zigzag arrangement.

Soybean seeds with two embryos have been observed by Owen.<sup>29\*</sup> These occurred in a Chinese variety to the extent of .44 percent (based on a sample of 5,000 seeds). There apparently exists a tendency for the abnormality to be inherited in this variety. An occasional double embryo seed was also observed by Owen in the Mandarin and Manchu varieties. The two embryos inclosed within the same seed coat were not identical, as pointed out by Owen, since in progenies segregating for cotyledon color two cotyledons were of one color and two of the other color. Hence it appeared likely that two ovules were fertilized and developed independently within the same seed coat.

As stated above, the soybean seed has two cotyledons. In tests at the Illinois Station a three-cotyledonous seedling (Fig. 1) occurred in the Virginia variety. This seedling was propagated in the field and seed was saved. When tested in the greenhouse, six seedlings (3.3 percent) out of a total of 182 showed a third cotyledon. In two of these, two of the three cotyledons were not completely divided. In ad-

dition one seedling had four cotyledons which were not completely divided. Since the percentage of such types is higher than has been observed before at this Station in this or any other variety, it would appear that there is a tendency for this abnormality to be inherited.

### METHOD OF REPRODUCTION

The soybean is normally a self-fertilized plant. The flowers are perfect, producing both pollen grains and ovules. As pollination occurs when the flower opens or a little before, there is very little chance for pollen from other flowers on the same plant or on different plants



FIG. 1.—A SOYBEAN PLANT WITH THREE COTYLEDONS

Such plants are rare. The variation is probably inherited. It will be noticed that this plant also has three primary simple leaves, while plants with two cotyledons have only two such leaves.

to enter and effect fertilization. Nevertheless a small amount of natural crossing does occur, as will be shown later. Since the soybean plant is almost exclusively self-fertilized, it is pure for its hereditary characters unless of course it is a hybrid or the offspring of a hybrid. The principles of breeding that apply to self-fertilized crops, such as wheat, oats, and barley, apply as well to the soybean. .

### EXTENT OF NATURAL CROSSING IN SOYBEANS

There is considerable evidence for the occurrence of natural crossing in the soybean. Piper and Morse<sup>34\*</sup> found in a bulk lot of seed

certain oddly colored seeds some of which produced plants whose progeny showed segregation in various seed and plant characters. These authors did not determine the amount of natural crossing but believed it to be "small, perhaps not one individual in two hundred." Woodhouse and Taylor<sup>54\*</sup> grew seventy-five or more plots, each derived from a single plant, and found one of these to be a hybrid. They concluded that "natural crosses do not occur on the plains of India to such an extent as that noted by Piper and Morse in America." Hayes and Jones<sup>16\*</sup> selected single plants from a mixed variety and found that the progeny of each bred quite true to the parental type. They suggested natural crossing as one way in which a variety may become mixed but stated that, "No clear cases of natural crosses are known to the writers to occur in soy beans but it is not unlikely that crossing does sometimes take place."

During the course of certain genetic studies on soybeans, Woodworth<sup>60\*</sup> observed a few plants whose progeny segregated for various plant characters. In an attempt to get at the amount of crossing more accurately, two experiments were conducted. In the first, white-flowered plants were planted between purple-flowered plants and seed saved only from the plants bearing white flowers. When these were tested the next year, none of them were found to be hybrid. In the second experiment cotyledon color was used as the criterion of hybridity in place of flower color. Plants of a green-cotyledon variety were planted in rows in such a way as to be entirely surrounded by plants of a yellow-cotyledon variety. Thus ample opportunity was afforded for natural crossing to occur. As green cotyledons are recessive to yellow in inheritance, and as cotyledon color is a character manifested in the seed, a natural cross between green ♀ and yellow ♂ would result in a yellow-cotyledon seed borne on a plant of the green variety. Each pod of the green plants was examined separately and in a total of 7,480 pods 3 pods, or .04 percent, contained hybrid seeds. Since crossing can occur between yellow ♀ and green ♂ also, this percentage becomes .08. This is much lower than the percentage given by Piper and Morse,<sup>34\*</sup> but considerable variation in the percentage of natural crossing may be expected in different varieties, localities, and seasons. Garber and Odland<sup>8\*</sup> determined the extent to which different varieties of soybeans cross when grown in adjacent rows. Under these conditions they found that natural crossing was .14 percent in 1922 and .36 percent in 1923. The conclusion appears justified, therefore, that a limited amount of natural crossing occurs in soybeans but it is considerably less than 1 percent.

Plants whose progeny segregate may also arise as a result of mutation. Since germinal changes usually occur in only one gamete at a time hybrid plants would be the result of the union of the changed with the normal gamete, whether the mutation were recessive or dominant to the original. It is difficult if not impossible to state definitely whether a particular segregating progeny is the result of mutation or of a natural cross. However, in the case of a mutation there will be segregation usually for only one character, while in the case of a natural cross many characters may be segregating at the same time.

Natural crosses are believed to be responsible for many of the mixtures occurring in our common varieties. At first the mixtures are mechanical, resulting from the drill or the threshing machine. As these mechanical mixtures grow alongside and in contact with typical plants in the same field, there is abundant opportunity for natural crosses to occur. When natural hybrids are produced, many more off-types are added owing to segregation and recombination. Hence it is not surprising that our standard varieties as commonly grown become badly mixed in a few years.

Natural crossing in soybeans is believed to be the work of small insects. Thrips (*Thrips tabaci*) have been observed crawling in and out of soybean flowers. Honey bees, too, have been observed in soybean fields, and it is known that they work on the flowers.

Experiments conducted at the Illinois Station indicate that plants growing in contact with one another are more likely to be crossed than plants not in contact but separated by only a few feet. This is further evidence that natural crossing is due largely to small insects that travel only between plants that are growing in contact with one another.

#### METHOD OF MAKING CROSSES ARTIFICIALLY

The small size of the soybean flower makes artificial crossing a difficult and tedious operation. The writer has found that this work can be greatly facilitated by the use of a low-power binocular microscope that can be strapped to the head, thus leaving both hands free. Only three other instruments are needed; namely, a needle, pair of fine-pointed forceps, and a small pair of scissors with fine points. Best results have been secured by hybridizing flowers in the afternoon from 3 to 7 o'clock. Also, it has been found best to emasculate and pollinate a flower the same afternoon. There appears to be no advantage in delaying pollination until the following morning or afternoon.

Emasculation is the most difficult part of the operation. The flower is so small that great care must be exercised to avoid injuring the



minute and delicate organs. Also the flower may be self-pollinated in the process of removing the anthers. With the flower held in one hand the sepals may be pushed down with the needle or forceps held in the other hand and either broken off with the forceps or cut off with the scissors. The sepals removed, the corolla may be readily pulled out with the forceps, thus exposing the ring of ten stamens around the pistil (Fig. 2, *B*). The anthers are removed with the needle. With care, one is able to remove several at a time. It is best to count them



FIG. 2.—STAGES IN THE ARTIFICIAL HYBRIDIZATION OF SOYBEANS

(A) Flower in the advanced bud stage ready for emasculation. (B) Flower from which the sepals have been trimmed down and the corolla removed to show the stigma surrounded by a ring of ten stamens; when the stamens are removed, the flower is ready to be pollinated. (C) Pollinated flower covered and protected by fastening a leaf over it with a pin. As the leaf is left attached to the plant, transpiration continues, thus tending to keep the mutilated parts from drying out.

as they are taken out so as to be sure that all ten have been removed. The style is bent like a goose neck and in consequence the delicate stigmatic surface faces the base of the flower. For this reason it is particularly easy to self-pollinate the flower, for the anthers, on being removed, are often broken and the needle, with attached pollen, may touch the stigmatic surface and thus effect pollination.

Pollination is a relatively simple process, but it is often difficult to find sufficient pollen in the right stage of development. Fresh-looking flowers that have just opened are best to use. The flowers are pulled or cut off the plant, the sepals and corolla removed, and the anthers examined with the aid of the binocular microscope to see whether they have burst open and whether the pollen grains seem separate (not massed together) and in viable condition. If the pollen grains appear in the right condition, the flower is caught in the forceps and

rubbed over the stigma of the emasculated flower. Sometimes a hand lens with higher magnification than the binocular microscope is used to determine whether any pollen grains are in contact with the stigmatic surface. Then a leaf, which is left attached to the plant, is pinned over the flower to protect the exposed and injured parts from excessive evaporation (Fig. 2, C). Finally, a small label, bearing the parent numbers and date, is placed on the stem just below the flower. The instruments are dipped in alcohol before work is started on the next flower.



FIG. 3.—SOYBEAN PLANTS GROWN IN GREENHOUSE FOR USE IN HYBRIDIZATION

One-gallon jars were used, and one or two plants were grown in each jar. Artificial light from 500-watt bulbs was used in the early stages of plant growth to induce good vegetative development, then the lights were shut off to induce flowering.

Soybean crosses can be made in the greenhouse as well as in the field provided artificial light is used to obtain sufficient plant development (Fig. 3). Without artificial light the plants are small and dwarf-like; they bear few flowers, which appear not to develop and open normally and which fertilize in the very early bud stage. Without artificial light a successful cross in the greenhouse was a rare occurrence, but where light was used, the percentage of successful crosses compared favorably with the percentage ordinarily obtained under field conditions.

## INHERITANCE IN SOYBEANS

For many reasons the soybean is a good plant to work on from a genetic standpoint. There are numerous types differing in various seed and plant characters; the plant is almost entirely self-fertilized; under favorable conditions a single plant may produce several hundred seeds; and hundreds of plants may be grown within a small area. The main drawback to genetic studies in this plant is the small size of the flower, making artificial crossing a difficult and tedious operation. Nevertheless considerable progress has been made in a genetic analysis of the soybean. The genetic relations of seed-color types have been worked out fairly completely, and the same may be said of many plant characters. While much remains yet to be done, much has been accomplished during the relatively short time the crop has been studied.

### SEED CHARACTERS

#### Cotyledon Color

In the soybean the cotyledons are of two colors, yellow and green. Since the cotyledons are a part of the embryo of the seed, they belong to the next generation and therefore give expression, prior to germination of the seed, to the character of the next generation with respect to cotyledon color. Piper and Morse<sup>35\*</sup> as early as 1909 observed the color differences in cotyledons and noted further that both yellow and green cotyledon seeds occurred on the same plant. When such plants were tested, three kinds of plants were found in the progeny; namely, those bearing only yellow cotyledon seeds, those bearing only green cotyledon seeds, and those bearing both kinds; and the ratio was approximately 1:1:2 respectively. These results, while not conclusive, indicated that yellow was a simple Mendelian dominant to green.

Very different results were secured by Terao.<sup>44\*</sup> In his crosses the cotyledon color of the hybrid progeny was the same as that of the female parent in every case, and there was no evidence of segregation in succeeding generations. He thus found cotyledon color in soybeans to be maternal in inheritance.

To explain these results Terao suggested that there were two kinds of chlorophyl represented by the two cotyledon colors; one that always remains green, and one that changes to yellow on the ripening of the beans. The former was designated as (*G*) and the latter as (*Y*). If the female parent possessed (*G*) or (*Y*), the hybrid progeny, down at least to the  $F_3$  generation (as far as the experiment was carried), would have green or yellow cotyledons respectively.

Maternal inheritance of cotyledon color in the soybean has been

substantiated by Piper and Morse<sup>35\*</sup> and more recently by Owen.<sup>30\*</sup> These workers used the Medium Green variety as the green cotyledon parent. Owen made a cross between Mandarin (yellow) and Progeny No. 56 (green), which was a selection of the Medium Green variety; and between Aksarben (yellow) and Progeny No. 56. In both crosses the green cotyledon variety was used as the male parent. All the seeds borne by the hybrid plants had yellow cotyledons. A third cross between Manchu and Medium Green varieties behaved in a similar manner.

The observations of Piper and Morse, referred to above, pointed to the fact that there is, in some cases, a real segregation in cotyledon color. This was confirmed by Woodworth,<sup>57\*</sup> who found evidence for two (duplicate) genes for yellow cotyledon. A cross was made reciprocally between a variety with yellow and a variety with green cotyledons, and in  $F_1$  the seeds had yellow cotyledons, showing the yellow color to be dominant. In  $F_2$  a ratio of 15 yellow to 1 green was obtained, and when the  $F_2$  yellows were tested by their  $F_3$  progeny the expected three types of progeny were obtained in approximately the expected proportions; namely, (1) those breeding true for yellow, (2) those segregating in a 15:1 ratio, and (3) those segregating in a 3:1 ratio. The green cotyledon beans, when tested, bred true for green.

In interpreting these results use was made of an analogous case in the garden pea. While the seeds of the garden pea are still immature, the cotyledons of both yellow- and green-cotyledon varieties have both yellow and green pigments (Bunyard, see Darbishire,<sup>4\*</sup> page 131 of reference). As the peas ripen, the green pigment fades out in yellow varieties but persists in green varieties. Yellow-cotyledon varieties, therefore, are first green, then turn yellow, and differ from the green-cotyledon varieties in having a gene that causes the green pigment to fade out as the peas mature. The situation in the soybean is quite similar. All soybeans are green while immature, and as the ripening period approaches, the varieties become differentiated by the fading out of the green pigment in varieties with yellow cotyledons and the persistence of the green pigment in varieties with green cotyledons. The yellow varieties, therefore, possess a gene or genes that cause the green pigment to disappear at maturity, and these are dominant to those that permit the green pigment to remain.

Soybean varieties with yellow cotyledons differ in the number of genes for yellow. Some possess only one gene; for example, Auburn (Woodworth<sup>57\*</sup>), and others possess two such genes. Owen<sup>30\*</sup> recently used the Mandarin, Aksarben, Ito San, Manchu, and a Japanese gla-

brous variety as parents in crosses and found them all to possess two (duplicate) genes. Woodworth<sup>59\*</sup> added Midwest, S.P.I. 20406, S.P.I. 65345, Ilsoy, Wea, and twelve other types introduced from China to the list of the two-gene varieties. Only four varieties have been found that possess only one gene. These are Auburn (above mentioned), Mikado, Wilson, and an introduction from China designated Progeny 2262. More recently five more varieties have been added to the list of two-gene varieties and one more to the list of one-gene varieties. Therefore, of the 33 varieties studied, 28, or 84.8 percent, possess two genes for yellow cotyledon. This situation is the opposite of what might be expected. After examining the various possibilities of accounting for the preponderance of two-gene varieties, Woodworth<sup>59\*</sup> concluded that at that time there was no satisfactory explanation.

The symbols originally used for these duplicate genes for yellow cotyledons were *D* and *I*. Recently these have been changed to  $D_1$  and  $D_2$  respectively. The corresponding recessives are  $d_1$  and  $d_2$ . These genes are independent in inheritance and hence are borne on different pairs of chromosomes. So far as the character manifestation is concerned, they appear to be exact duplicates of each other.

There are, therefore, two kinds of green cotyledon varieties; namely, (1) a kind which in crosses with yellow types shows no segregation in cotyledon color (maternal green); and (2) a kind which in crosses with yellow types shows segregation and is differentiated from yellow by genes residing in the chromosomes (genetic green). The first type is a light or yellowish green, the second, a deep chromium green. So great is the difference in the intensity of the green color in these two types that they can be fairly well distinguished (on this basis alone) without the necessity of making test crosses.

More recent work (Veatch and Woodworth<sup>48\*</sup>) at the Illinois Station on cotyledon color indicates that the maternal green carries genes  $D_1$  and  $D_2$  for yellow cotyledon on its chromosomes. Among the soybean crosses recently made was one between genetic green ♀ and maternal green ♂. The crossed seeds were yellow just as tho a yellow cotyledon type had been used as the male parent. Furthermore, when the  $F_1$  plants were grown, segregation for cotyledon color occurred in a ratio of 15 yellow to 1 green showing that the maternal green parent had contributed duplicate genes for yellow cotyledon to the hybrid. Segregation for other characters in which the parents differed proved that the parents were as indicated above. Also many other crosses of the same kind have been made always with the same result. There is good evidence, therefore, that the maternal green soybean is a genetic yellow so far as chromosomal cotyledon genes are concerned.

In the above article Veatch and Woodworth postulated that another type of maternal green could be produced, tho so far as known it did not exist at that time. Reference is here made to the type which carries genes  $d_1$  and  $d_2$  for green cotyledon on the chromosomes, a maternal green which behaves as a genetic green when used as the male parent in crosses. It is believed that this type has now been produced. The procedure outlined in the above article was carried out as follows: A cross was made between maternal green ♀ and genetic green ♂. In the  $F_2$  plants of this cross all seeds had green cotyledons because of maternal inheritance, but we should expect segregation in cotyledon chromosomal genes, resulting in a difference in the intensity of the green color. Theoretically, fifteen-sixteenths of the seeds should be light green and one-sixteenth a deep chromium green. This color difference was observed and it was found possible to classify the seeds into these two groups in approximately a 15:1 ratio. It was thought that the deep chromium green seeds represented the type desired because of their resemblance to the regular genetic greens. Accordingly these were planted and plants grown. Test crosses were made by applying pollen from these plants to stigmas of genetic green plants. The resulting seeds were green instead of yellow, thus proving that the ♂ parent brought genes  $d_1d_2$  to the cross rather than genes  $D_1D_2$ . We have therefore produced a soybean that behaves in crosses not only as a maternal green when used as ♀ parent, but also as a segregating green when used as ♂ parent.

The above relationships among cotyledon types may be briefly set forth in the following outline:

*Yellow cotyledon*

One gene,  $D_1$  or  $D_2$

Two genes,  $D_1$  and  $D_2$

*Green cotyledon*

Genetic,  $d_1 d_2$

Maternal

Genetic yellow,  $D_1 D_2$

Genetic green,  $d_1 d_2$

As stated earlier, in hybrid plants segregating for cotyledon color both yellow and green cotyledon seeds occur on the same plant. The distribution of seeds with yellow or green cotyledons is random over the plant, and in pods containing two or more seeds the combinations of yellows and greens follow the laws of chance. These facts were brought out in a study by the writer of plants segregating in a 3:1 or a 15:1 ratio. Pods were carefully picked off the plants by hand, and classified into 1-seeded, 2-seeded, 3-seeded, and 4-seeded pods. Each

TABLE 1.—ACTUAL DISTRIBUTION OF YELLOW AND GREEN COTYLEDON SEEDS AMONG THE VARIOUS POD TYPES COMPARED WITH EXPECTED DISTRIBUTION

Ratios	1-seeded pods		2-seeded pods			3-seeded pods			4-seeded pods					
	Yellow	Green	2 yellow	1 yellow 1 green	2 green	3 yellow	2 yellow 1 green	1 yellow 2 green	3 green	4 yellow	3 yellow 1 green	2 yellow 2 green	1 yellow 3 green	4 green
Observed 3:1 ratio...	1 695	496	1 267	695	134	423	329	114	15	13	12	2	1	
Expected ratio.....	3	1	9	6	1	27	27	9	1	81	108	54	12	1
Expected numbers...	1 643	548	1 179	786	131	371.5	371.5	124	14	8	12	6	1	..
Observed 15:1 ratio...	436	25	334	33	1	115	23	45	..	1	1	..	60	..
Expected ratio.....	15	1	225	30	1	3 375	675	45	..	50 625	13 500	1 350	..	..
Expected numbers...	432	29	323	43	1	114	23	1	..	..	..	..	..	..

pod was shelled by hand and the number of yellow and green cotyledon beans noted. The various combinations of cotyledon colors in the four types of pods are given in the headings of Table 1. The expected ratio of yellow to green in 1-seeded pods is 3:1 or 15:1, according as segregation is occurring for one or two genes. The expected ratio of combinations in 2-seeded pods is the terms of the binomial raised to the second power,  $(3 + 1)^2$  or  $(15 + 1)^2$ ; in 3-seeded pods, the terms of the binomial raised to the third power,  $(3 + 1)^3$  or  $(15 + 1)^3$ ; and in 4-seeded pods, the terms of the binomial raised to the fourth power,  $(3 + 1)^4$  or  $(15 + 1)^4$ . A study of the observed numbers compared with the expected numbers calculated on the basis of these ratios (Table 1) shows rather close correspondence. The results on the 15:1 ratio plants would have shown closer agreement with the expected had larger numbers been obtained.

### Coat Color

There are four main seed-coat colors in soybeans; namely, black, brown, green, and yellow. Various combinations of these colors on the same bean give rise to bicolor types or, more rarely, tricolor types; and a mottled appearance is presented, sometimes showing definite and characteristic patterns. The black pigment, according to Owen,<sup>32\*</sup> is a very intense purple and belongs to the general class of anthocyanins; the brown pigment is closely related to quercetin; and the green and yellow are plastid pigments.

In inheritance the black and brown pigments are genetically independent of green and yellow. Black is dominant to brown, and in  $F_2$  a ratio of 3 black to 1 brown is obtained. Green is dominant over yellow, and in  $F_2$  a ratio of 3 green to 1 yellow is obtained.

The situation becomes much more complicated when black or brown is crossed with green or yellow. Beans are called self-black or self-brown when the whole bean including the hilum is covered with black or brown pigment. Most green and yellow beans have black or brown hilums and may be thought of as black or brown beans in which the black or brown pigment is confined to the hilum. There are, however, a few types in which the hilums are entirely devoid of black or brown pigment—the hilums are yellow or green, the same as the seed coat. Hence, when self-black is crossed with a green type with black hilum there is no gene for pigment involved but rather a gene for restriction or inhibition of pigment, designated as *I*. Since the green type carries *I*, it is dominant and appears in  $F_1$  to the exclusion of self-black, which carries *i*. There are genes effecting different degrees of inhibition.



Owen<sup>32\*</sup> has demonstrated the existence of a multiple allelomorphic series effecting inhibition consisting of  $I^h$ ,  $I^i$ ,  $I^k$  and  $i$ .  $I^h$  inhibits all black and brown pigment so that none is visible on the seed coat even in the hilum.  $I^i$  permits black or brown pigment to appear in the hilum but prevents its occurrence on the seed coat.  $I^k$  restricts black and brown pigment still less, allowing it to spread out from the hilum as a center so as to form a "saddle" characteristic of the Black Eyebrow variety. Finally,  $i$  permits pigment to cover the whole seed coat, resulting in a "self" colored seed such as we have in black- and brown-seeded varieties. However, Stewart<sup>39\*</sup> was not able to distinguish between types carrying  $I^h$  and types carrying  $I^i$ , and on the basis of his evidence he would revise the allelomorphic series thus:  $I$ ,  $I^k$ , and  $i$ . Nevertheless there are yellow and green types that have no black or brown pigment at all, even in the hilum, as well as those that have these pigments only in the hilum, and it is important to differentiate between them genetically, as Owen has done. To make the symbols conform to present usage it is suggested that they be written  $I$ ,  $i^i$ ,  $i^k$ , and  $i$ .

A self-black or self-brown seed coat may cover up green or yellow pigments. In other words, genes  $G$  (green) or  $g$  (yellow) may be present but fail to produce a green or yellow seed coat, as the case may be, because of the presence of  $i$ , which permits complete extension of the black or brown colors. Thus in a cross between a yellow-seeded strain, designated as A.K. 114, and Ogema, a self-brown variety, the seeds of the  $F_1$  plant were green. The green coat color must have come from the brown parent. The yellow parent contributed  $i^i$ , which in the  $F_1$  plant restricted the brown pigment to the hilum, thus permitting the green color to appear. Other brown varieties and a few black varieties that have been studied with respect to the plastid pigment present are as follows:

BROWN		BLACK	
Variety	Gene	Variety	Gene
S.P.I. 65388.....	$g$	Sooty.....	$g$
Recessive glabrous.....	$g$	Black Eyebrow.....	$g$
Virginia.....	$G$	Ebony.....	$g$
412 G.....	$g$	Wisconsin Early Black.....	$g$

It is clear that the constitution of black or brown varieties with respect to genes  $G$  and  $g$  can be readily determined by crossing with yellow varieties. If the brown or black parent carries yellow, the hybrid will be yellow; if it carries green, the hybrid will be green.

The genetic relationships of black and brown pigments in the hilum and the effect of other genes on these colors will be discussed in detail in the next section.

### Hilum Color

Nagai,<sup>25\*</sup> Woodworth,<sup>57\*</sup> and Owen<sup>32\*</sup> postulated two complementary genes for black pigment formation in the seed coat and hilum. These were designated *C* and *L* by Nagai, *B* and *H* by Woodworth, and *R*<sub>1</sub> and *R*<sub>2</sub> by Owen. Owen's symbolism appears to be preferable.

In Woodworth's early experiments<sup>57\*</sup> which led to the suggestion of complementary factors for black hilum, a cross was made between a strain with black hilum and a strain with colorless hilum. In the F<sub>2</sub> of this cross, black and brown hilum plants occurred in the ratio of 9:7. As pointed out in that publication, the ratio probably was 9 black: 6 brown:1 colorless, but on account of mottling of the seed coat the plants with brown hilums could not be distinguished from plants with colorless hilums, and consequently they were classed together; hence the ratio 9:7.

The black hilum parent was considered to have the genetic constitution *R*<sub>1</sub>*R*<sub>2</sub>, and the colorless hilum parent, *r*<sub>1</sub>*r*<sub>2</sub>. In F<sub>2</sub> the expected types and proportions would be as follows:

16	{	9 <i>R</i> <sub>1</sub> <i>R</i> <sub>2</sub> black hilum
		3 <i>R</i> <sub>1</sub> <i>r</i> <sub>2</sub> brown hilum
		3 <i>r</i> <sub>1</sub> <i>R</i> <sub>2</sub> brown hilum
		1 <i>r</i> <sub>1</sub> <i>r</i> <sub>2</sub> colorless hilum

Just recently a cross was made at this Station between Illini [brown hilum (*R*<sub>1</sub>*r*<sub>2</sub>)] and a dominant glabrous type [brown hilum (*r*<sub>1</sub>*R*<sub>2</sub>)]. The seeds of the F<sub>1</sub> plant had black hilums (*R*<sub>1</sub>*r*<sub>2</sub>.*r*<sub>1</sub>*R*<sub>2</sub>). In F<sub>2</sub> of 187 plants 97 had black hilums, 77 brown, and 13 colorless. The expected numbers on the basis of a 9:6:1 ratio are 105:70:12 respectively. There was no mottling in this cross to interfere with the separation of colorless from colored hilum types. In this particular type of colorless hilum there is no gene for brown pigment, and hence no color can be produced except the plastid pigment, which is yellow or green according to whether the seed-coat color is yellow or green. Restriction genes then have no effect because there is no brown or black pigment for them to restrict. In appearance this type is the same as the other type which is colorless because of the action of *I*, but the two types may differ greatly in genetic constitution.

Substantiating evidence for the complementary relationship of *R*<sub>1</sub> and *R*<sub>2</sub> has been furnished by recent crosses between types with brown hilums. Thus the F<sub>1</sub> plant produced by a cross between AK 114 (dark brown hilum) and Illini (light brown hilum) bore seeds with black hilums. Similar crosses involving these and other varieties with brown hilum are given below:

Cross No.	Parents	F <sub>1</sub> hilum color
2	Chimera × S.P.I. 65345.....	Black
8	Wea × Virginia.....	Black
31	Wea × 435 B.....	Black
32	Chimera × 435 B.....	Black
36	Dunfield × S.P.I. 65388.....	Black
37	Illini × 435 B.....	Black
40	Recessive glabrous × S.P.I. 54592.....	Black
47	Illini × Virginia.....	Black
58	435 B × Columbia.....	Black
101	AK 114 × Wea.....	Black
104	Illini × Olive Green.....	Black
128	AK 114 × Illini.....	Black

One parent in each of these crosses has dark brown hilum and the other parent light brown hilum. The difference in the intensity of hilum color is due to the genes *Tt* for tawny vs. gray pubescence. Types with *T* have dark brown hilums, and types with *t* have light brown hilums. One parent in each cross contributes one complementary gene  $R_1$ , and the other parent contributes the other complementary gene  $R_2$ , both of which are necessary for black hilum. The light brown hilum type is considered to be  $R_1r_2t$  and the dark brown hilum type,  $r_1R_2T$ . The F<sub>1</sub> plant would therefore be  $R_1r_2t \cdot r_1R_2T$ .

Obviously not all crosses between types with brown hilum will produce hybrids with black hilum. Crosses between types with light brown hilums ( $R_1r_2t$ ) will produce again this same type; and crosses between types with dark brown hilums ( $r_1R_2t$ ) will produce again this same type. Black hilum is not produced in either of these crosses, because either  $R_1$  or  $R_2$  is involved in both parents and both must be present to produce black.

In the above reference (Woodworth<sup>57\*</sup>) the cross studied was  $R_1R_2T$  (black hilum, tawny pubescence) ×  $r_1r_2t$  (colorless hilum, gray pubescence). In the F<sub>2</sub> of this cross no plants were obtained of the constitution  $R_1R_2t$  (black hilum, gray pubescence). The results then obtained indicated that *T* not only changes gray pubescence to tawny pubescence, but also reacts with  $R_1$  to give black pigment. Consequently *T* was considered either to be identical to, or completely linked with, *H* (now called  $R_2$ ). Since then types with black hilum and gray pubescence have been found. The hilum, tho black, does not appear quite the same as it does in the typical black hilum of constitution  $R_1R_2T$ . The gene *t* seems to reduce the amount of black pigment, confining it more to the center of the hilum and leaving the area near the margin more or less free of this pigment. This type of hilum is called dilute or imperfect by Owen<sup>32\*</sup> and Stewart,<sup>39\*</sup> and according to these

authors has the constitution  $R_1r_2t$ . However, if  $R_1$  and  $R_2$  are necessary for black, then the so-called imperfect type of hilum must have both  $R_1$  and  $R_2$ . Furthermore there are types with black coats and gray pubescence, and these must have the constitution  $R_1 R_2 t$ . They may be thought of as crossover types. No soybeans representing the other crossover type of constitution  $r_1r_2T$  are at present known to the writer, but it is quite likely that they will ultimately be produced, if, indeed, they are not already in existence. Furthermore, if, according to Owen and Stewart,  $r_1R_2$  represents a brown and  $r_1r_2$  a very light brown or buff, then a cross of two browns could give only brown again, not black. In view of the above considerations the following revisions are suggested even tho it is admitted that the available evidence may not fully justify them.

<i>Hilum color (with i')</i>	<i>Symbols</i>	<i>Coat color (with i)</i>	<i>Symbols</i>
Black.....	$R_1R_2T$	Black.....	$R_1R_2T$
Black.....	$R_1R_2t$	Black.....	$R_1R_2t$
Dark brown.....	$r_1R_2T$	Dark brown.....	$r_1R_2T$
Light brown.....	$R_1r_2t$	Light brown or buff.....	$R_1r_2t$
Colorless hilum.....	$r_1r_2T$ (or $t$ )	Yellow or green.....	$r_1r_2T$ (or $t$ )

The genes for purple and white flowers ( $Ww$ ) have also been found to influence black and brown seed-coat or hilum colors. Owen<sup>32\*</sup> considered  $W$  to be complementary to  $r_2$ , but Stewart<sup>39\*</sup> found it necessary to consider  $W$  to be complementary to  $R_1$  in order to avoid certain inconsistencies in the use of formulae. With  $R_1$ ,  $W$  reacts to give imperfect black in the seed coat, while  $w$  with  $R_1$  gives a buff color.

Stewart<sup>39\*</sup> found evidence for another series of multiple allelomorphs affecting coat color: namely,  $R_1$ ,  $r_1$ , and  $r_1^o$ . Nagai<sup>25\*</sup> had previously reported that reddish brown ( $o$ ) was recessive to light brown ( $O$ ).  $R_1$  with  $R_2$  produces black pigment as has been stated above;  $r_1$  with  $R_2$ , light brown; and  $r_1^o$  with  $R_2$ , a reddish brown. Gene  $r_1$  is dominant to  $r_1^o$ ,  $R_1$  to  $r_1$  and  $r_1^o$ , thus fulfilling the conditions of a multiple allelomorphic series.

The production of black mottling on a self-brown seed coat was explained by Nagai and Saito<sup>26\*</sup> as due to the gene  $M$ ,  $m$  being without effect. Owen<sup>32\*</sup> described a natural hybrid that segregated in a ratio of 3 black to 1 brown, but the seeds of the heterozygous plants were speckled with brown.

#### Abnormal Hilum

In the soybean the seed normally separates from the pod at the point of attachment, leaving a clean, straight surface at the hilum or seed "scar." In the Soysota variety (Fig. 4), however, there is an

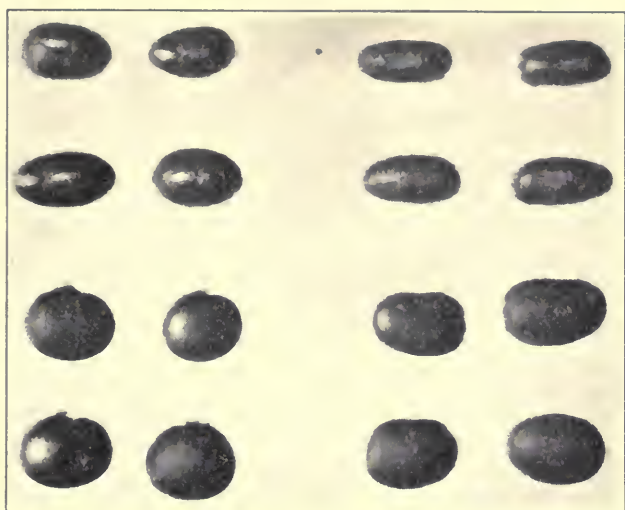


FIG. 4.—NORMAL AND ABNORMAL HILUMS

In most soybean varieties the hilum separates from the pod leaving a clean smooth surface, as shown by seeds of the Virginia variety (right). In the Soy-sota variety (left) the seeds have a rough hilum owing to adherence of a portion of the pod tissue to the hilum. In inheritance this is a simple recessive to the normal condition.

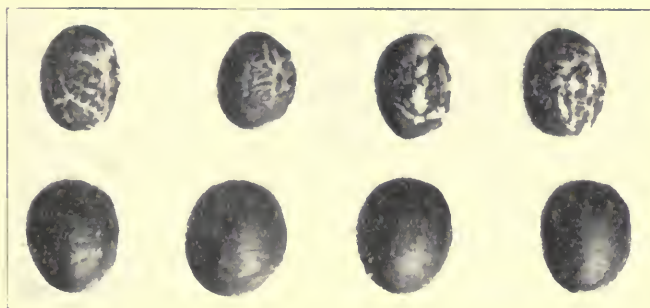


FIG. 5.—BEANS WITH DEFECTIVE AND ENTIRE SEED COATS

In most soybeans the outer seed coat is entire and completely covers the seed. In others the outer, thicker coat is defective in that it does not completely cover the seed, exposing the thin, inner coat. The latter is objectionable, as the seed is thus deprived of the protection that the outer coat should afford. In the upper row are shown seeds of glabrous type with defective coats; in the lower row are seeds of Ogema variety, having entire coats.

abnormal hilum owing to the tissues being torn on separation of the seed from the pod. Owen<sup>32\*</sup> found this type of hilum to be a simple recessive to the normal. The symbols  $Nn$  were used to represent the genes involved.

### Defective Seed Coats

In normal soybeans the seed coats may be said to be entire in the sense that they completely cover the seed. If, however, one examines them closely, he will find defects in the outer layer ranging from a pin point in size to large cracks. Owing to the growth of the cotyledons, the margins of the crack are spread apart in some strains of soybeans, exposing comparatively large areas of the inner white layer. Sometimes this happens in such a way as to give a net-like appearance to the seed coat (Fig. 5). This apparently was the explanation of the so-called "black and white" soybean, a sample of which was sent to this Station several years ago by W. J. Morse, of the U. S. Department of Agriculture.

Defective seed coats have been observed in black, brown, buff, and yellow seeds, and rarely in green seeds. In some yellow and green seeds mottled with brown pigment the defects occur mostly in the brown areas, as Stewart and Wentz<sup>40\*</sup> found. The character is undesirable, for in the defective areas the very thin inner coat cannot furnish the protection against unfavorable weather conditions and organisms causing disease that is afforded by the thick, heavy, strong, outer coat.

Stewart and Wentz<sup>40\*</sup> observed this character in the seeds produced by a few  $F_2$  plants of a cross between Wisconsin Black and Mandarin varieties. The  $F_2$  ratio was 51 normal to 5 defective. This suggested a 15:1 ratio, which was interpreted as follows: defective seed coat was found only in plants having  $i$ , the gene for lack of restriction of pigment; therefore  $I$  was assumed to prevent  $de$ , the gene for defective seed coat, from expressing itself. The  $F_2$  classes can then be represented as follows:

$$16 \begin{cases} 9 I De, \text{ normal} \\ 3 I de, \text{ normal (except for mottled areas on the seed coat)} \\ 3 i De, \text{ normal} \\ 1 i de, \text{ defective} \end{cases}$$

The  $F_3$  results gave substantiating evidence for this interpretation. Since all plants bearing defective seeds had gray pubescence and none were found with tawny pubescence, it was assumed that there was complete linkage between  $de$  and  $t$ . On this hypothesis the Mandarin carries the gene  $de$  for defective seed coat, but it is prevented from ex-

pressing itself by *I* also carried by this variety; and Wisconsin Black has the constitution *iDe*. Hence neither parent was characterized by defective seed coats, but segregation and recombination following the cross brought about the particular combination of genes which permitted them to occur in certain  $F_2$  plants.

### Mottling of Seed Coat

A few years ago the seed of many yellow- and green-seeded soybean varieties showed considerable mottling. Seeds with black hilums were black-mottled, and seeds with brown or colorless hilums were brown-mottled. The mottling consisted of patches, blotches, or bands of black or brown pigment, irregular in outline and extent, superimposed on a ground color of yellow or green.

In 1924 Woodworth and Cole<sup>62\*</sup> described the character and recorded studies on the appearance of mottling on seeds of the same plant. Seeds in the same pod showed striking similarity in the extent and even in the particular pattern of mottling, but when these seeds were planted, the plants grown, and resulting seed studied, there appeared to be no evidence of the inheritance of the parent pattern or of the amount of mottling. The causal factors were believed to be physiological rather than genetic. In the same year Hollowell<sup>15\*</sup> reported results of studies on mottling carried on at various points in Iowa. Rich soils were found to favor mottling, while on thin or poor soils very little or no mottling developed. Also, crowded plants mottled much less than plants given ample space in which to grow.

Owen<sup>28\*</sup> concluded after an extensive investigation of this subject that mottling is due both to hereditary and environmental factors. Among the environmental factors believed to be important were mentioned abnormal physiological conditions resulting in a concentration of sugars, or at least in an unbalanced nutritive condition, type of soil, amount of space between plants, fertilizers, inoculation, and shading. In general the more favorable the conditions for growth the more the mottling, but there were many exceptions. No definite conclusions were drawn regarding the hereditary factors. Selection against mottling was effective in some cases, and certain strains seemed more susceptible to mottling than others. In artificial hybrids it appeared that certain of the factors belonging to the restriction series *i* and *I* were not completely dominant, and mottling was therefore allowed to develop. The pubescence color was found in one instance to influence the extent of mottling, tawny pubescence increasing it, gray pubescence decreasing it. However, Owen could not designate any par-

ticular factor as being the most important in causing mottling. The problem had certain genetic aspects, but the environmental effects were always quite evident.

Some attention was given to the mottling problem at the Illinois Station, beginning in 1924, to determine whether any genetic aspects were involved and whether selection would have any effect. Considerable variation had been observed in the Manchu variety (Fig. 6) in the extent of mottling. Some plants showed none at all, other showed



FIG. 6.—MANCHU SOYBEANS: (ABOVE) MOTTLED, (BELOW) NONMOTTLED

Some varieties tend to mottle more than others, but the amount of mottling is affected greatly by growing conditions. In general the more favorable the conditions, the more the mottling. Of late years farmers have not complained much of their soybeans showing this character. Probably one reason is the wider use of strains that show little tendency toward mottling.

a slight amount, and still others were described as being considerably mottled. In any plant exhibiting mottling there was considerable variation in the pattern and amount of the black pigment on individual seeds, an observation which had been made by the other workers on this problem. In order to represent the extent of mottling on the seeds of a single plant by one figure so as to treat the data quantitatively, the seeds were first placed in the following five classes:

- (a) No mottling whatever
- (b) Less than  $\frac{1}{4}$  of seed coat covered by black pigment
- (c) From  $\frac{1}{4}$  to  $\frac{1}{2}$  of seed coat covered by black pigment
- (d) Seed coat more than  $\frac{1}{2}$  but not fully covered by black pigment
- (e) Seed coat fully covered by black pigment.

The number of seeds in each class was counted and expressed as a percentage of the total. Then each percentage was multiplied by its respective factor as follows: Class (a), 0; (b), 1; (c), 2; (d), 3; and (e), 4. These products were added, and the sum expressed in a single



figure the extent to which the seeds of a plant were mottled. This method admitted of comparing different plants and different progenies in the amount of the mottling shown.

In the beginning, the plants used as parents were simply distinguished on the basis of mottling by such descriptive terms as "non-mottled," "very little mottling," "considerable mottling," and the like. The progeny of these plants, however, were classified and evaluated according to the method outlined above. From the results given in Table 2 it can be seen that two nonmottled plants, 2052-7 and 2052-11, gave progeny with the lowest amount of mottling; while the progeny of plant 2064-9, which was also nonmottled, had a mean value of 116.5, only slightly less than the progeny of 2070-18, which was described as "very little mottling." Little of significance can be gained from this table except that the parent plants having no mottled seed produced progenies that showed the least amount of mottling.

TABLE 2.—COMPARISON OF PARENT PLANTS AND THEIR PROGENIES IN EXTENT OF MOTTLING OF SEED COAT

Parent	Character of parent seed	Progeny No.	Number of plants	Mean mottling <sup>1</sup>
2020-2.....	Considerable mottling	2512	32	146.75 ± 3.94
2020-12.....	Very little mottling	2514	37	180.46 ± 3.79
2020-24.....	Considerable mottling	2517	36	170.81 ± 4.39
2020-25.....	Very little mottling	2518	33	141.78 ± 5.35
2052-7.....	Nonmottled	2519	26	75.09 ± 2.52
2052-11.....	Nonmottled	2520	34	79.50 ± 1.92
2061-16.....	Mottled	2523	31	146.88 ± 4.49
2064-9.....	Nonmottled	2524	28	116.51 ± 2.49
2070-18.....	Very little mottling	2528	21	119.58 ± 3.09

<sup>1</sup>See text for method of calculation.

To continue the experiment use was made of progenies 2517, 2518, and 2519 because they represented high, intermediate, and low averages respectively and their parents stood in almost the same relative position with respect to mottling. Plants were selected to represent the extremes as well as the intermediates of each progeny. Also the class of seeds of each selected plant was kept separate in planting, so as to determine whether any differences could be detected in the offspring. The results are given in Table 3.

There are several items of interest that may be deduced from this table. The extent of mottling shown by the offspring of 2519 is the lowest, and this is significant inasmuch as they trace back to a non-mottled grandparent. However, there is very little or no difference between the offspring of 2517 and 2518, in spite of the fact that the grandparent of the former was considerably mottled and the grandparent of the latter very little mottled. Furthermore the several classes

TABLE 3.—COMPARISON OF SELECTED PROGENIES WITH ONE ANOTHER AND OF DIFFERENT CLASSES OF SEED IN EXTENT OF MOTTLING OF SEED COAT

Parents of 1925 crop	Mottling of parent	Type of seed planted <sup>1</sup>	Number of plants	Mean mottling
2517-8.....	93.5	0-0	7	92.38 ± 4.88
		0- $\frac{1}{4}$	14	35.15 ± 4.09
		$\frac{1}{4}$ - $\frac{1}{2}$	2	72.65 ± 0.88
		$\frac{1}{2}$ -1	2	75.05 ± 4.36
2517-9.....	169.4	0-0	1	74.67 ± 0.00
		0- $\frac{1}{4}$	11	66.81 ± 6.18
		$\frac{1}{4}$ - $\frac{1}{2}$	5	97.28 ± 4.37
		$\frac{1}{2}$ -1	6	94.92 ± 9.76
2517-13.....	179.3	0-0	3	91.48 ± 3.03
		0- $\frac{1}{4}$	16	102.17 ± 7.39
		$\frac{1}{4}$ - $\frac{1}{2}$	3	104.86 ± 5.61
		$\frac{1}{2}$ -1	5	130.19 ± 14.33
2517-16.....	244.5	0- $\frac{1}{4}$	9	97.88 ± 9.26
		$\frac{1}{4}$ - $\frac{1}{2}$	6	125.07 ± 9.51
		$\frac{1}{2}$ -1	16	105.46 ± 3.63
2517-19.....	219.5	0- $\frac{1}{4}$	11	110.99 ± 7.02
		$\frac{1}{4}$ - $\frac{1}{2}$	4	98.65 ± 6.29
		$\frac{1}{2}$ -1	13	76.81 ± 7.53
2517-24.....	94.1	0-0	9	93.84 ± 5.88
		0- $\frac{1}{4}$	21	105.03 ± 5.61
		$\frac{1}{4}$ - $\frac{1}{2}$	2	66.68 ± 1.98
		$\frac{1}{2}$ -1	2	110.01 ± 1.03
2517-25.....	212.9	0- $\frac{1}{4}$	12	103.41 ± 6.32
		$\frac{1}{4}$ - $\frac{1}{2}$	6	117.05 ± 15.14
		$\frac{1}{2}$ -1	9	103.47 ± 7.37
2517-27.....	178.8	0- $\frac{1}{4}$	20	108.75 ± 12.95
		$\frac{1}{4}$ - $\frac{1}{2}$	5	106.92 ± 3.57
		$\frac{1}{2}$ -1	10	115.34 ± 6.63
2517-33.....	98.3	0-0	8	103.25 ± 4.69
		0- $\frac{1}{4}$	15	116.40 ± 4.14
		$\frac{1}{4}$ - $\frac{1}{2}$	4	108.58 ± 3.64
		$\frac{1}{2}$ -1	2	125.45 ± 10.13
2518-6.....	193.8	0- $\frac{1}{4}$	13	115.73 ± 3.55
		$\frac{1}{4}$ - $\frac{1}{2}$	8	111.78 ± 7.89
		$\frac{1}{2}$ -1	13	118.31 ± 5.82
2518-12.....	140.1	0-0	..	.....
		0- $\frac{1}{4}$	20	121.89 ± 2.71
		$\frac{1}{4}$ - $\frac{1}{2}$	9	104.18 ± 9.47
		$\frac{1}{2}$ -1	2	117.39 ± 6.41
2518-14.....	141.5	0- $\frac{1}{4}$	24	122.94 ± 5.55
		$\frac{1}{4}$ - $\frac{1}{2}$	7	115.34 ± 10.61
		$\frac{1}{2}$ -1	8	126.07 ± 7.25
2518-15.....	197.5	0- $\frac{1}{4}$	16	113.55 ± 3.77
		$\frac{1}{4}$ - $\frac{1}{2}$	8	111.69 ± 5.63
		$\frac{1}{2}$ -1	13	116.47 ± 3.21
2518-19.....	193.6	0-0	..	.....
		0- $\frac{1}{4}$	15	109.87 ± 4.31
		$\frac{1}{4}$ - $\frac{1}{2}$	8	113.28 ± 4.50
		$\frac{1}{2}$ -1	9	113.44 ± 8.75
2518-20.....	47.8	0-0	19	96.42 ± 8.86
		0- $\frac{1}{4}$	11	72.36 ± 11.08
2518-24.....	51.6	0-0	17	112.78 ± 2.36
		0- $\frac{1}{4}$	13	115.48 ± 6.51
2518-26A.....	00.0	0-0	5	100.46 ± 6.36
2518-5.....	97.9	0-0	3	93.30 ± 11.56
		0- $\frac{1}{4}$	20	99.89 ± 14.83

TABLE 3.—*Concluded*

Parents of 1925 crop	Mottling of parent	Type of seed planted <sup>1</sup>	Number of plants	Mean mottling
2518-34.....	144.2	0- $\frac{1}{4}$	20	104.06 ± 5.45
		$\frac{1}{4}$ - $\frac{1}{2}$	7	112.78 ± 4.15
		$\frac{1}{2}$ -1	4	87.02 ± 6.34
2519-3.....	74.9	0-0	10	31.61 ± 4.26
		0- $\frac{1}{4}$	18	27.94 ± 2.53
		$\frac{1}{4}$ - $\frac{1}{2}$	3	52.13 ± 8.40
2519-8.....	36.3	$\frac{1}{2}$ -1	1	22.78 ± 0.00
		0-0	19	14.27 ± 1.89
		0- $\frac{1}{4}$	8	25.59 ± 2.10
2519-9.....	37.4	0-0	23	13.47 ± 1.93
		0- $\frac{1}{4}$	10	11.98 ± 2.12
2519-12.....	92.7	0-0	6	26.38 ± 3.25
		0- $\frac{1}{4}$	19	20.83 ± 2.88
		$\frac{1}{4}$ - $\frac{1}{2}$	2	7.07 ± 0.61
		$\frac{1}{2}$ -1	1	27.39 ± 0.00
2519-14.....	94.7	0-0	7	19.89 ± 3.91
		0- $\frac{1}{4}$	17	17.16 ± 2.14
		$\frac{1}{4}$ - $\frac{1}{2}$	..	.....
2519-18.....	93.4	$\frac{1}{2}$ -1	2	24.92 ± 4.71
		0-0	8	19.83 ± 4.09
2519-21.....	15.4	0- $\frac{1}{4}$	18	26.90 ± 2.68
		0-0	20	25.78 ± 2.55
2519-26.....	77.5	0- $\frac{1}{4}$	9	29.49 ± 5.38
		0-0	7	28.36 ± 1.72
2519-27.....	75.9	0- $\frac{1}{4}$	16	15.84 ± 1.53
		$\frac{1}{4}$ - $\frac{1}{2}$	4	36.37 ± 3.37
		0-0	9	19.77 ± 2.52
Bulk Manchu.....	.....	0- $\frac{1}{4}$	20	13.38 ± 1.79
		0-0	20	54.55 ± 4.73
		0- $\frac{1}{4}$	20	52.67 ± 5.76
		$\frac{1}{4}$ - $\frac{1}{2}$	20	96.61 ± 2.30
		$\frac{1}{2}$ -1	20	86.41 ± 9.61

<sup>1</sup>0-0 = seeds with no mottling on seed coat.

0- $\frac{1}{4}$  = seeds with  $\frac{1}{4}$  or less of seed coat covered with black pigment.

$\frac{1}{4}$ - $\frac{1}{2}$  = seeds with more than  $\frac{1}{4}$  but less than  $\frac{1}{2}$  of seed coat covered with black pigment.

$\frac{1}{2}$ -1 = seeds with  $\frac{1}{2}$  or more of seed coat covered with black pigment.

of seeds of any parent plant gave very much the same kind of progeny with respect to extent of mottling. That is to say, the seeds of a particular plant, regardless of the amount of mottling each seed exhibited, are alike genetically and produce the same kinds of plants.

Finally, attention may be drawn to the data on plants produced from seeds picked out of a bulk lot of Manchu. The seeds were classed as were those of the individual plants and the progeny of each class compared in amount of mottling. Plants coming from class (a) seeds (no mottling) averaged 54.55 and from class (b) seeds, 52.67, while plants from classes (c) and (d), having considerable mottling, averaged 96.61 and 86.41 respectively.

It would appear from these data that the problem of mottling has some genetic aspects. In a variety that mottles considerably, as did the Manchu at the time this experiment was conducted, the selection of in-

dividual plants showing little or no mottling may be effective in reducing greatly the amount of mottling. At the outset it might be advisable to pick out from a bulk lot a number of seeds exhibiting no mottling and to grow plants from these seeds apart from the rest of the crop. These plants can then be harvested and threshed separately, and any showing little or no mottling can be continued. Thus a strain may be developed by selection that lacks the objectionable feature of mottling exhibited by the original variety.

More recently, for reasons that are not entirely clear, mottling has not appeared to an extent sufficient to attract attention. Perhaps the wider use of varieties not subject to mottling has been an important factor.

### Bloom on Seed Coat

Most soybean varieties are characterized by a comparatively smooth seed coat, tho they differ widely in the degree of smoothness. Some are rather dull in appearance, while others are bright and shiny. In



FIG. 7.—SEEDS OF THE SOOTY VARIETY SHOWING "BLOOM" ON THE SEED COAT

On the seeds in the upper row the bloom is unmolested. On the seeds in the lower row a portion of the bloom is scraped off, showing the smooth seed coat beneath. In inheritance, bloom is dominant to no bloom, and three genes,  $B_1$ ,  $B_2$ ,  $B_3$ , appear to be necessary for its expression.

some types, however—for example, Wild soybean (*S. ussuriensis*) Sooty, Harbin Nos. 222 and 223 (strains secured from Harbin Agricultural Experiment Station, Harbin, Manchuria) and probably others—there is a distinct "bloom" covering the entire seed coat (Fig. 7). The bloom can be easily brushed or scraped off, thus exposing the comparatively smooth seed coat beneath. All the types mentioned above are black-seeded, but at the Illinois Station there is a sample of the Wild soybean that is brown-seeded, and these seeds also show the bloom.

In a cross between Sooty and Manchu the  $F_1$  seeds were black-hilum yellow and covered with bloom. In the  $F_2$  generation the following results were obtained:

<i>Type</i>	<i>Number of plants observed</i>	<i>Number of plants expected</i>	<i>Expected ratio</i>
With bloom.....	243	241	3
Without bloom.....	78	80	1
Total.....	<u>321</u>	<u>321</u>	<u>4</u>

The data thus indicate that the two parent varieties differed by one gene for the character.

In another cross quite different results were secured. The parents were Dunfield, a yellow bean with light brown hilum, and S.P.I. 65388, a small-seeded, self-brown type. Neither parent showed the bloom. Seeds produced by the  $F_1$  plants closely resembled those of the  $F_1$  plants in the cross above described. They were yellow with black hilum and were covered with bloom. In the  $F_2$  generation the following results were obtained:

<i>Type</i>	<i>Number of plants observed</i>	<i>Number of plants expected</i>	<i>Expected ratio</i>
With bloom.....	119	116	27
Without bloom.....	155	158	37
Total.....	<u>274</u>	<u>274</u>	<u>64</u>

The actual results obtained fit very closely the expected results on the basis of a 3:1 ratio in the first cross and a 27:37 ratio in the second. The facts can be interpreted genetically if we assume that there are three genes involved, designated as  $B_1$ ,  $B_2$ , and  $B_3$ , all three of which must be present together to manifest the bloom; if any one of these is not present the character does not develop. On this assumption the Sooty variety possesses all three genes, the Manchu only two. In the case of the cross between Dunfield and S.P.I. 65388, one of these parent varieties must carry two genes and the other the third gene necessary for the character to manifest itself. It is hoped that further studies now in progress will help to establish whether this is the correct interpretation.

While the linkage relations of this character have not been fully investigated, it is independent of the following character pairs:  $Ll$ ,  $Ii$ ,  $Gg$ ,  $Ww$ , and  $Tt$ .

## PLANT CHARACTERS

### Flower Color

Soybean flowers are purple or white. While variations in intensity and grade of color are observable in the purple-flowered varieties, no

attempt has been made in this country to separate them phenotypically or genetically. In crosses purple ( $W$ ) is dominant to white ( $w$ ), and a simple ratio of 3 purple to 1 white is obtained in  $F_2$  (Woodworth<sup>58\*</sup>). Takahashi and Fukuyama<sup>43\*</sup> found a dihybrid ratio of 9 purple, 3 purplish red, and 4 white in an  $F_2$  generation.

### Stem Color

In the seedling stage soybean stems are either purple or green. The color in purple stems is most abundant just below the cotyledons. As the plants develop, the color fades out in the stems and accumulates in the nodes and the petioles of the leaves. Purple-stemmed plants bear purple flowers and green-stemmed plants bear white flowers (Woodworth<sup>58\*</sup>). No exception has been found to this relationship, the same gene probably being responsible for both characters. Hence stem color of the seedling is a reliable indication of the flower color to be shown later by the plant.

### Pubescence Color

Practically all soybean varieties are pubescent; that is, the stems, leaves, and pods are covered with fine hairs which are either brown (tawny) or gray. Tawny pubescence ( $T$ ) is dominant to gray ( $t$ ) in crosses, and in  $F_2$  a simple ratio of 3 tawny to 1 gray is obtained. In most cases there is no difficulty in distinguishing the two colors; a plant is either tawny or gray, not both; but in the Morse variety many plants have been observed that cannot be classified so definitely. The pubescence color is often intermediate between tawny and gray, and sometimes both colors appear to be present on the same plant. This is a problem needing further investigation.

### Glabrousness

Two distinct soybean types are glabrous, that is, lack pubescence or hairiness. These glabrous types are interesting genetically because of their relation in inheritance to each other and to the pubescent type. In crosses with pubescent varieties one glabrous type behaves as a dominant while the other behaves as a recessive. In each case the ratio is a 3:1, showing that a single factor pair is involved. Nagai and Saito,<sup>26\*</sup> who discovered the dominant type, designated it by the symbols  $P_1p_1$ , and Stewart and Wentz<sup>41\*</sup> who discovered the recessive type, used the symbols  $P_2p_2$ . By crossing the two types, Woodworth and Veatch<sup>63\*</sup> were able to get at the genetic relationship between them. The  $F_1$  plants were glabrous, and in  $F_2$  a ratio of 13 glabrous to 3 pubescent plants was obtained. On the basis of these results it was

postulated that  $P_2$  is responsible for pubescence,  $p_2$  for no pubescence or glabrousness (recessive), and that  $P_1$  is a factor inhibiting the production of pubescence,  $p_1$  having no effect on  $P_2$ . This factorial interpretation was substantiated by the  $F_3$  results. Hence, factorially, the dominant glabrous type is  $P_1P_1P_2P_2$ , and the recessive glabrous type,  $p_1p_1p_2p_2$ . The pubescent type is  $p_1p_1P_2P_2$ . By appropriate crosses a third glabrous type may be isolated; namely,  $P_1P_1p_2p_2$ .

Gene  $P_1$  also inhibits plant growth as well as pubescence. Glabrous soybeans ( $P_1P_2$ ) are smaller, shorter, and yield less than most pubescent varieties ( $p_1P_2$ ). This fact has been noted by Nagai and Saito<sup>26\*</sup> and by Owen.<sup>31\*</sup> Veitch<sup>47\*</sup> studied three crosses between pubescent varieties and the dominant glabrous type and found that the  $F_1$  plants were below the average of the parents in vigor. Maturity also



FIG. 8.—PORTION OF ROW OF SOYBEAN PLANTS BELONGING TO AN  $F_2$  GENERATION OF A CROSS BETWEEN ILLINI AND A DOMINANT GLABROUS TYPE

The difference in height and vigor is striking. The taller, larger plants are pubescent, like the Illini parent; the smaller plants are glabrous. The gene  $P_1$  inhibits not only pubescence but also normal vigor and plant development.

was affected by the gene  $P_1$ , the  $F_1$  plants being later than the average of the parents. In the  $F_2$  generation the most vigorous plants were pubescent and the least vigorous were the glabrous plants. The pubescent plants were 60 to 100 percent taller than the glabrous plants (Fig. 8), and they were three to five times higher in weight of seed (yield) and number of seed. It was interesting to note that the  $F_2$  glabrous plants averaged higher in most cases than the glabrous parents, and that the  $F_2$  pubescent plants averaged higher in all cases than the pubescent parents; also that certain extreme  $F_2$  glabrous plants had more vigor as measured by plant height and yield than cer-

tain pubescent plants,  $F_2$  or parent. Evidently the genes for vigor were not the same in the two parent types.

Furthermore it appeared that  $P_1$  did not always inhibit vigor to the extent it did in the glabrous parent. There probably were modifying genes involved in the cross, the effects of which are not inhibited or depressed by  $P_1$ . Finally,  $P_1$  was apparently completely dominant over its allelomorph  $p_1$ , there being no significant difference in the development of the glabrous  $F_2$  plants that were heterozygous and those that were homozygous for  $P_1$ .

The recessive glabrous type ( $p_1p_2$ ) discovered and described by Stewart and Wentz<sup>41\*</sup> is also low in vigor and yield, much lower in the plantings at the Illinois Station than is the dominant type. Lack of vigor in the recessive strain cannot be due to  $P_1$  since  $P_1$  is not present; nor to  $p_1$  since  $p_1$  does not have such an effect in the presence of  $P_2$ ; but more likely it is due to the presence of  $p_2$ . The heterozygous pubescent type ( $p_1p_1P_2p_2$ ) appears to be just as vigorous and productive as the homozygous pubescent type ( $p_1p_1P_2P_2$ ), as Wentz and Stewart<sup>49\*</sup> have shown. Therefore  $P_2$  is apparently completely dominant over its allelomorph  $p_2$ . Since the recessive glabrous type is lower in vigor and production than the dominant glabrous type, it would seem that  $P_2$  has a greater effect in producing plant development than  $P_1$  has in depressing it.

### Leaf Shape

The shape of the leaflets of most soybean varieties has been described by Piper and Morse<sup>35\*</sup> as ovate-lanceolate. A few types are known with leaflets that are described by the same authors as narrowly lanceolate or almost linear (Fig. 9). Takahashi and Fukuyama<sup>43\*</sup> have studied the hybrids between the normal and narrow types. In their studies the  $F_1$  generation was found to be intermediate, and in  $F_2$  a ratio of 1 broad or ovate to 2 intermediate to 1 narrow or linear was obtained.

Crosses between normal and narrow-leaf types have been made at the Illinois Station with essentially similar results except that the broad shape was partially dominant and the  $F_2$  generation was made up of two main types, broad and narrow, in a 3:1 ratio. There were a few  $F_2$  plants, however, that seemed to be intermediate in leaf shape between the two parents. The symbols  $Na$ ,  $na$ , are suggested for this character pair.

### Number of Leaflets

As noted in the section on description of the soybean, the compound leaf generally is made up of 3 leaflets, but occasionally 4 or 5



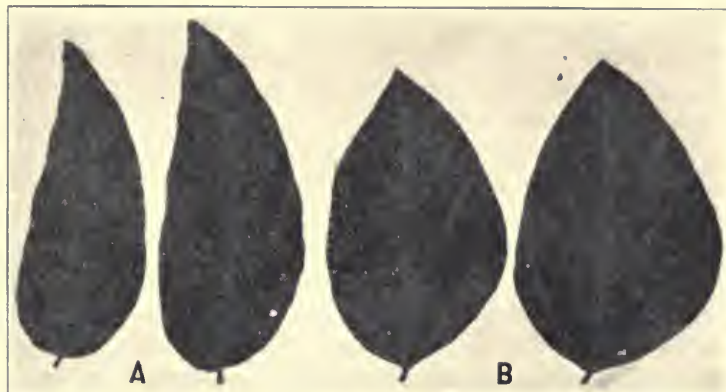


FIG. 9.—NARROW AND BROAD SOYBEAN LEAFLETS

Most soybeans have broadly lanceolate leaflets as in B, but a few have narrowly lanceolate, almost linear, leaflets as in A. Narrow leaves are recessive to the normal in inheritance.



FIG. 10.—NORMAL AND EXTRA LEAFLETS

In soybeans compound leaves with three leaflets are the most common, but occasionally compound leaves with four or five leaflets are found. A strain of Manchu is known which breeds true for this characteristic, tho the proportion of compound leaves with extra leaflets is not high. This abnormality is inherited but the method of inheritance appears to be rather complex.

leaflets are observed (Fig. 10). Takahashi and Fukuyama<sup>43\*</sup> discovered a strain in which 73 percent of the compound leaves on the main stem had extra leaflets. When this strain was crossed to the normal, the percentage of compound leaves with extra leaflets on the main stem of the hybrid was 52. Thus only partial dominance was shown. However, in  $F_2$  a ratio of 3 plants with extra leaflets to 1 normal was obtained. The extra leaflet character has also been observed by the writer in a strain of the Manchu variety. All plants of this strain show the character, and counts on 6 plants gave 27.12 percent extra leaflets. In the  $F_2$  generation of a cross between this type and Sooty (all normal leaflets) a ratio of 36 plants with extra leaflets to 335 plants with normal leaflets was obtained. This corresponds to a 1:9.3 ratio. The  $F_1$  plants were grown in the greenhouse, and it was not noted whether they bore compound leaves with extra leaflets or not. On the  $F_2$  plants classed as bearing extra leaflets only one compound leaf with extra leaflets was usually found. This case is evidently different genetically from the case reported by the Japanese workers.

Occasionally plants in other varieties have been observed with one or more extra leaflets, but the variation does not appear to be inherited.

### Height of Plant

Extensive studies on inheritance of size in the soybean have not been made, but two cases have been reported in which definite segregation in plant height was observed. Woodworth<sup>58\*</sup> described a natural hybrid that was segregating in the ratio of 3 tall, luxuriantly growing, late-maturing plants (*S*) to 1 short, stocky, early-maturing plant (*s*). Stewart<sup>38\*</sup> reported the discovery of a dwarf type in soybeans that behaved in inheritance as a simple recessive to the normal. This type of dwarf, according to Stewart, seldom reached a height of more than 10 inches, was spindly, weak, and bore only 4 or 5 pods; while the normal plants in the same segregating line were large and vigorous, attaining a height of about 2 feet.

### Maturity

Soybean varieties differ greatly in the time at which they mature. This character usually has a complicated mode of inheritance because it is determined by numerous genes. An exception to this statement was reported by Woodworth<sup>58\*</sup> in describing a progeny of plants that conspicuously segregated for two plant sizes, tall and short, in a 3:1 ratio. Coupled with plant size was a difference in time of maturity.

The tall type matured usually about two weeks later than the short type. In this instance late maturity was dominant. Studies made by Veatch<sup>46\*</sup> tended to confirm this, but Owen<sup>31\*</sup> found the  $F_1$  of crosses between early and late types to resemble the early in time of maturity more than the late, and in  $F_2$  the range in maturity due to segregation covered the entire parental range.

### Sterility

Occasionally very small, dwarf-like soybean plants are found that bear few or no pods. They are sterile or practically so. In many cases they appear to be diseased, probably with mosaic, but the writer has made no particular study of them. Owen<sup>27\*</sup> described a sterile type in which both ovules and pollen grains were nonfunctional. After flowering time the plants took on a dark green color, the leaves became thick, and sometimes the stems became greatly enlarged. The sterile type was discovered in a progeny of Manchu soybeans. Segregation into 3 normal to 1 sterile was definite and clear cut, and it appeared that a single gene mutation was responsible. Probably many of the small, dwarf-like plants occurring as rogues in fields of soybeans are due to genetic factors. If completely sterile they are automatically eliminated, but their occurrence in the field at all strongly suggests the presence of normal plants heterozygous for sterility that are constantly producing sterile plants as a result of segregation and recombination.

### Variegation

In the  $F_3$  generation of a hybrid a single plant was found at the Illinois Station with variegated leaves (Fig. 11). Neither parent possessed this character, and it is supposed that the variegation arose as a mutation. When the progeny of this plant were grown, all plants showed the character. In crosses with the normal the variegated type proved to be recessive. Results in  $F_2$  were as follows:

<i>Cross No.</i>	<i>Parents</i>	<i>Normal plants</i>	<i>Variegated plants</i>
43	Elton × Variegated.....	123	49
44	Variegated × Recessive glabrous.....	129	20
46	Variegated × Recessive glabrous.....	90	20
	Total.....	342	89

While the deviation from expected numbers on a 3:1 basis is rather large, it is believed that variegation ( $v_1$ ) is a simple recessive to the normal in inheritance. The wide deviations from expected in crosses 44 and 46 are likely due to errors of classification. The recessive gla-

brous plants are small and weak, and their leaves are dull and drab, appearing to lack the normal amount of chlorophyll. Hence, it was impossible to determine whether the  $F_2$  glabrous plants were variegated, and they were all recorded as normal. This type of variegation is best observed under field conditions in plants that are about half grown. It does not appear in the leaves first produced on the seedling plant

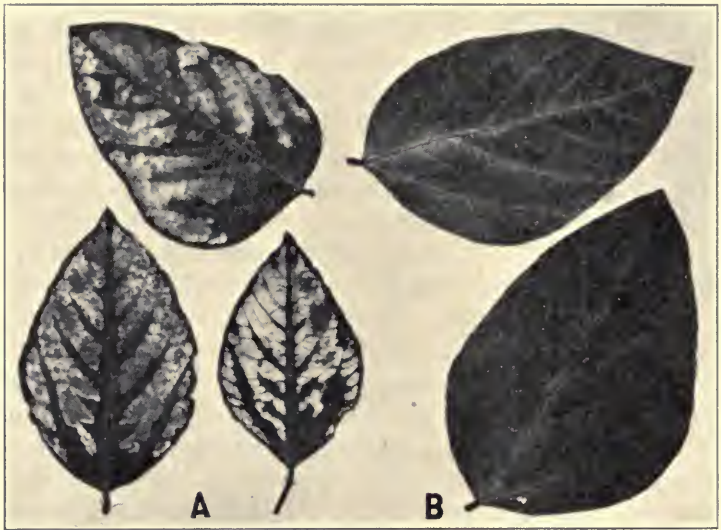


FIG. 11.—(A) VARIEGATED LEAFLETS COMPARED WITH (B) NORMAL LEAFLETS

The gene responsible for this type of variegation has been designated  $v_1$ , and is recessive to the normal  $V_1$ . This character probably arose as a mutation. It was found in the  $F_3$  generation of a cross and it bred true from the beginning.

nor in new leaves put out as the plant is attaining full growth. Hence only a part of the leaves of a plant are affected and the reduction in chlorophyll is small. Tho no definite tests have been made, it has not been observed that variegated plants are any less vigorous or productive than normal plants.

Takagi<sup>42\*</sup> has reported a type of soybean with greenish yellow leaves which appeared in one-sixteenth of the  $F_2$  progeny of a cross between two normal, green-leaved parents. Takagi has assumed that two complementary genes,  $A$  and  $B$ , for normal leaves are involved,  $A$  being brought in by one parent,  $B$  by the other parent; and that only in the absence of both factors does the chlorotic type appear. The  $F_2$

ratio was substantiated by growing the  $F_3$  progeny. Plants of the chlorotic type are stunted in growth and bear only small, faintly colored seeds.

### Fasciation

There is, in many different kinds of plants, a peculiar condition in which the stem is flattened and often abnormally enlarged as if by the adhering or growing together of two or more ordinary stems (Fig. 12). This condition is called fasciation. A strain of fasciated soybeans, having the characteristically flattened stems has been described



FIG. 12.—STEM AND PODS OF A FASCIATED SOYBEAN PLANT

This type came from Japan (Takagi<sup>42\*</sup>). The stem is wide and flattened as if two or more stems had grown together. All the pods were borne at the top of the plant. This character is recessive to the normal.

by Takagi.<sup>42\*</sup> In crosses with the normal type fasciation was recessive, and in  $F_2$  a ratio of 3 normal to 1 fasciated was obtained.

### Pod Color

Soybean pods exhibit a wide variety of pod-color types, ranging from light straw yellow thru various shades of gray and brown to black. No attempt has been made to describe the many different color types or to study their inheritance. Two general types have been distinguished, designated dark and light. Dark pods are mostly black or



FIG. 13.—DETERMINATE AND INDETERMINATE TYPES OF GROWTH

A close view of a stem from each of the two plants shown in Fig. 14. The stem at the right (determinate) is terminated by a long flower stalk bearing several pods, that at the left (indeterminate) has only one pod at the tip. The pod-bearing habit is an important factor in yield of seed.



FIG. 14.—(A) INDETERMINATE AND (B) DETERMINATE POD-BEARING HABIT IN THE SOYBEAN

These plants came from a progeny segregating for these habits. The parent of this progeny had the habit shown by A; hence the indeterminate habit is dominant.

nearly so, while by light pods is usually meant pods ranging from a very light tan thru straw yellow to light brown.

In inheritance dark pods are dominant to light, and in  $F_2$  a ratio of 3 dark to 1 light is obtained (Piper and Morse<sup>35\*</sup> and Woodworth<sup>58\*</sup>). The symbols *Ll* are used for this factor pair.

### Pod-Bearing Habit

In the main there are two modes of pod formation (Fig. 13) in the soybean, according to Etheridge, Helm, and King;<sup>5\*</sup> namely "a dense array of pods on the central stem, terminating there in a blunt apex, with a thin dispersal on the lateral branches; and a sparse and comparatively even distribution of pods over all branches and stems, a diminishing frequency toward the tip of the central stem being notable." These authors placed more than a hundred soybean varieties and strains into one or the other of these classes with respect to pod-bearing habit.

These two methods of pod formation are very well illustrated in Fig. 14. The two plants there shown were sibs, members of the same progeny, the parent of which had the habit of growth shown by the plant at the left. Hence the pod-formation habit represented by B is dominant to the habit represented by A. The hereditary behavior is further indicated by the fact that the progeny, from which the two plants pictured in Fig. 13 descended, segregated for pod-bearing habit as follows: type B, 69 plants; type A, 19 plants. Thus a single factor difference appears to be involved. Type B may be termed indeterminate and type A determinate. The symbols *Dt*, *dt* are suggested for this character pair.

### LIST OF GENES IN SOYBEANS

The following list of genes is given for convenience of reference. No pains have been spared in the attempt to make it complete and up-to-date. The author has taken the liberty to assign symbols to certain characters that had been investigated by other workers but not named and also to change slightly certain other symbols in order to bring them into line with current usage.

- B*<sub>1</sub>, *B*<sub>2</sub>, *B*<sub>3</sub>, genes for "bloom" on seed coat
- D*<sub>1</sub>, one of duplicate genes for yellow cotyledons; *d*<sub>1</sub>, green cotyledons
- D*<sub>2</sub>, one of duplicate genes for yellow cotyledons; *d*<sub>2</sub>, green cotyledons
- De*, normal seed coat; *de*, defective seed coat
- Df*, normal; *df*, dwarf type
- Dt*, indeterminate; *dt*, determinate
- E*, early maturity; *e*, late maturity
- F*, normal stem development; *f*, fasciated or flattened stem
- G*, green seed coat; *g*, yellow seed coat
- I*, *i*<sup>h</sup>, *i*<sup>k</sup>, *i*, multiple allelomorphic series for inhibition of black and brown pigment in seed coat
  - I*, total inhibition; seeds show no black or brown pigment even in hilum; identical with *I*<sup>h</sup>
  - i*<sup>i</sup>, partial inhibition; permits pigment only in hilum; identical with *I*<sup>i</sup>
  - i*<sup>k</sup>, partial inhibition; responsible for Black Eyebrow pattern; identical with *I*<sup>k</sup>
  - i*, no inhibition; seeds are entirely black or brown

- L*, dark-colored or black pods; *l*, light-colored pods  
*M*, responsible for black mottling on a self-brown seed coat; *m*, no mottling  
*N*, gene for normal hilum such as is found in most soybean varieties; *n*, abnormal hilum such as is found in the Soysota variety  
*Na*, broad leaflet of most varieties; *na*, narrow leaflet  
*P*<sub>1</sub>, inhibition of pubescence, causing glabrousness; *p*<sub>1</sub>, no inhibition  
*P*<sub>2</sub>, gene for pubescence; *p*<sub>2</sub>, no pubescence  
*R*<sub>1</sub>, *r*<sub>1</sub>, *r*<sub>1</sub><sup>o</sup>, multiple allelomorph series for seed-coat color  
     *R*<sub>1</sub>, complementary with *R*<sub>2</sub> for black seed coat or hilum  
     *r*<sub>1</sub>, complementary with *R*<sub>2</sub> for brown seed coat or hilum; recessive to *R*<sub>1</sub>  
     *r*<sub>1</sub><sup>o</sup>, reddish brown seed coat; recessive to *R*<sub>1</sub> and *r*<sub>1</sub><sup>o</sup>  
*R*<sub>2</sub>, complementary with *R*<sub>1</sub> for black seed coat or hilum; *r*<sub>2</sub>, recessive to *R*<sub>2</sub>  
*S*, tall, late-maturing type; *s*, stocky, early-maturing type  
*St*, normal production of seed; *st*, sterility  
*T*, tawny or brown pubescence color; *t*, gray pubescence color  
*V*<sub>1</sub>, normal chlorophyll development; *v*<sub>1</sub>, variegation  
*W*, purple flower color; *w*, white flower color  
*X*, extra leaflets in compound leaf; *x*, normal number, three

### LINKED CHARACTERS IN SOYBEANS

Artificial crosses are difficult to make in soybeans; hence back crosses are impractical as a means of determining crossover values in this plant. A type of soybean carrying a large number of independent recessive characters would be of great value as a linkage tester. Whenever the linkage relations of a character or characters are desired, a cross could be made with the tester, and as large an  $F_2$  population as practicable could be grown and studied. The segregating characters could then be classified, two at a time, and the extent noted to which the ratio deviated from that signifying independence. With the convenient and accurate formulae and tables now available for determining crossover values on  $F_2$  data, it can no longer be considered a handicap in linkage studies in the soybean to be confined to studies of the  $F_2$  generation.

In the soybean there are many characters which, tho recessive in inheritance, do not seem to reduce the vigor of the plant. Certain high-yielding standard varieties possess many recessive characters; as, for example, gray pubescence, white flowers, light-colored pods, light brown hilums, and the like. Glabrous plants, however, are low in vigor, and such types are undesirable for linkage testers because of the low yield of seed. With the exception, therefore, of such genes as *p*<sub>2</sub> (causing glabrousness) and *st* (causing sterility) it would seem feasible to accumulate a considerable number of recessive characters in one type.

A provisional chromosome map of soybeans showing linkage relations of a few factors is given in Fig. 15.

In Group I, *R*<sub>2</sub> and *T* are represented as being completely linked.



However, since types with the constitution  $R_2t$  are known, they can be thought of as crossover types. The linkage then may not be absolutely complete, tho no crossovers have been observed in crossbreeding experiments. Owen<sup>31\*</sup> found about 6 percent crossing over between  $E$  and  $T$ . Also, according to Stewart and Wentz,<sup>40\*</sup>  $de$  for defective seeds is completely linked with  $t$ . Hence to date four genes have been

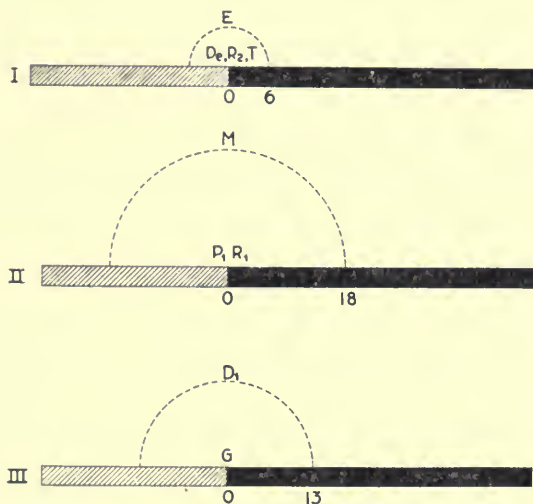


FIG. 15.—CHROMOSOME CHART SHOWING THE THREE GROUPS OF LINKED GENES THAT HAVE BEEN WORKED OUT THUS FAR IN THE SOYBEAN

In Group I genes  $De$ ,  $R_2$ , and  $T$  are all at the same locus, while gene  $E$  is represented as being six units away. Without further information it is not known on which side of the  $De$ ,  $R_2$ ,  $T$  locus  $E$  lies; hence the semicircle. A similar plan is followed for the other groups. The idea is borrowed from the plan used by corn geneticists led by Dr. R. A. Emerson at Cornell University.

identified in Group I, three of which have the same locus, and the fourth gene is located approximately 6 units away.

In Group II,  $P_1$  and  $R_1$  are represented as being completely linked (Owen<sup>31\*</sup>). Factor  $M$  for mottling is located 18 units from  $P_1$  and  $R_1$ . Thus to date only three factors have been located in this group. Only two factors,  $D_1$  and  $G_1$  have been located in Group III. Published data indicate about 13 percent crossing over (Woodworth,<sup>57\*</sup> Owen<sup>30\*</sup>) in Group III.

The chromosome number in soybeans is given as 20 for the haploid and 40 for the diploid condition by Tischler,<sup>45\*</sup> who refers to the work of Karpetschenko.<sup>17\*</sup>

## VARIATION IN SOYBEANS

By variation is meant deviation, with regard to a specific character or quality, from what may be taken as the original type. The type is usually considered to be the average expression of the character, and any deviation from this average constitutes a variation no matter how small or how large. Variation implies a difference in one respect or another. If a parent plant is heterozygous, there is variation among the offspring and certain of the offspring may even differ from the parent. Plants may also vary because of differences in growth conditions. Variations furnish the sole basis for improvement. Without variation, no improvement is possible.

From a plant-breeding standpoint there are two main kinds of variation, heritable and nonheritable. The nonheritable variations are often called modifications or fluctuations, and they are due to the unequal influences of growth conditions, such as differences in soil type, soil fertility, moisture, etc. Differences in growth conditions are reflected in differences in size of plant, branching, height, and rate of growth. Soybean plants having plenty of space in which to develop send out many branches, whereas crowded plants usually have only a main stem with no branches. Such changes are not inherited, and hence affect only the crop being grown. It would be of great advantage to the plant breeder in making initial selections and in testing the progeny of these selections if the growth conditions were identical for every plant in the field or plot. In such a case the breeder could be reasonably sure that any variations observed would be due to heritable changes. However, this ideal situation does not and cannot exist, and the breeder must devise ways and means of testing his plants in order to demonstrate heritable differences in spite of the ever-present and universal lack of uniformity in the plant environment.

Heritable variations are of two kinds; namely, mutations and those due to segregation and recombination. Mutations have been defined as heritable differences that do not result from segregation and recombination. By far the greater number of mutations affect one gene at a time. The wild soybean, for example, has purple flowers. By mutation the element or gene in the germplasm responsible for purple flowers was changed so that it produced white flowers. Usually such a change occurs in only one gamete at a time, and when the changed gamete unites with an unchanged gamete, the result is a hybrid which, in the illustration just cited, would have purple flowers. When the hybrid reproduces, however, segregation occurs, and it is to be expected that one-fourth of the progeny will be white-flowered. It is quite likely that

many of the numerous variations in individual characters observable today among soybean varieties have originated thru mutation, but it is certain that in some cases, as in those involving complementary relationships, hybridization was necessary to bring about visible differences.

Piper and Morse<sup>35\*</sup> describe an instance in which a brown-seeded variety arose as a mutation from a yellow-seeded variety. "The Trenton is a brown-seeded variety found in a field of the yellow-seeded Mammoth grown in Kentucky. Grown side by side at the Arlington Experimental Farm, the two sorts were indistinguishable by any other character than the seed color." This could be readily explained by assuming that the gene  $i^y$  carried by the Mammoth variety mutated to  $i$ , thus permitting the brown pigment of the Mammoth hilum to extend over the whole seed coat to produce a brown bean.

Many of the characters the mode of inheritance of which was described under the section on inheritance in soybeans have been due, according to the various authors, to mutation. Thus Stewart and Wentz<sup>41\*</sup> believe that the recessive glabrous type designated by the symbol  $p_2$  likely arose as a mutation. Stewart<sup>38\*</sup> found a dwarf soybean which was most probably a mutation. The list could be greatly extended. Below are a few mutations that have come under the observation of the writer during the course of several years:

- Dark pod to light pod
- Normal plant size to dwarf
- Normal green plant to variegated
- Black hilum to brown hilum (this occurred in Ebony, a black-seeded variety)

In addition to the above a few somatic mutations have occurred resulting in "chimeras" of various kinds (Fig. 16). One of the most interesting of these was a small plant the stem of which was half purple and half green from base to tip (Fig. 17). This plant was discovered in one of the plantings at the Illinois Station by Dr. Leo Clemente, now of the University of the Philippines. The line separating the two stem colors was very sharp and distinct. The purple side of the plant bore purple flowers and the green side white flowers, a result to be expected because of the close relationship between stem color and flower color. A few seeds have been found with one green and one yellow cotyledon, also the result of somatic mutation. These are, of course, of no importance from a plant-breeding standpoint since they cannot be perpetuated, but they are of considerable genetic interest.

The cause of mutations is not known. Various attempts have been made by different means in different organisms to induce mutative

changes artificially. The most successful of these has been the use of X-rays. The changes induced by the X-rays are recessive and detrimental, but it is significant that these are the same in nature and appearance as those occurring naturally from time to time in the same material. It appears, therefore, that X-rays may be a means of speeding up the process. Quite recently Patterson and Muller<sup>33\*</sup> have suc-



FIG. 16.—A TYPE OF VARIEGATION IN THE SOYBEAN

This was discovered for the first time in 1930. A few leaves were entirely white and a few were entirely green, but most of them were part white and part green, as shown above. The plant from which these leaves came is a chimera.

ceeded in inducing dominant changes in the fruit fly (*Drosophila melanogaster*). It appears that the use of X-rays in improving plants has possibilities for the future, but for the present it must be considered to be in the experimental stage. So far as the writer knows, no work of this kind has been done on the soybean. The soybean breeder is fortunate in having an abundance of variations on which to work. Much remains to be done in the way of utilizing the varieties and strains at present available for improvement thru hybridization and selection without resorting to the use of X-rays.

Not many years ago the idea was entertained by some people that selection, if carried on continuously for a period of years, caused heritable changes in the direction of selection. This idea has special reference to normally cross-fertilized material. While accepting the fact that such changes may have accompanied selection, they have now been interpreted in other ways. A character is the manifestation of a gene

or genes resident in the germplasm, and a character must appear before selection can become operative. Hence selection can scarcely be said to induce mutations when such heritable changes had already taken place in the germplasm before the plant was subjected to selection.

Furthermore the occurrence of mutations cannot be ascribed to a need for them on the part of the plant. Proof of this statement



FIG. 17.—A YOUNG SOYBEAN PLANT WITH HALF ITS STEM  
PURPLE AND HALF GREEN

The purple side (left) later produced purple flowers and the green side (right) white flowers. This is a chimera, and probably arose as a mutation which occurred at a very early stage in the development of the embryo. It was discovered by Dr. Leo Clemente, now of the University of the Philippines, while at the University of Illinois.

is furnished by some results obtained at the Illinois Station in an experiment on breeding soybeans for high and low oil content. This experiment will be described more fully in a later section, but sufficient mention will be made here to illustrate the point. Several hundred soybean plants of the Manchu variety were analyzed for oil content. Considerable variation was found, most of which was probably due to

growth conditions. That some of this variation was genetic was indicated by the fact that progeny tests of high and low parents revealed significant differences of 2 to 3 percent oil. No correlation was found between oil content and yield of seed. Therefore slight differences in oil content can have no selective value from the standpoint of the survival and well-being of the plant. In this variety at various times in the past and for no known reasons mutations have occurred affecting

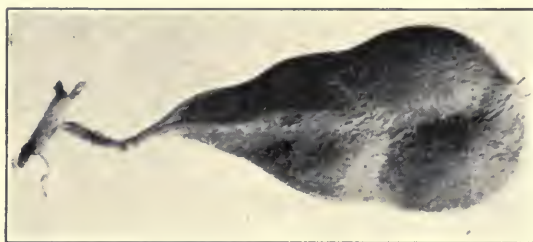


FIG. 18.—TWO SOYBEAN PODS THAT HAVE GROWN TOGETHER

The soybean flower usually has a single pistil, but this double pod may have developed from a double ovary. It is probably not inherited.

oil content, and as a result the variety has become a mixture of types so far as this character is concerned. The occurrence of heritable variations for oil content would never have been detected had analyses not been made.

The same may be said concerning resistance to plant diseases. Mutations occur from time to time regardless of whether the variety is ever subjected to attacks of the causal organism or not. Consequently, when such attacks occur, plants are found that are partially or wholly resistant and hence survive and propagate their kind. Thus resistant varieties are produced. Resistance to a plant disease, then, is not a character that has been produced by a need for it on the part of the individual plant, for the character existed prior to such need. Also, if after the first attacks of the causal organism further mutations occur in the direction of more complete resistance, it seems reasonable to suppose that the same cause or causes responsible for the initial variations have brought about the further germinal changes, rather than that these changes are due to the presence of the causal organism.

Thus mutations occur from time to time, producing certain new characters or quantitative changes in others without provocation, need, or apparent cause. All that the breeder can do is to watch for them and when they occur isolate and study them to see if these mutant forms are more valuable than the type from which they came.

In soybeans very few abnormalities, such as albinos and yellow plants, are found when compared with the number observed in corn following self-fertilization. This should not be taken to mean that such mutations rarely occur in soybeans, but rather that when they occur they are almost immediately subjected to natural selection and they either perish or survive on their merits. In a cross-fertilized crop like corn, on the other hand, such abnormalities can be carried along indefinitely in the heterozygous condition, and as additional mutations are constantly occurring and none is eliminated, they tend to accumulate in the variety. It may be said, then, that self-fertilization is good for the soybean plant in that it tends continually to purge it of defective germplasm, and thus to keep it remarkably free from abnormal types.

It is extremely difficult, if not impossible, to get at the rate of mutation for various characters in the soybean. The number of mutations in any organism is usually so small that several hundred thousand or even millions of cases must be observed in order to determine the rate of change with any degree of accuracy. Stadler<sup>36\*</sup> has made a study of the mutation rate in corn for factors affecting aleurone color and endosperm texture, and he finds significant differences in the rate for different genes. His procedure may be illustrated by the method used to determine the rate of mutation of *R*, one of the genes for aleurone color in corn. Crosses on a quantity basis were made between a colorless aleurone type *ACrPr* ♀ and a purple aleurone type *ACRPr* ♂. All the kernels on the crossed ears should have been purple, and this was the case except when the gene *R* mutated to *r*, giving rise to colorless aleurone. The ratio of such colorless aleurone kernels to the purple aleurone kernels gives the mutation rate of this gene. Crosses can be very easily made in corn, and large numbers can be obtained particularly in cases involving endosperm characters. On the other hand, in the soybean crosses are made with great difficulty. This in itself precludes the use of Stadler's method for getting at mutation rates in soybeans. Furthermore cotyledon color is the only character so far known for which cases running into the thousands can be easily obtained in segregating generations. This fact, however, does not help in getting at mutation rates even for cotyledon genes, owing to the above-mentioned difficulty of making crosses and to the inability to distinguish, in segregating generations, green cotyledon beans due to mutation from those due to recombination. Hence there appears to be at present no adequate method by which mutation rates for various genes in soybeans can be determined.

Other heritable variations are those due to hybridization, which result in segregation and recombination. The breeder desires to find ways of inducing variation so as to make it occur more frequently



FIG. 19.—TWIN SOYBEAN PLANTS AND SEED PRODUCED BY THEM

These plants grew together as one plant on the same root but bore different kinds of seed. Hence these are not identical twins. There were probably two embryos within the same seed coat, and they produced different kinds of seed because of a different genetic constitution.

than it would occur ordinarily by mutation. Hybridization is one of these ways. Hayes and Garber<sup>13\*</sup> state that the only practical means possessed by the breeder of inducing variation is thru hybridization. Bettering the conditions of growth induces greater development but these changes are not inherited. Since, as stated above, the cause is unknown, the breeder does not know how to produce them. Also, the



use of X-rays in causing mutations, while a promising method for the future, must be considered experimental probably for many years to come. Hence hybridization will likely continue for some time to be the only practical means in the hands of the breeder of producing heritable variations.

How does hybridization induce variation? This is brought about as a result of segregation and recombination. When a hybrid, such as  $AaBb$ , is self-fertilized, four kinds of progeny will result, two of which will be like the original parents, namely,  $Ab$  and  $aB$ . The other two will be different. One will possess both genes  $A$  and  $B$ , and the other neither of these genes ( $ab$ ). Thus new types have resulted from the cross. Both these new types might have been produced by mutation, but the breeder might have waited in vain for them to be produced in that way. By crossing, nature is given a chance to produce them in a relatively short time.

In the illustration given above only two factors were used. Segregation and recombination following a cross between two soybean varieties is much more complex since there are not only the numerous genes involved for characters, such as color of flower, pod, pubescence, and seed, but also genes for such characters as type of plant, maturity, size of seed, and height of plant. The quantitative characters just mentioned are quite complicated in inheritance, many genes being involved for each. Various combinations of all these genes give rise to numerous types which are different not only from the parents but from one another. An idea of their complexity may be gained by referring to the statement made later in this bulletin regarding the number of types resulting from selfing, starting with hybrids heterozygous for varying numbers of genes. By reference to the general formula there given (page 345), it can be seen that by crossing two varieties differing by only ten genes as many as 1,024 different types will result. Thus hybridization is a practical means of inducing heritable variations by recombining in various ways characters already in existence.

Furthermore under certain conditions hybridization may give rise to entirely new characters. This comes about thru the complementary relationship of certain genes. It was shown under the section on inheritance that by crossing two brown hilum varieties, a black hilum type could be produced. This was explained as follows: two genes are necessary to produce black; namely,  $R_1$  and  $R_2$ . When one parent carries  $R_1$  and the other  $R_2$  the hybrid, containing both  $R_1$  and  $R_2$ , will be black. Then in addition to recombining in different ways characters already present in the parents, hybridization may give rise to entirely new characters, not of course as mutation does it, by a change in the

germinal material, but by combining two sets of germplasm, one of which contains genes complementary to those of the other.

### SELECTION AS A METHOD OF BREEDING

Selection is a choice of the best. It is one of the most powerful tools in the hands of the breeder for effecting improvement. Effective selection presupposes the occurrence of variations. One discovers a plant that is different in some particulars from its neighbors. It may be taller, have more branches, more pods, or it may have merely a different color of flower, pod, or pubescence. It is selected, isolated from the group, and when planted separately it may breed true to the particular difference or differences for which it was selected, and thus a new type is produced.

### COMPOSITION OF VARIETIES

Varieties of soybeans are, as a rule, relatively pure; that is, all the plants of a given variety are alike. This is due to the fact, mentioned earlier, that the soybean is a self-fertilized plant. However, if one walks thru a field of soybeans all planted to the same variety and examines the plants, he will find a greater or less number of off-type plants, so called because they are different in one or more of the characteristics that distinguish the growing plant of one variety from that of another. There may be a difference in flower color, pubescence color, pod color, or habit of growth. If later one were to examine the threshed seed, he might also discover seeds having coat or hilum colors that are not typical of the variety.

How do these mixtures occur? There are at least three different ways: (1) By mechanical means. Where several varieties are grown in a neighborhood, the threshing machine carries seeds from one farm to another. If farmers change from one variety to another, they are often not careful to clean out the drill or seed room thoroly. (2) By natural crossing. When mechanical mixtures have occurred, and the off-type plants are growing alongside and in contact with the typical plants of the variety, natural crosses occur to a certain extent, as pointed out earlier in this bulletin. When the hybrids grow and reproduce they will not breed true but, owing to segregation and recombination, will give rise to numerous types. (3) By mutation. As pointed out under the heading of variation, mutations may occur tho they are probably rare. Nevertheless instances are recorded of germinal changes taking place in soybeans, thus giving rise to new types.

If mechanical mixtures are avoided, no natural crosses can give

rise to mixed types. Mutations, tho beyond the control of the grower, occur too rarely to be an important factor in causing mixtures. Hence the grower can keep his variety relatively pure by taking care that no off-type seeds get into the variety by mechanical means, and by roguing them out if by chance some do get in, thus reducing greatly the chances for natural crossing.

If the variety is pure for its characters, self-fertilization results in its breeding strictly true. The composition of the variety then remains the same so long as the condition of purity is maintained. If, however, hybrids are produced by natural crossing and thereafter propagated by self-fertilization, the tendency is for the progeny of the hybrid, after several generations, to consist almost entirely of pure types.

This principle can perhaps be made clearer by an illustration. Suppose we start with a plant which is heterozygous for gene  $A$ , having, therefore, the constitution  $Aa$ . When self-fertilized, it will produce the following types in the following ratio:  $1 AA: 2 Aa: 1 aa$ . Now, if each plant of this progeny produces four individuals, the next generation will consist of the following types and proportions:  $3 AA: 2 Aa: 3aa$ . The pure types,  $AA$  and  $aa$ , make up 75 percent of the total, and the heterozygous type,  $Aa$ , only 25 percent. In the preceding generation the ratio of homozygous to heterozygous was 1:1. If this problem is carried further it can be readily determined that the homozygous type will increase and the heterozygous type will decrease, until it can be said that the progeny of the original hybrid, for all practical purposes, consists of only two types,  $AA$  and  $aa$ , in equal numbers. Stated in general terms the proportions of the pure and impure types in the progeny after  $n$  generations would be  $2^n - 1 AA: 2 Aa: 2^n - 1 aa$ , where  $n$  is the number of generations, counting the  $F_2$  generation as the first.

It should be emphasized that self-fertilization does not reduce the progeny of the hybrid to homozygosity, but rather to a *mixture* of homozygous types. The number of homozygous types resulting from continued self-fertilization depends on the number of heterozygous factors in the original hybrid parent. In the example cited, there were two pure types. If the original parent were heterozygous for  $B$  as well as  $A$  ( $AaBb$ ) there would be four pure types: namely,  $AABB$ ,  $AAbb$ ,  $aaBB$ , and  $aabb$ . The general formula  $2^m$ , where  $m$  is the number of heterozygous factors in the original parent, can be used to calculate the number of different pure types that would result. This is better shown as follows:

Number of heterozygous genes.....	1	2	3	4	5	$m$
Number of homozygous types.....	2	4	8	16	32	$2^m$

Thus if a plant were heterozygous for 10 pairs of genes,  $2^{10}$  or 1,024 pure types would be produced as a result of self-fertilization. This emphasizes the importance of natural crossing in causing mixtures in the variety.

#### NATURAL PURIFYING METHOD OF SELECTION

There is a method of handling hybrids which is based on the principle just explained. This has been variously called the "Svalöf method," the "bulked population method," and the "natural purifying method." The plan (Fig. 20) generally followed is to bulk the plants of the first segregating generation instead of harvesting and threshing

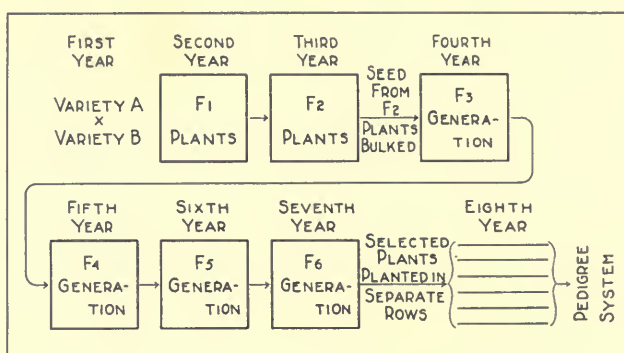


FIG. 20.—STEPS IN THE NATURAL PURIFYING METHOD

Hybrid plants from natural or artificial hybrids are bulked together and a plot grown each year from seed produced by the hybrid population of the previous year. This process is continued for several years. Then single plant selections can be made with fair assurance that such plants will be homozygous for their characters and will therefore breed true, the heterozygous types having been gradually eliminated as a consequence of the principle of self-fertilization. The selected plants can then be carried along by the pedigree system.

them separately. The seed is planted in bulk, the plants again bulked, and the same procedure is repeated for several generations. After 6 to 10 generations the breeder can make selections from such a population of plants with fair assurance that any plants selected will be pure for the combination of characters carried, and will therefore breed true when tested by their progeny. Furthermore, during the purifying period all the plants are subjected in each generation to natural selection and the very poorest are eliminated. Hence any plants selected may be considered not only to be pure but also to be among the best so far as yield and vigor are concerned.

This method has certain advantages. One of these concerns the time element. It requires little of the breeder's time and attention to carry along the material during the purifying period. Also, the hybrids from many different crosses can be put together and continued as one population. No time is required for a careful study till the selections are made and tested. Another advantage is that the lot of seed can be divided after the second or third generation has been grown and the smaller lots sent to parts of the state which differ in soil type and climatic conditions. During the purifying period natural selection would tend to favor those types that are best adapted to the particular locality. Hence the task of selecting good, desirable types will be lightened by whatever nature has done in the way of preserving the best and eliminating the poorest.

The "natural purifying method" of selection can be used for the improvement of soybeans, since the soybean is a self-fertilized crop. The method has not been used to any extent at the Illinois Station because the pedigree system, in which the progeny of each hybrid is studied carefully for several generations, has been preferred. Such a careful study is necessary when one wishes to learn about the mode of inheritance of characters. Furthermore selections can be made at any time and tested to see whether they breed true for the combination of characters desired. However, the "natural purifying method" can be used with natural or artificial hybrids, and soybean growers who are interested in soybean improvement may use it on the progeny of natural hybrids that occur in their fields from time to time.

#### PEDIGREE SELECTION METHOD

In a variety which has become mixed in any one or all of the ways described above, numerous types exist that differ in size, maturity, and yield as well as in color of flower, seed, or pod. For the most part these types can be considered pure for their characters, and the differences they exhibit are inherited. Such a mixed variety can be considered a mixture of pure types. If now the breeder selects from such a mixture a number of single plants, keeps the seed of each plant separate, grows a row of plants from each parent plant, and continues to keep the progenies separate, he is practicing pedigree selection (Fig. 21), so-called because the pedigree of the strain can be traced back to a single parent plant.

The success of this method depends greatly on the first or initial selection. If the parent plant is pure for its characters, the progeny it produces is spoken of as a pure line, because it is produced as a

result of self-fertilization. When the pure line is separated or isolated from the group, it is useless to select further within the line, since such selection has been found to have no effect. All that selection can do, therefore, in a self-fertilized crop like soybeans, is to separate the pure lines of which the original variety or type was composed. This is why so much importance is placed on the initial selections, and why

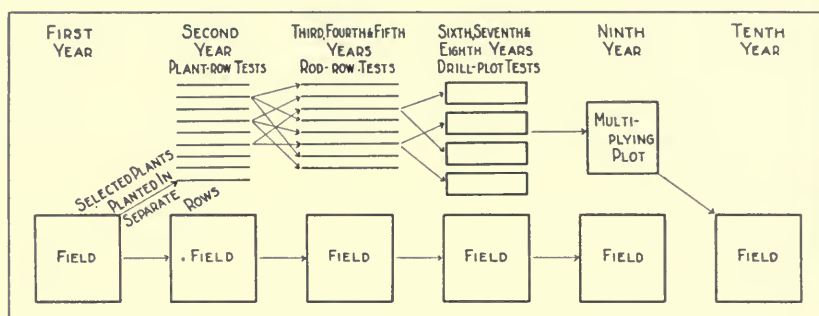


FIG. 21.—STEPS IN THE PEDIGREE SELECTION METHOD

Selected plants from a variety or hybrid population are planted in separate rows. The best are chosen by inspection and tested in rod rows for three or more years. The poorest are discarded and the best are advanced to drill plot tests. Finally the best strain is multiplied in a multiplying plot for general field planting. Many superior strains have been isolated from existing varieties by some such plan as this.

as large a number of plants as possible should be selected at the beginning. If 1,000 plants are chosen for test, the chances of finding an improved type are ten times as great as if only 100 plants are selected.

Variation in growth conditions in different parts of the field makes selecting plants for test difficult and uncertain. Plants that appear superior to the rest in yield may be so because of more space in which to grow or more fertility in that particular spot of soil, and not because of a better genetic constitution for yield. In other words, two plants may appear different but breed the same, or appear alike but breed differently. Differences in appearance will not be reproduced in the progeny unless they are the result of a difference in genetic constitution.

Pedigree selection is responsible for the discovery of many improved types of soybeans. The Illini variety originated from a single plant selected from the A.K. variety (Fig. 22). The parent plant bred true from the start, and since the resulting strain had certain desirable

characters, such as high yield and early maturity, it was multiplied and distributed. Mansoy is a selection from Manchou, Ilsoy from Ebony, and Virginia from the Morse variety.



FIG. 22.—A FIELD OF ILLINI SOYBEANS ON THE UNIVERSITY OF ILLINOIS SOUTH FARM

One of the outstanding characteristics of this variety is its uniformity in growth habit.

#### MASS SELECTION METHOD

Mass selection differs from pedigree selection in that the selected plants are bulked and threshed together and the seed planted as one lot of seed (Fig. 23), instead of the seed of each plant being kept separate as in the latter method. Oftentimes a seed plot is maintained which is planted to the seed of the selected plants; this may be a corner of the general field. Before harvest the breeder goes thru the seed plot and again selects the best plants, which are again bulked as before, and another seed plot planted. The remainder of the plants in the first seed plot can be harvested together, threshed, and the seed used for commercial planting. This process may be repeated indefinitely.

Mass selection is simple and has the further advantage of requiring little time on the part of the breeder as compared with that necessary in the pedigree method. If, however, hybrid plants are selected, they will segregate and cannot be eliminated from the seed plot except by further selection. In the case of pedigree selection the whole row coming from the hybrid plant can be eliminated. Furthermore, if we think of the population as being a mixture of pure lines which vary in yielding capacity, each around its own respective average, continued

mass selection of the higher yielding lines tends, theoretically at least, to eliminate first the lowest ones, then those near the average of the whole group, and finally all but one line which is the very best. When the population thus is made up of a single line, further selection would have no effect, as explained in the preceding section. To reach this point under mass selection requires a considerable number of generations, many more, likely, than the practical results would justify. That is to say after a period of five or six years the breeder may have been able to eliminate, by mass selection, all but the best yielding half dozen

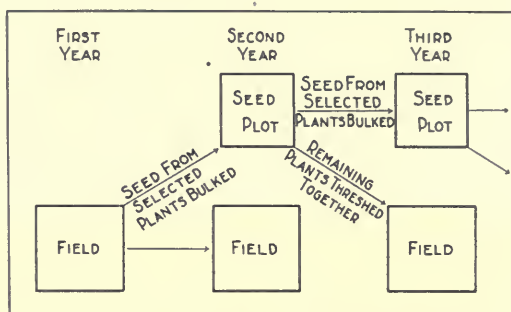


FIG. 23.—STEPS IN MASS-SELECTION METHOD

This method is simple and easily carried out. It is particularly effective in purifying a variety that has become badly mixed with other types. It may also be used to isolate the better yielding line or lines from the plant population, but a long period of time is required for this, and furthermore improvement is very slow if it can be noticed at all within a period of a few years.

lines. The difference between these, if any, may be so slight as to make it immaterial whether the population is reduced to a single line. It should be kept in mind that the lines we are concerned with here are alike with respect to plant characters, so that when mixed together they present a uniform appearance, and that any differences they exhibit are due to genes affecting size, vigor, yield, and the like. Such quantitative differences are very generally confused with differences in growth due to soil fertility or soil type, and under field conditions it is difficult and oftentimes impossible to distinguish between the heritable and the nonheritable quantitative variations. For these reasons it may be a waste of time to continue mass selection beyond a certain point.

Aside from any improvement in yield which may result, mass selection is quite effective in purifying a mixed population of soybeans or



of any other self-fertilized crop. For example, if for various reasons a field of Illini beans becomes badly mixed and it is desired to purify them, the grower can select a large number of plants which are typical of the variety in every particular, thresh them together, and plant the bulked seed separate from the rest of the field. If none of the selected plants is a natural hybrid, the next crop will be pure and true to type; but if a few natural crosses have occurred, as may have been the case, a few mixtures will be observed in the next crop. If these mixtures carry plant characters which make them easily distinguishable from the typical plants, they can be pulled and removed from the field. In case, however, plants off-type in seed characters occur, they cannot be distinguished from the rest until harvest, and then they can be picked out and discarded. It may be necessary to repeat this process in order to make sure that all mixtures have been removed.

Pedigree selection is still more effective than mass selection in purifying a variety of soybeans. Each selected plant is planted in a sepa-

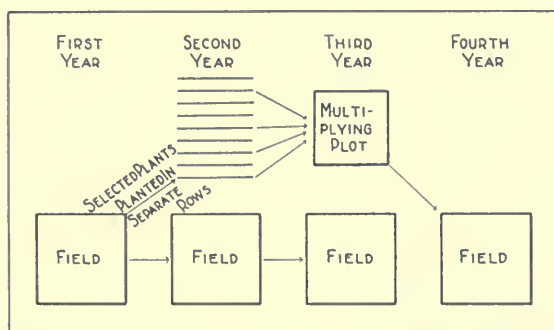


FIG. 24.—STEPS IN A MODIFIED METHOD OF MASS SELECTION

Instead of bulking the seed from selected plants as in the mass-selection method, the selected plants are harvested and threshed separately and the seed planted in separate rows the following year. The rows that are inferior for any reason or are segregating for one or more characters can be eliminated and the rest can be harvested together for planting a multiplying plot the next year. This is a good way to purify a variety having many dominant characters.

rate row and every plant of the progeny examined with respect to plant and seed characters. Any row found to be different from the type in any way or to be segregating for any character is discarded, and the typical true-breeding rows are massed together to make a pure stock of seed (Fig. 24). Thus only one generation with pedigree selection is required to attain a high degree of purity in the stock.

## CROSS-FERTILIZATION OR HYBRIDIZATION AS A METHOD OF BREEDING

It was shown earlier that self-fertilization tends to separate the genes present in the hybrid and distribute or assort them to different strains. Hence self-fertilization may be looked upon as an analytical method which breaks or tears down the combination of genes piled up or assembled in the hybrid. By way of contrast cross-fertilization may be considered to be a synthetic method which brings together or synthesizes the genes that have been separated or assorted to different lines. Cross-fertilization offers an opportunity for the greatest number of favorable genes to be combined into one type. Hence types may be said to be synthesized by cross-fertilization and analyzed by self-fertilization.

Plant-breeding has for its major problem the bringing together into one type of all the characters that are considered desirable from the standpoint of production. No type now known contains all these characters expressed to the highest degree. For example, a strain selected from the A.K. variety of soybeans is a good yielder, stands up well, and is early maturing, but in certain seasons it shatters badly. Two methods are available for improving this strain. One method is to examine the strain for plants that show little or no shattering in the hope that such plants, if any are found, represent heritable variations in the direction of nonshattering. If, however, the strain is pure for the shattering, no progress can be made by selection. The other method is to cross the strain with another variety that is quite resistant to shattering in the hope of being able to isolate from among the hybrids pure types that are good in yield, early, and erect as well as nonshattering. All these characters involved in the cross are probably determined by a large number of genes. It is a difficult problem, therefore, to grow and study enough plants in the  $F_2$  and  $F_3$  generations to justify the hope of finding types having the particular combination desired, especially since the expression of these characters may be modified to so great an extent by differences in soil fertility and soil type. Nevertheless progress is being made in overcoming these difficulties by learning more about the soybean plant itself, the mode of inheritance of the characters, and ways of testing plants in the field to obtain more accurate comparisons.

Hybridization makes it possible oftentimes to produce types that are superior or inferior to either parent with respect to a given character. This is referred to as *transgressive segregation*. The phenomenon of transgressive segregation occurs when the character involved

is determined by many genes some of which reside in one parent, some in the other. In such a case the parents are not thought of as being at the extremes for the expression of the character, that is, one parent very low or small, the other very high or large; but rather as intermediate or nearly so, tho between this situation and that in which one parent represents the extreme in one direction and the other parent the extreme in the other direction all possible gradations in intermediacy may occur.

A cross between two soybean varieties involving the hard seed-coat character is a good example of transgressive segregation. Seeds of the Dunfield variety when placed in water imbibe water very quickly and swell. Seeds of a strain designated S.P.I. 65388 have very hard seed coats, and imbibe water only after being soaked for several days. When, however, the seed coats are cut or scratched, water enters and the seeds swell. Hence the varieties differ in something that tends to make the seed coat impervious to water. In the crosses between these varieties it was found that the seeds of the  $F_1$  hybrid were intermediate between the two parents in this respect, tho resembling the Dunfield somewhat more than the other parent. In the  $F_2$  plants considerable variability occurred, as might have been expected. There were not only all possible gradations between the parents in the ability to imbibe water, but a few plants were even harder than the hard parent and a few even softer than the soft parent. Even tho it might be considered that the parents stood at practically the extremes for this character, yet a few  $F_2$  plants were found that transgressed the limits of the parents. Thus hybridization offers opportunity not only for combining desirable characters into one type, but also for bringing together or piling up genes for a given character, some of which are contributed by one parent and some by the other, resulting in the expression of the character to a higher or lower degree than it appeared in either parent.

Another phenomenon often accompanying hybridization is called *hybrid vigor*. This phenomenon may be defined as the stimulating effect resulting from a cross between different types, causing the hybrids to excel the parents in general vigor, size, or other characteristics. It has been variously called "vigor due to crossing," "hybrid vigor," "stimulus of heterozygosis," "heterozygotic stimulation," and "heterosis."

Hybrid vigor is particularly noticeable in hybrids between inbred strains of corn, a normally cross-fertilized crop. As a result of continuous self-fertilization strains have been produced that are inferior

to ordinary varieties of corn in general vigor, size, and yield. When however, these selfed lines are crossed, the hybrids usually excel the parents in these qualities and often even the ordinary varieties from which the parent lines originated. Hence this method of breeding corn is receiving considerable attention at the present time, particularly by the corn-belt experiment stations and the U. S. Department of Agriculture.

The phenomenon of hybrid vigor is not, however, confined to corn and other cross-fertilized crops. It is exhibited to a certain extent in self-fertilized crops as well. The first report of heterosis in soybeans was given by Wentz and Stewart,<sup>50\*</sup> who found in the hybrid ( $F_1$ ) of some crosses considerable increases in height of plant over the average of the parents. A few hybrids, however, were even below the parental average in this character. In crosses exhibiting heterosis the hybrids were below the parents in height during the first half of the growing period, but during the latter half and particularly during the last three weeks of the period the hybrids grew faster than the parents and finally exceeded them. Still greater evidences of hybrid vigor were shown by the hybrids in yield of seed, the percentage increases over the parents ranging from 59.58 to 394.37. The number of hybrid plants grown and studied was small, ranging from 1 to 3, and the number of parent plants, 1 to 5. In some cases the male parent plants were not available for comparison, but the authors stated that even if they be assumed to show a high yield of seed, there would still be good evidence for the occurrence of hybrid vigor.

Studies on hybrid vigor involving more crosses and more characters than the preceding were made by Veatch<sup>46\*</sup> at the Illinois Station. Sixteen crosses were compared with the average of the two parents and with the better parent in the following characters: yield of seed, number of seeds, average seed weight, percentage of abortive seeds, number of pods per plant, number of seeds per pod, plant weight, straw-grain ratio, plant height, total stem and branch length, number of nodes, average internode length, and number of days from planting to flowering. As might be expected, there was considerable variation among the hybrids as to the extent of hybrid vigor. The average of all the hybrids was higher in all characters studied than the average of all the parents; but in the following characters the average of the hybrids was exceeded by the average of all the better parents: average seed weight, number of seeds per pod, straw-grain ratio, and average internode length. The characters in which the hybrids exceeded, on the average, even the better parents, and therefore the characters in

which hybrid vigor was shown, were the following: number of pods per plant, plant weight, plant height, total stem and branch length, number of nodes, days from planting to flowering, seed weight or yield, and number of seed (Fig. 25). While these data are also based on only 1 to 4 hybrid plants of each cross and the same number of parent plants, yet, taken together with those of Wentz and Stewart just described, it is clear that a certain amount of hybrid vigor is shown by many soybean varietal crosses.

Granting that the phenomenon of heterosis is exhibited in certain soybean crosses, we have the problem of the utilization of this vigor

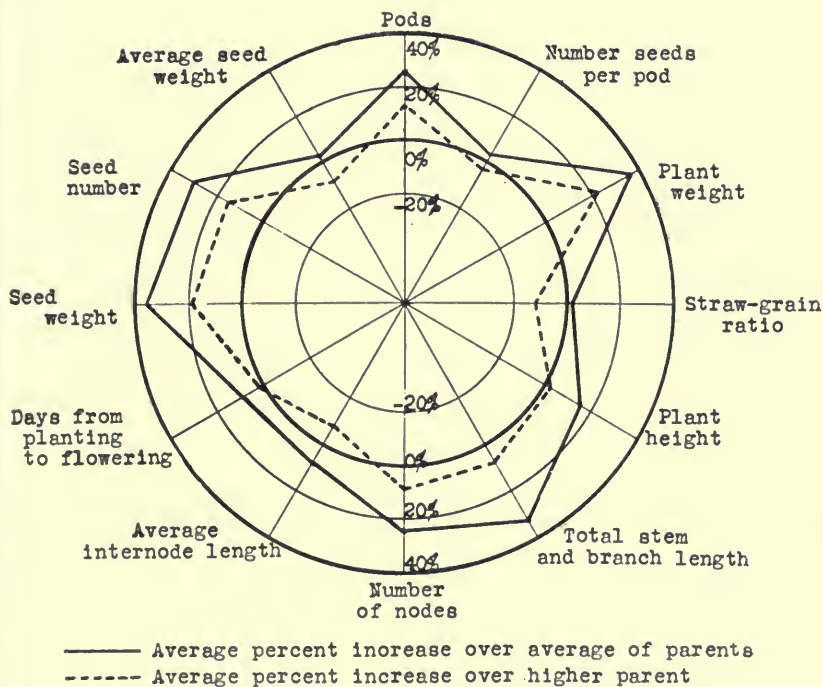


FIG. 25.—EXTENT OF HYBRID VIGOR IN SOYBEANS

Hybrid vigor occurs in certain characters and certain crosses in soybeans but it has not yet been utilized for increased production. In this diagram the light innermost circle represents 20 percent below the average of the parents; the next, a heavy line, represents the average of the parents; the next light line represents 20 percent above the average, and so on. The position of the hybrids is represented by the two polygons. The average of the hybrids exceeded the parental average for every character, but it exceeded the average of the higher parents only in number of pods, plant weight, plant height, total stem and branch length, number of nodes, number of days from planting to flowering, weight of seed, and number of seed. (From Veitch<sup>48</sup>)

for increased production. The soybean hybrids will not breed true. Unlike the horticulturist who is working with a plant that can be propagated by budding, cuttings, etc., thus passing on the benefits of hybrid vigor from generation to generation in undiminished extent, the soybean breeder must either first render his material homozygous for whatever genes are responsible for the hybrid vigor or else he must produce the hybrids anew each year. The latter method is out of the question because of the difficulty of making soybean crosses. The former method with various modifications that may be devised is the only one that has promise. With respect to yield the question may be put thus: What are the possibilities of isolating a type homozygous for genes responsible for the high  $F_1$  yield by selecting the highest yielding plants from among those of the  $F_2$  generation? The answer is that such a type should be expected, provided the Mendelian interpretation of heterosis as being due to dominant growth genes is the correct one, and provided further that linkage of genes does not exist to prevent random assortment and recombination of the genes involved. On account of the large number of genes probably involved, it would be impossible to grow and study enough  $F_2$  plants to have any chance of securing the particular combination which is homozygous for all the genes for which the  $F_1$  was heterozygous. Aside from this, there is the matter of random gene assortment. With 20 pairs of chromosomes in the soybean we should not expect linkage to hinder this process to the extent that it probably does in corn, which has only 10 pairs of chromosomes. At any rate, the chances are better in the soybean than in corn for the occurrence of independent pairs of genes and hence for independent assortment of these genes to the gametes. For the practical utilization of hybrid vigor, however, it is not necessary that the all-homozygote should be located and isolated. If a type could be obtained from among the hybrids that would breed true for 10, or 5, or even 2 favorable genes more than were carried by the better parent, some improvement would thereby have been brought about.

With the object of determining to what extent the  $F_2$  plants exhibited the vigor of the  $F_1$  parent, Veatch<sup>46\*</sup> made a study of the  $F_2$  generation of four crosses in yield of seed, number of seeds per plant, height of plant, and number of days from planting to flowering. Unfortunately the  $F_1$  and  $F_2$  generations could not be grown the same season, but comparisons of the two hybrid generations were made thru the parental types by interpolation. With respect to yield the  $F_2$  plants were found to extend from the lowest variate of either parental line to the highest variate or above. In one cross a particular  $F_2$  plant

yielded 67.38 grams, while the best plant of either parent yielded 58.27 grams. This difference was probably due to soil conditions. In another cross, however, the extreme yield of 111.17 grams was given by an  $F_2$  segregate, and this yield was more than twice as great as that of any plant in the parental lines or of any other plant in the  $F_2$  population. It would seem that this was too great a difference to be accounted for by soil differences, yet when this extremely high yielding  $F_2$  segregate was tested the next year by its progeny, it failed to transmit its marked reproductive propensity.

It must be granted that the method of comparing  $F_1$  and  $F_2$  generations by interpolation is far from satisfactory, but when this was done in the above case, it was found that three of the four  $F_1$ 's were above their respective  $F_2$ 's in average yield. In all but one of the  $F_2$  populations, however, there were extreme variates that yielded twice as much as the  $F_1$  plants (interpolated yields). This situation held very well for each of the other characters studied tho the excess of the extreme  $F_2$  variates over the interpolated  $F_1$  results was not quite so much. The next year many other extreme  $F_2$  segregates were tested by their progeny, in addition to the two mentioned above, but the results were disappointing. They performed no better than their parents. Probably soil variation is responsible for these results. More accurate methods of testing and comparing hybrid parents and progenies are needed in order to make definite progress in the utilization of hybrid vigor for increased production.

## BREEDING FOR SPECIAL FEATURES

### OIL AND PROTEIN CONTENT

One of the most important considerations in connection with the improvement of the soybean is that of modifying the composition of the bean, especially with regard to its oil content. The Illinois Station has demonstrated the possibility of effecting profound changes in the composition of corn with regard to protein and oil by continuous selection. The question arose as to whether these same methods used so effectively in modifying the composition of corn could be applied to the soybean, recognizing the fact that corn is a cross-fertilizing plant while the soybean is a self-fertilizing plant.

To test this point an experiment\* was started with the Ebony variety. Seed from ten plants from each of several plant rows grown in 1914 were analyzed for oil and protein. The row showing erect type,

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\*This work was done by Dr. L. H. Smith and Dr. A. M. Brunson.

vigor, and the greatest variability in protein content, Strain 13-13, was selected as the foundation of the High- and Low-Protein strains, and similarly the row exhibiting erect type, vigor, and the greatest variability in oil content, Strain 13-29, was selected as the foundation of the High- and Low-Oil strains. Thus the two protein strains originated from a single plant and the two oil strains originated from a different single plant of the same variety.

In the spring of 1915 seed from the 5 plants showing the highest percentage of protein of the 10 plants analyzed from Strain 13-13 were planted in Rows 1 to 5, comprizing the High-Protein selection. Similarly seed from the other 5 analyzed plants of Strain 13-13 showing the lowest percentage of protein were planted in plant Rows 6 to 10, and this comprized the corresponding Low-Protein selection.

In like manner seed from the 5 plants of Strain 13-29 showing highest percentage oil was planted in Rows 11 to 15 to form the High-Oil planting, and the seed from the 5 plants of the same strain showing lowest percentage oil was planted in Rows 16 to 20 to form the Low-Oil planting.

The later procedure was as follows: The 20 best plants of each row were selected by inspection, cut, and bagged separately, then later threshed, weighed separately, and the seed stored in glass jars. Composites of each of the 20 rows were then made and analyzed for protein and oil. The 20 plants of the row in the High-Protein selection having the highest percentage of protein were then analyzed individually, and the 5 highest of these were selected to plant the 5 High-Protein rows for the following year. Similarly the highest or lowest 5 plants of the row showing highest or lowest composite were selected in each of the other 3 strains to plant the following year. In this manner all 5 rows of one strain any year were planted from 5 mother plants, all grown in one plant row the year before.

The data obtained in this experiment are summarized in Tables 4 and 5. Table 4 shows the composition each year of the seed planted and the corresponding crop harvested with respect to protein content in the High-Protein and Low-Protein strains, and Table 5 shows similar results with respect to oil content in the oil strains.

In general the results show rather conclusively that selection has had no effect in these strains, either in the high or the low direction. As an average, the six crops of the Low-Protein strain were even higher than the six crops of the High-Protein strain, tho the difference was only .37 percent. In oil content the average analyses for the two strains showed a difference of only .10 percent. These results tend to



TABLE 4.—PROTEIN CONTENT OF SEED AND OF CROP THEREFROM FOR THE HIGH-OIL AND LOW-PROTEIN STRAINS

Year	High protein		Low protein	
	Seed	Crop	Seed	Crop
1915.....	42.85	41.47	40.29	42.23
1916 <sup>1</sup> .....	.....	.....	.....	.....
1917.....	43.11	38.96	40.53	42.36
1918.....	41.49	44.34	41.43	43.55
1919.....	47.56	39.28	41.24	39.03
1920.....	40.70	39.45	37.85	39.11
1921.....	42.04	41.41	38.72	40.84
Average.....	42.96	40.82	40.01	41.19

<sup>1</sup>No crop.

confirm those obtained in similar investigations on other species in indicating the futility of attempting to modify characters by selective breeding within pure lines propagated by self-fertilization.

Since selection for protein and oil within pure lines of soybeans appeared to have no effect, an experiment was started by the writer in 1922 to determine if strains differing in oil content could be isolated from a single variety. The Manchu variety was chosen for this experiment. On examining the beans it was found that two types existed, namely, those with black hilums and those with brown hilums. In 1922 over 200 plants were grown from each type of seed, the plants were threshed separately, and the seed of each analyzed for oil. In Tables 6 and 7 respectively the plants from black-hilum beans and from brown-hilum beans are classified with respect to oil content. The means, standard deviations, and coefficients of variability were not very different for the two groups.

Correlation coefficients were calculated for yield per plant and percentage of oil. These were, for the black-hilum group,  $r = .119 \pm .042$ , and for the brown-hilum group,  $r = .037 \pm .041$ . The results indicate that in this material no relation exists between the percentage of oil in the bean and the yield per plant.

TABLE 5.—OIL CONTENT OF SEED AND CROP THEREFROM FOR THE HIGH-OIL AND LOW-OIL STRAINS

Year	High oil		Low oil	
	Seed	Crop	Seed	Crop
1915.....	17.85	17.39	16.94	17.29
1916 <sup>1</sup> .....	.....	.....	.....	.....
1917.....	18.04	16.19	16.62	16.26
1918.....	16.89	16.53	15.44	16.37
1919.....	16.67	18.83	15.63	18.41
1920.....	19.18	19.09	17.95	19.23
1921.....	19.68	18.38	18.38	18.33
Average.....	18.05	17.74	16.82	17.64

<sup>1</sup>No crop.

TABLE 6.—FREQUENCY DISTRIBUTION OF 256 SOYBEAN PLANTS IN  
PERCENTAGE OF OIL  
(Progeny 1590, black hilum Manchu)

Range	Mid-value	Frequency
17.75-18.24.....	18.0	5
18.25-18.74.....	18.5	5
18.75-19.24.....	19.0	15
19.25-19.74.....	19.5	27
19.75-20.24.....	20.0	36
20.25-20.74.....	20.5	53
20.75-21.24.....	21.0	65
21.25-21.74.....	21.5	35
21.75-22.24.....	22.0	14
22.25-22.74.....	22.5	1
		<u>256</u>

Mean = 20.50  
Standard deviation = .90  
Coefficient of variability = 4.39

In order to determine whether high or low percentages of oil, as the case may be, shown by the parent plants would be transmitted to the progeny, several of the extreme variates in each group were planted in the spring of 1923. The high parents chosen were all but one over 21 percent in oil content and the low parents were all below 19 percent. In Tables 8 and 9 are given the means and variation constants of the progenies along with the analyses of the parent plants. In general high parents produced relatively high progeny and low parents, low progeny, tho there were a few exceptions. For example, Plant 1590-10 analyzing 21.35 percent gave a progeny of plants varying around a mean of 17.85, and Plant 1590-162, with an analysis of 17.82, produced a progeny giving the high mean analysis of 19.70 percent. On the whole, however, it can be stated that the initial selection was the important one, and that after the high and low strains were separated from the population no further increases or decreases were accomplished by selection.

TABLE 7.—FREQUENCY DISTRIBUTION OF 271 SOYBEAN PLANTS IN  
PERCENTAGE OF OIL  
(Progeny 1591, brown hilum Manchu)

Range	Mid-value	Frequency
17.75-18.24.....	18.0	0
18.25-18.74.....	18.5	7
18.75-19.24.....	19.0	24
19.25-19.74.....	19.5	53
19.75-20.24.....	20.0	63
20.25-20.74.....	20.5	79
20.75-21.24.....	21.0	37
21.25-21.74.....	21.5	7
21.75-22.24.....	22.0	1
22.25-22.74.....	22.5	0
		<u>271</u>

Mean = 20.10  
Standard deviation = .68  
Coefficient of variability = 3.40

TABLE 8.—ANALYSES OF PARENT PLANTS SELECTED FOR HIGH OIL CONTENT AND ANALYSES OF THEIR PROGENIES

Parent No.	Analysis of parent	Progeny No.	Number plants analyzed	Mean percent oil
1590-5.....	21.23	2018	25	18.66 ± .08
6.....	21.52	2019	15	19.15 ± .11
10.....	21.35	2021	20	17.85 ± .22
14.....	21.61	2022	21	19.50 ± .08
16.....	21.56	2023	20	18.97 ± .08
17.....	21.78	2024	24	19.20 ± .09
19.....	22.59	2025	19	19.57 ± .07
22.....	21.54	2026	24	18.62 ± .04
28.....	21.53	2027	18	19.33 ± .10
35.....	21.96	2028	19	19.86 ± .11
43.....	21.07	2029	24	19.97 ± .13
44.....	21.56	2030	10	19.96 ± .09
48.....	21.91	2031	20	19.44 ± .10
57.....	21.20	2032	18	19.61 ± .09
62.....	21.84	2033	11	20.10 ± .11
65.....	21.75	2034	14	19.50 ± .17
69.....	21.88	2036	18	19.74 ± .11
77.....	21.98	2038	20	20.18 ± .11
84.....	21.57	2039	12	20.20 ± .09
89.....	21.82	2040	16	19.54 ± .15
91.....	21.79	2041	9	19.19 ± .08
92.....	21.77	2042	22	19.58 ± .07
136.....	21.82	2045	12	20.35 ± .08
171.....	21.79	2047	17	19.89 ± .10
175.....	21.72	2049	12	20.60 ± .10
191.....	21.62	2050	18	20.19 ± .13
197.....	21.67	2052	24	18.99 ± .11
204.....	21.68	2053	9	20.15 ± .07
208B.....	21.77	2054	21	19.85 ± .08
258.....	21.63	2055	18	18.95 ± .09
1591-12.....	20.98	2056	16	18.73 ± .12
19.....	21.16	2057	19	19.64 ± .09
25.....	21.64	2058	12	19.19 ± .12
33.....	21.99	2059	12	19.64 ± .13
37.....	21.10	2060	18	19.22 ± .08
62.....	21.17	2062	23	19.92 ± .10
65.....	21.09	2063	19	19.73 ± .07
74.....	21.35	2064	19	19.00 ± .91
112.....	21.24	2065	18	19.41 ± .11
119.....	21.17	2066	15	19.38 ± .11

TABLE 9.—ANALYSES OF PARENT PLANTS SELECTED FOR LOW-OIL CONTENT AND ANALYSES OF THEIR PROGENIES

Parent No.	Analysis of parent	Progeny No.	Number plants analyzed	Mean percent oil
1590-8.....	18.33	2020	24	15.29 ± .09
67.....	18.38	2035	10	17.49 ± .11
72A.....	18.16	2037	16	18.10 ± .07
96.....	17.99	2043	16	15.88 ± .10
162.....	17.82	2046	17	19.70 ± .08
172.....	17.96	2048	20	16.40 ± .25
195.....	18.09	2051	19	17.00 ± .11
1591-57.....	18.73	2061	14	15.57 ± .19

For planting in 1924 seven progenies were chosen. To show how they compared with the original parents in percentage of oil, and the reason for using them to continue the experiment, Table 10 is presented. Significant differences are apparent in the mean analyses of the progenies described as high and low. It was obviously impossible,

TABLE 10.—PEDIGREE, PERFORMANCE, AND OTHER INFORMATION ON PROGENIES SELECTED FOR STUDY OF OIL CONTENT

Original parent	Parent analysis	Progeny No.	Mean percent oil of progeny	Hilum color	Reason for selection
1590-8.....	18.33	2020	15.29 ± .09	Black	Low analysis
96.....	17.99	2043	15.88 ± .10	Black	Low analysis
136.....	21.82	2045	20.35 ± .08	Black	High analysis
172.....	17.96	2048	16.40 ± .25	Black	Medium analysis
175.....	21.72	2049	20.60 ± .10	Black	High variability
1591-57.....	18.73	2061	15.57 ± .19	Brown	High analysis
62.....	21.17	2062	19.92 ± .10	Brown	Low analysis
					High analysis

on account of the expense, to continue all progenies, but the seven given in Table 10 were continued another generation by using a few plants as parents that represented the lowest, middle, and highest points of the range. The results are shown in Table 11. Again low progenies produced low, high progenies, high. The progeny described in Table 10 as being of medium oil content with high variability

TABLE 11.—COMPARISON OF ANALYSES OF PROGENIES WITH THOSE OF THEIR PARENTS WITHIN THE SAME LINE, 1924 CROP

Progeny No.	Mean analysis of progeny (1923)	Analysis of parent plants of 1924 crop	Mean analysis of progeny (1924)
2020.....	15.29 ± .092	15.70 16.30 14.44 14.54 14.77 16.15	14.84 ± .06 15.45 ± .06 15.00 ± .09 14.84 ± .06 14.96 ± .07 14.95 ± .06
2043.....	15.88 ± .102	15.92 16.48	15.57 ± .07 15.27 ± .04
2045.....	20.35 ± .086	19.98 21.05 20.54	17.79 ± .08 18.24 ± .11 18.44 ± .07
2048.....	16.40 ± .252	19.96 16.45 14.27 14.99 15.58 18.00 19.41	17.16 ± .11 14.88 ± .05 15.19 ± .06 14.63 ± .05 14.95 ± .06 16.03 ± .12 16.89 ± .10
2049.....	20.60 ± .109	21.32 20.70 19.96 21.10	18.22 ± .10 18.23 ± .13 17.76 ± .14 17.93 ± .13
2061.....	15.57 ± .194	16.60 15.49 14.29 17.03 14.87 15.58	15.17 ± .08 14.78 ± .08 15.28 ± .09 15.53 ± .08 14.58 ± .05 15.42 ± .14
2062.....	19.92 ± .108	19.63 18.44 21.05 20.52 19.13 19.93	18.01 ± .09 15.31 ± .10 18.40 ± .07 19.13 ± .10 18.06 ± .07 17.59 ± .07

(Progeny 2048) gave variable results, but in general high variates gave rise to high progenies, low variates to low progenies, thus giving evidence of segregation for oil content. The parent plant was likely heterozygous for factors affecting oil content and in consequence the progeny showed segregation. From such a segregating progeny it is possible to isolate types which differ in percentage of oil, but after these have been isolated selection is powerless to effect further improvement.

It is of interest to follow further the behavior of this variable progeny. Plants from three progenies of the 1924 crop were tested in 1925.

TABLE 12.—COMPARISON OF ANALYSES OF PARENTS AND ANALYSES OF PROGENIES DESCENDED FROM LINE 2048, WHICH SHOWED HIGH VARIABILITY IN OIL CONTENT

Percent oil of parents	Mean percent oil of 1924 progenies	Analysis of parents of 1925 crop	Mean percent oil of 1925 progenies	Analysis of parents of 1926 crop	Mean percent oil of 1926 progenies
19.96.....	17.16 ± .11	16.42 16.42 17.05 18.98 16.72 18.86 17.20	18.70 ± .09 19.10 ± .12 19.94 ± .10 20.19 ± .09 19.36 ± .07 19.18 ± .06 19.60 ± .06	... {21.24 18.94	19.62 ± .12 19.63 ± .05
14.99.....	14.63 ± .05	14.67 14.21 14.52 15.03 14.23 15.01 14.35	16.75 ± .07 16.58 ± .06 17.15 ± .07 16.83 ± .05 16.64 ± .05 16.91 ± .07 16.18 ± .09	... {18.07 16.36	16.96 ± .07 17.17 ± .11
18.00.....	16.03 ± .12	17.60 14.88 17.08	18.26 ± .23 15.54 ± .19 17.52 ± .36	... {17.43 16.56 16.34 14.97	19.97 ± .04 19.13 ± .14 16.14 ± .08 16.29 ± .07
16.45.....	14.88 ± .05				
14.27.....	15.19 ± .06				
15.58.....	14.95 ± .06				
19.41.....	16.89 ± .10				

The results are given in Table 12. It is clear from this table that the progeny giving an average analysis of 17.16 in 1924 differed genetically from the progeny giving an average analysis of 14.63, based on the behavior of the progeny. It is also clear that the progeny analyzing 16.03 in 1924 must have been segregating for factors affecting oil content, as the resulting progenies in 1925 differed significantly in average analyses. Furthermore, when certain of these were carried further by using the highest and the lowest plants of certain progenies as parents, the result was the production of high-analysis progenies and low-analysis progenies differing by about 2 percent. Also, in the case of

TABLE 13.—PERCENTAGE OF OIL IN STRAINS A, B, C, D, AND BULK MANCHU FOR YEARS 1922-1930

Strain	No. of original parent	Percent oil of original parent 1922	Oil content							
			1923	1924	1925	1926	1927	1928	1929	1930
A.....	1590-175.....	21.72	20.60	18.03	19.25	20.60	19.33	22.37	20.37	18.48
B.....	1591-62.....	21.17	19.92	19.64	20.38	18.69	21.72	20.37	20.37	19.87
C.....	1590-8.....	18.33	15.29	17.66	16.92	16.91	19.37	17.29	17.29	17.93
D.....	1591-57.....	18.73	15.57	17.26	16.86	16.05	20.61	16.81	16.81	17.98
Manchu.....	.....	.....	.....	17.68	18.45	18.04	17.96	.....	20.29	20.12

highest and lowest parent plants complete regression to the mean of the type was shown by both progenies in every case, indicating homozygosity for factors for oil content. Hence it may be concluded that in a mixed or segregating population of plants for oil content, selection of single plants is effective in separating out the various types, but after they have once been isolated from the group and from one another, no further effect is obtained.

After the analyses were obtained on the 1924 crop, certain progenies were composited which could be traced back to a single original plant. Four lines or strains were thus formed, designated as A, B, C, and D. Lines A and C were characterized by black hilums; Lines B and D, by brown hilums. Lines A and B exceeded Lines C and D by about 2 percent of oil on the average, and this difference has been maintained quite uniformly until 1930 (Table 13) when Line A showed less than 1 percent more oil than Lines C and D. Seasonal variations have been quite marked; however, in a season favoring high oil, as in 1928, both the high and low lines were increased, but the same relative difference was maintained between them. Likewise in 1924 the conditions favored low oil content; consequently, both high and low lines were lowered but they still differed by 2 to 3 percent. The unselected Manchu beans which have been carried on for comparison have varied considerably from season to season, but in general their oil content has been between the analyses of the high and low lines. An exception to this occurred in 1930, when the oil content of the unselected Manchus was higher even than that of the high lines.

The application of these findings is clear. Since selection within a pure line is without effect, some progress may be made by isolating different lines from a variety that has not undergone previous selection. In such a variety germinal changes for oil content may have occurred at various times in the past, remaining, of course, unknown until chemical analysis is applied. After the strains have been isolated from the group and found to breed true, it is needless to attempt further improvement by reselecting within the strain.

Since selection was powerless to effect any further improvement in oil content within the strain, hybridization was resorted to. The high-analysis strains, A and B, were approximately 2 percent higher in oil than the low-analysis strains, C and D. Would it be possible by crossing A and B or C and D to produce a type higher in oil than the parents in one case and lower in oil than the parents in the other case, on the principle of transgressive segregation discussed earlier in this bulletin? This would be possible only in case the oil content of Strains

A and B or of Strains C and D were due to different genetic factors. Since selection brought about no further improvement, it seemed worth while to try the method of crossing.

Accordingly crosses were made between Strains A and B and between C and D. Crosses were also made between A and D, A and C, and C and B in order to get some information on the inheritance of oil content. The oil content of the  $F_1$  plants (Table 14) was in most cases between the analyses of the two parents. An exception to this occurred in the cross  $A \times C$ , as the  $F_1$  progeny were higher even than

TABLE 14.—COMPARISON OF  $F_1$  PLANTS WITH PARENT STRAINS IN PERCENTAGE OF OIL, 1927

Type	Number of plants	Average analysis	Type	Number of plants	Average analysis
A.....	8	19.50	C	9	17.95
B.....	2	20.08	B	7	20.61
$F_1 (A \times B)$ .....	2	19.63	$F_1 (C \times B)$	3	19.16
A.....	6	19.58	C	11	16.93
D.....	11	18.63	D	10	17.74
$F_1 (A \times D)$ .....	3	19.50	$F_1 (C \times D)$	3	17.67
A.....	6	19.28	....	..	....
C.....	8	17.97	....	..	....
$F_1 (A \times C)$ .....	4	19.85	....	..	....

the higher parent. This fact might suggest that the parents contributed complementary genes for oil content so that in the  $F_1$  generation there was a combination of genes more favorable for oil production than existed in the higher parent in the homozygous condition. However, this suggestion was not confirmed by the  $F_2$  results (Table 15). The average of 51  $F_2$  plants in Rows 1050 and 1051 was 22.03 percent, and the average of 33  $F_2$  plants of the same cross in Rows 1053 and 1054 was 21.72 percent. The range of the entire 84  $F_2$  plants was from 19.78 to 23.76. Ten plants of A, Row 1049, averaged 22.77 percent and 9 plants of A, Row 1055, averaged 21.98 percent; while 8 plants of parent C, Row 1052, averaged 19.84 percent. The parents ranged in oil content from 19.33 to 24.17 percent. Thus even with 84  $F_2$  plants no evidence was obtained to indicate that a type higher than the higher parent in oil content could be produced from this cross. Hence the  $F_1$  of this cross was higher than the higher parent owing probably to environmental influences rather than to a more favorable combination of genes for oil content than existed in the higher parent.

Much the same could be said about the  $F_2$  progeny of the other crosses grown. The extremes of 31  $F_2$  plants of cross  $A \times B$ , both high-analysis strains, were within the fluctuating variations of the two



parents. In crosses between high and low strains, as  $A \times D$ ,  $A \times C$ ,  $C \times B$ , and  $B \times C$ , the same thing was true, with the single exception that an  $F_2$  plant in cross  $C \times B$ , with an analysis of 18.68 percent, was lower than any plant of the low-analysis parent  $C$ . However, in the cross  $C \times D$ , low-analysis parents, both the upper and lower extremes

TABLE 15.—COMPARISON OF  $F_2$  PROGENIES WITH THEIR PARENTS IN PERCENTAGE OF OIL, 1928

Cross	Row	Type	Number plants analyzed	Average percent oil	Range	
					From	To
$A \times B$	1037.....	A	3	21.36 ± .35	20.14	22.08
	1040.....	A	10	23.72 ± .22	22.22	25.36
	1034.....	B	10	23.48 ± .09	22.32	24.51
	1035, 1036.....	$F_2$	19	22.84 ± .15	20.99	24.45
	1038, 1039.....	$F_2$	12	21.94 ± .10	21.23	23.09
$A \times D$	1040.....	A	10	23.72 ± .22	22.22	25.36
	1048.....	A	10	22.46 ± .15	21.39	23.54
	1043.....	D	11	20.94 ± .08	19.86	22.32
	1044.....	D	9	21.07 ± .05	20.79	21.38
	1045.....	$F_2$	23	22.27 ± .12	20.46	23.38
	1046, 1047.....	$F_2$	37	22.28 ± .08	20.17	24.25
$A \times C$	1049.....	A	10	22.77 ± .12	21.90	24.17
	1055.....	A	9	21.98 ± .15	20.44	22.67
	1052.....	C	8	19.84 ± .10	19.33	20.74
	1050, 1051.....	$F_2$	51	22.03 ± .07	19.78	23.76
	1053, 1054.....	$F_2$	33	21.72 ± .09	20.25	23.16
$C \times B$	1065.....	C	10	19.70 ± .06	19.29	20.48
	1067.....	B	10	21.91 ± .11	20.71	23.01
	1066.....	$F_2$	28	20.68 ± .10	18.68	22.06
$B \times C$	1068.....	B	10	21.87 ± .12	21.07	22.82
	1072.....	B	10	21.38 ± .13	20.47	22.15
	1071.....	C	10	18.79 ± .08	17.93	19.51
	1075.....	C	9	19.06 ± .12	18.19	19.62
	1069, 1070.....	$F_2$	43	20.91 ± .64	19.05	22.63
	1073, 1074.....	$F_2$	37	20.87 ± .11	18.07	22.62
$C \times D$	1080.....	C	10	19.45 ± .12	18.20	20.39
	1083.....	D	10	19.81 ± .12	19.17	20.88
	1081, 1082.....	$F_2$	38	19.80 ± .09	17.91	21.39
	1084, 1085.....	$F_2$	29	20.07 ± .14	17.46	22.26
	1086.....	$F_2$	11	19.86 ± .23	18.05	21.95

of the parents were exceeded by certain plants of the  $F_2$  generation. There appeared, therefore, to be good indication of transgressive segregation in this cross, particularly when these facts are considered along with the results obtained in the  $F_3$  generation.

For the purposes of determining whether any segregation occurred with respect to genes for oil content, and to secure further evidence for transgressive segregation indicated in a case or two in the  $F_2$  generation, the extreme  $F_2$  segregates were tested by their  $F_3$  progeny in comparison with plants of the original parental strains. The results are shown in Table 16. In the  $F_3$  plants of the cross  $A \times B$ , both high strains, there is no evidence of genetic differences and none of trans-

TABLE 16.—COMPARISON IN PERCENTAGE OF OIL OF F<sub>3</sub> PROGENIES WITH THEIR PARENTS, 1929

Cross	Type of parent	Analysis of parent	Number plants of progeny analyzed	Row No.	Average percent oil of progeny	Range	
						From	To
A × B.....	A	.....	10	330	20.13 ± .14	19.51	21.97
	A	.....	10	336	20.21 ± .06	19.36	20.68
	B	.....	10	333	21.06 ± .09	20.17	21.91
	B	.....	10	339	20.11 ± .13	19.12	21.44
	High	24.33	10	331	20.22 ± .16	18.50	21.67
	Low	21.69	10	332	20.27 ± .13	19.34	20.97
	High	24.45	10	334	20.26 ± .16	18.77	21.53
	Low	21.23	10	335	20.56 ± .20	18.79	21.66
	High	24.10	10	337	20.31 ± .19	19.70	20.98
	Low	21.43	10	338	19.96 ± .09	19.40	20.61
	A × D.....	A	.....	10	342	20.27 ± .08	19.37
A		.....	10	348	21.00 ± .10	19.66	21.88
A		.....	10	354	20.26 ± .14	18.88	21.03
D		.....	10	345	16.08 ± .19	13.60	16.95
D		.....	10	351	17.17 ± .11	16.09	17.90
High		24.34	10	343	19.19 ± .14	18.28	20.21
Low		20.68	10	344	19.38 ± .18	17.64	20.34
High		24.00	10	346	19.11 ± .12	18.44	20.17
Low		20.60	7	347	18.17 ± .15	17.07	18.63
High		24.58	10	349	20.66 ± .27	20.33	21.10
Low		20.46	10	350	18.01 ± .13	17.27	19.82
High		24.25	10	352	19.77 ± .13	18.68	20.61
Low		21.76	10	353	18.75 ± .17	17.13	20.58
A × C.....	A	.....	10	354	20.26 ± .14	18.88	21.03
	A	.....	10	360	20.64 ± .06	20.18	21.13
	C	.....	10	357	17.16 ± .15	15.55	17.92
	C	.....	10	363	17.99 ± .15	16.59	18.71
	High	23.76	10	355	20.04 ± .16	18.24	20.93
	Low	19.78	10	356	17.54 ± .16	16.72	19.35
	High	23.32	10	358	20.36 ± .05	19.85	20.97
	Low	20.72	10	359	19.22 ± .13	18.20	20.51
	High	23.16	10	361	20.91 ± .09	20.34	21.64
	Low	20.25	10	362	18.36 ± .16	16.75	19.49
C × B.....	C	.....	10	377	17.05 ± .13	16.09	17.81
	C	.....	10	383	16.63 ± .14	15.77	18.15
	B	.....	10	380	20.00 ± .24	17.24	21.59
	B	.....	10	386	20.28 ± .09	18.13	19.60
	High	22.06	10	378	19.25 ± .14	18.29	20.19
	Low	19.50	10	379	18.68 ± .13	17.64	19.48
	High	22.15	10	381	20.88 ± .10	19.84	21.71
	Low	19.38	10	382	18.25 ± .17	17.46	20.04
	High	22.62	10	384	19.02 ± .20	17.55	20.78
	Low	18.07	10	385	18.68 ± .29	15.81	20.89
	C × D.....	C	.....	10	387	17.64 ± .04	17.16
D		.....	7	390	17.22 ± .03	16.99	17.66
D		.....	10	394	16.77 ± .07	16.39	17.25
High		21.39	8	388	17.32 ± .06	15.71	19.07
Low		17.91	10	389	17.15 ± .10	16.19	17.85
High		22.26	10	391	17.19 ± .11	16.36	18.08
Low		17.46	10	392	15.82 ± .16	14.66	17.30

gressive segregation. There was complete regression to the same mean in progenies from both high and low selections. It may therefore be concluded from these data that Strains A and B have the same genetic constitution with respect to oil content.

In crosses between high and low strains, as A × D, A × C, and C × B, there were distinct evidences of segregation. Many progenies from high F<sub>2</sub> segregates were significantly different from those from low F<sub>2</sub> segregates. However, no progenies were lower than the low

parent or higher than the high parent. Hence these crosses, so far as they were carried in this experiment, were of no value in producing types with either lower or higher oil content than that of the parents. To express these facts genetically we may assume that the high strains possess the genetic complex  $X + AB$  and the low strain the genetic complex  $X + Ab$  or  $X + aB$ . The  $F_1$  hybrid between these would likely be intermediate between the parents in oil content, and this was found to be the case. Segregation and recombination, furthermore, cannot produce any  $F_2$  segregates that are higher or lower in oil content than the parents, and this also appeared to be the case in the crosses mentioned above.

As stated above, the only cross that showed evidence of transgressive segregation in the  $F_2$  generation was that between C and D. Data on the  $F_3$  generation of this cross furnished a small amount of confirmatory evidence on this point. The highest  $F_2$  segregate of this cross contained almost 5 percent more oil (Table 15) than the lowest  $F_2$  segregate (22.26 percent as compared with 17.46 percent) and about 1.38 percent more oil than the highest variate of the parents; and the lowest  $F_2$  segregate contained .74 percent less oil than the lowest variate of the parents. In the  $F_3$  generation the progeny of the highest  $F_2$  segregate (22.26 percent oil) varied about a mean of 17.19 percent, about the same as the average of the parent strains; and the progeny of the lowest  $F_2$  segregate (17.46 percent oil) varied around a mean of 15.82 percent, about 1.5 percent lower than the parental average. There was, therefore, more than 1 percent difference between the means of these two progenies, a difference of some statistical significance. Thus there appeared to be a slight indication of transgressive segregation in the direction of low oil content but not in the direction of high oil content.

Soybeans with low oil content are desired especially for hog feeding, as too much oil tends to produce "soft" pork. It has not been definitely determined how low the percentage in the soybean should be to prevent this effect, but indications point to a range of tolerance of 5 to 8 percent. Since in the cross  $C \times D$ , both low oil strains, there seemed to be evidence of transgressive segregation for oil content on the low side (one of the progenies in  $F_3$  varying around a mean significantly lower than the parental analyses, 15.82 percent as compared with 16.77 to 17.64 for the parent strains), there seemed to be some hope of making more progress in producing types with lower oil content by hybridization than by selection. When, however, several individual plants in this  $F_3$  progeny were tested in 1930, the resulting prog-

enies (Table 17) were quite similar and varied around a mean quite close to the analyses of the parent strains grown adjacent to them. These results were not only disappointing from the standpoint of de-

TABLE 17.—COMPARISON OF  $F_4$  PROGENIES WITH THEIR PARENTS IN PERCENTAGE OF OIL, 1930

Parent	Analysis of parent	Number of plants of progeny analyzed	Mean percent oil of progeny	Range	
				From	To
93812-1.....	17.30	10	17.97 ± .01	17.11	19.43
2.....	15.81	10	18.16 ± .01	16.64	19.28
3.....	14.70	22	17.89 ± .00	16.82	18.74
4.....	16.26	14	17.37 ± .01	16.31	18.68
5.....	15.99	10	17.65 ± .00	17.22	18.14
6.....	14.66	10	17.63 ± .01	16.17	18.37
7.....	16.33	17	18.21 ± .01	17.26	19.34
8.....	16.02	14	17.47 ± .00	16.71	18.35
9.....	15.68	6	17.97 ± .01	17.05	18.55
Line C) Original....	.....	..	17.93	.....	.....
Line D) parents.....	.....	..	17.98	.....	.....

veloping a soybean strain with a low oil content, but they also cast some doubt on the conclusions above drawn that transgressive segregation actually occurred in this cross on the low side.

Hence it cannot be definitely stated that the results obtained in these crosses demonstrated the occurrence of transgressive segregation for oil content, tho the  $F_2$  and  $F_3$  data on cross C × D seemed to indicate it. Hybridization, therefore, was not effective in producing true-breeding types of soybeans with higher or lower oil content than that of the parents so far as these experiments were concerned.

In the interpretation of these results certain limitations are recognized and admitted. The number of plants analyzed of any one strain or hybrid progeny was inadequate, but, owing to the expense and time required to make the analyses, it was impossible under the circumstances to handle a greater number. This limitation is felt especially when it is desired to carry forward and analyze the progeny of several extreme  $F_2$  segregates. The number of plants that should be analyzed each successive year thus increases in geometrical ratio, and the experiment spreads out like a fan, expanding with each succeeding generation. In the case of a character like height of plant or color, which can be taken and noted quickly, the limitation of numbers is scarcely felt.

Furthermore there is considerable variation in the analyses of individual plants of the same pure strain due to unequal effect of growth conditions. With the limited number of plants which it was possible

to analyze, the parent strains sometimes varied more than their hybrid progenies. However, no method of removing this ever-present variation presented itself; hence the amount of variation was calculated so that the progeny means could be compared in the light of their probable errors. In this connection too it is recognized that 10 or less is too small a number on which to calculate the probable error, but this was the only practical means of indicating the amount of variation since to publish the individual analyses would require an undue amount of space.

Finally, oil content in soybeans is a very complex character probably determined by a number of genes. For this reason the data do not admit of determining the mode of inheritance of oil content. It is believed that the high strains, A and B, differ genetically from the low strains, C and D, because (1) their means differed significantly, and (2) the hybrids between the high and low lines showed segregation in oil content. No attempt was made to estimate the number of genes which were responsible for the difference between the high and low strains.

The percentages of oil and protein have been determined for a large number of soybean varieties by various workers (Fellers<sup>6\*</sup>; Piper and Morse<sup>35\*</sup>; Stark<sup>37\*</sup>; Cole, Lindstrom, and Woodworth.<sup>2\*</sup>) The published analyses indicate that varieties differ greatly in oil and protein content. It is not known, however, to what extent these differences are genetic and therefore of value from the plant-breeding standpoint. Considerable evidence is at hand showing that the environmental factors greatly affect the composition of a variety. Indeed Stark<sup>37\*</sup> states that such factors may be responsible for greater differences in composition within the same variety than are usually found between varieties.

#### QUALITY OF OIL

The use to which soybean oil may be put depends greatly on its quality. Quality may, of course, include many things, but in soybean oil quality refers particularly to its drying property since so large a proportion of the soybean oil produced is used in paint manufacture. The capacity for rapid drying depends on the ability to combine with atmospheric oxygen, and this in turn, on the degree of saturation or unsaturation of the fatty acids in the oil. The more unsaturated the oil, the more quickly it combines with oxygen.

Drying quality is measured by the amount of iodine which the oil will absorb. The percentage of iodine absorbed is called the iodine number of the oil. The iodine number of linseed oil is about 180 while that of soybean oil is about 125 to 130. To make soybean oil a better dry-

ing oil, its iodine number must be raised. One method by which this may be brought about is by breeding.

In 1912 a selection experiment was started at the Wisconsin Station (Cole, Lindstrom, and Woodworth<sup>2\*</sup>) to determine whether any progress could be made in the direction of a high iodine number by selection within a pure line. Seeds of a single plant were analyzed for quantity and quality of oil. The progenies of this plant were grown in 1913, and each plant analyzed. Then the highest and lowest of these were selected in order to start a "high" line and a "low" line. Each year therefore for seven years the plant analyzing highest in the high line and lowest in the low line were used to continue these lines.

Selection resulted in the development of differences between the high and low lines in quality of oil as measured by the iodine number. The averages for the last three years of the experiment were as follows: high line, 133.7; low line, 124.9. These results were interpreted by the authors as due to the separation of two different genotypes within the original variety rather than as due to selection being effective within a pure line. That this interpretation is probably the correct one is indicated by the fact that while the individual plants of the original strain showed high variability in iodine number, they also varied in flower color, maturity, and type of plant.

Selection was based only on iodine number and at the end of the experiment the high line was purple-flowered, tall, late-maturing; while the low line was white-flowered, short, early-maturing. Hence the original type was probably heterozygous for genes affecting quality of oil as well as for genes responsible for plant characters; or else was a mixture of types, and selection did no more than to isolate or separate the types that were present. This was also the case, apparently, in the selection experiments at the Illinois Station for oil content described above.

Cole, Lindstrom, and Woodworth<sup>2\*</sup> reported that late maturity in soybeans seems to be correlated with high-quality oil. Probably this accounts for a certain amount, at least, of the difference between the two lines mentioned above. Another important point was that there seemed to be no relation between the quality and quantity of the oil. Therefore selection for quality did not tend to depress the quantity of oil present.

Leith<sup>23\*</sup> reported a similar effect of selection in isolating strains differing in iodine number. The difference between the two strains, 32-4-1 and 32-12-1, was small but probably significant. Leith emphasized the fluctuations shown by soybean strains in composition and

quality of the oil from year to year. This is in line with what other workers have found, and helps to bring out the extent to which the plant environment modifies the behavior of the soybean. However, strains differing in composition or quality of the oil owing to genes in the germplasm tend to maintain these same differences regardless of seasonal conditions.

### RESISTANCE TO DISEASE

The soybean is attacked by a large number of bacterial and fungous diseases but no one disease has as yet assumed serious proportions in this country. As the culture of the soybean continues, however, we may expect diseases to increase in number as well as in prevalence and in destructive effect on the crop. Hence breeding for disease resistance may become in the future a very important phase of soybean improvement.

Fortunately numerous instances are known of varietal resistance to certain bacterial and fungous diseases.

#### Bacterial Diseases

Clinton<sup>1\*</sup> reported observations on the occurrence of a bacterial leaf disease on the following varieties: Medium Yellow (Midwest), Wilson, Manhattan, Quebec 92, Quebec 537, and Ito San. The last-named variety was affected worse than the others. Unfortunately he did not mention other varieties which were presumably examined and not found infected. This was probably the same disease as the one to be mentioned next.

Woodworth and Brown<sup>61\*</sup> reported results of observations and experiments on varietal resistance and susceptibility to bacterial blight (*Bacterium glycineum*, n. sp.) of the soybean. Of 47 varieties grown and artificially inoculated under field conditions in 1918 about half were completely resistant and the remainder ranged from complete susceptibility to partial resistance. The experiment was repeated with a number of varieties in the greenhouse and similar results obtained. "Varieties Ebony, Elton, Habara, No. 8 (S.P.I. 20406), Mammoth yellow, Virginia, Cloud, Wilson, Medium yellow, and Ito San were under trial. All plants were sprayed with a water suspension of the bacterial blight organism shortly after the first compound leaf appeared. An examination made three weeks later showed about half of the plants of the Wilson variety, all but three of Medium yellow, and all of Ito San infected. The other varieties were completely resistant."

Observations made by Wolf<sup>51\*</sup> on the natural occurrence on a num-

ber of varieties of a closely related disease caused by *Bacterium sojae*, n. sp., failed to disclose any evidence of varietal resistance or susceptibility.

The most extensive study made with soybeans on varietal resistance and susceptibility to a disease was that made by Lehman.<sup>22\*</sup> As a result of random field observations and carefully executed artificial inoculations both on field and greenhouse plantings, Lehman was able to classify 56 varieties of soybeans with respect to their reaction to the bacterial pustule disease (*Bacterium phaseoli sojense*). This classification is as follows, the varieties being arranged in order of decreasing resistance, the least resistant at the bottom:

<i>Highest</i> (resistant)	<i>Intermediate</i>	<i>Lowest</i> (susceptible)
Columbia	Laredo	Hoosier
Mandarin	Chiquita	Midwest
Old Dominion	Mammoth Yellow	Medium Green
	Tarheel Black	Virginia
	Biloxi	Herman
	Otootan	Haberlandt
	Goshen Prolific	Pine Dell Prolific
	Southern Prolific	Hollybrook
		Minsoy
		Merko
		Yokoten

The Columbia variety, while the most resistant of all, was not immune, but showed some lesions when the conditions for infection were made as favorable as possible. However, the lesions were fewer in number, smaller, and slower in development than those of less resistant varieties, in addition to lacking certain features, such as the yellow halo, which were typical of lesions in other varieties. Hence, as pointed out by Lehman, the Columbia variety may prove to be a good parent to use in crossing experiments for the purpose of combining resistance to the bacterial pustule disease with desirable characters of other varieties.

### Fungous Diseases

The foliage of soybeans is also attacked by a fungous disease called "brown spot" (*Septoria glycines* Hemmi). It was first described in Japan by Hemmi.<sup>14\*</sup> Later Wolf and Lehman<sup>52\*</sup> in this country made a careful study of the disease and established the fact that the fungus causing the disease in America was identical with that causing the same disease in Japan. Wolf and Lehman noted differences among soybean varieties in relative resistance and susceptibility. The most susceptible were Black Eyebrow, Virginia No. 12, and several hybrids of Virginia.



Those showing only a moderate degree of infection were Austin, Wilson, Midwest, and Ito San. The most resistant varieties, that is, those showing only a slight amount of infection, were Mammoth Yellow, Haberlandt 38, Laredo, Biloxi, Lexington, Tokyo, Tarheel Black, and Chiquita.

Another fungous disease of the soybean is called Fusarium blight by Cromwell,<sup>3\*</sup> who made an extensive study of the disease as it occurred in North Carolina. In variety tests for indications of resistance the following varieties were used: Brown, Black Eyebrow, Virginia, Mammoth Yellow, Early Dwarf Green, Wilson, Barchet, Jet, Austin, Arlington, Guelph, Chiquita, Auburn, Manchu, Tokio, Peking, Tarheel Black, Haberlandt, and Medium Yellow (now called Midwest). All these varieties were susceptible except Black Eyebrow which, in two tests, showed considerable evidence of resistance. The Brown variety, however, tho infected, seemed to be able to tolerate infection better than any of the others. This variety, according to Cromwell, is the same as Mammoth Yellow except in seed color. Haberlandt also seemed to be able to develop well in spite of infection.

Evidence of varietal resistance and susceptibility to still another disease attacking the foliage of the soybean, namely, frog eye leaf spot caused by *Cercospora diazu* Miura, was furnished by Lehman.<sup>20\*</sup> Varieties which were attacked and therefore susceptible were Laredo, Ootoan, Biloxi, Manchu, Mammoth Yellow, Goshen Prolific, Virginia, Austin, Tarheel Black, Wilson, Tokyo, Haberlandt, and Chiquita. "Of this group, Ootoan and Biloxi are most susceptible; Chiquita, Tarheel Black, Wilson, and Mammoth Yellow are somewhat less susceptible. Early maturing varieties such as Dixie, Manchu, and Virginia, escape serious injury; while such late maturing varieties as Ootoan and Biloxi suffer most."

#### Mosaic Disease

Clinton<sup>1\*</sup> reported observations on a disease which from his description was probably the mosaic disease. The following varieties were found to be infected: Medium Green, Wilson, Swan, Kentucky, Mikado, O'Kute, Ito San, and Midwest. The last-named variety appeared to be infected worse than the others. Varieties, if any, which were not infected, and therefore considered resistant, were not mentioned.

More extensive studies and experiments were made on the mosaic disease of soybeans by Gardner and Kendrick<sup>10\*</sup> and Kendrick and Gardner.<sup>19\*</sup> These authors report that, "Mosaic has been noted on the following varieties of soybeans at La Fayette, Indiana: Midwest, or

Medium Yellow, Haberlandt, Manchu, Ito San, Mongol, Hurrelbrink, Mammoth Black, Habara, A.K., Arlington, Hoosier, Elton, Wea, Lexington, Black Eyebrow, Pinpu, 36847, Feldun, Dunfield, Soysota, Wilson Black, Mammoth Yellow, Brown, Virginia, and Tar Heel Black. The disease seems to be most prevalent in the Midwest, Haberlandt and Black Eyebrow varieties, and the symptoms seem to be most conspicuous in the Midwest variety." The varieties above named may be considered susceptible.

That the disease may be transmitted thru the seed has been proven by Gardner and Kendrick.<sup>10, 19\*</sup> In work reported in 1921 13 percent of the seed from mosaic plants transmitted the disease. In 1922 a plot was planted with seed from mosaic plants, and a similar plot with seed from healthy plants. In the former, of a total of 993 seedlings, 172, or 17 percent, showed mosaic; while in the latter there were no mosaic plants in 590. These results were confirmed by further studies. Furthermore, when seeds were taken from diseased plants of different varieties, and plants grown, it was found that varieties differed in their ability to transmit the disease. "The Midwest, Haberlandt, Black Eyebrow, A.K., and Arlington varieties apparently transmit the disease more readily than Feldun, Manchu, Lexington and Dunfield."

Studies made by these authors on secondary spread of mosaic brought out further evidences of varietal differences. In variety test plots which were equally exposed to infection and which showed no mosaic among the seedlings, counts made on August 7 to 14 ranged from .6 percent for Virginia to 90 percent for Midwest. Soysota also largely escaped infection, having only 2 percent. Among the most susceptible were Midwest (90 percent), Manchu (79 percent), Haberlandt (73 percent), Elton (64 percent), and Feldun (63 percent). It therefore seems clear from these results that varieties of soybeans differ greatly in relative resistance and susceptibility to this disease.

An important point brought out by Gardner and Kendrick was that seed from plants apparently free from mosaic produced practically 100 percent healthy seedlings. This was not always the case, however. For example, seed from 42 supposedly healthy plants was saved, and of these, 3 showed mosaic when tested. Probably such variable results were due to the difficulty of choosing plants absolutely free from the disease. Also single plants of the same variety seemed to vary considerably in the amount of mosaic in the progeny. For example, in the progenies of six single plant selections from the Midwest variety the amount of mosaic varied from 0 to 33 percent. This would seem to indicate that the variety is a mixture of types with respect to relative

susceptibility, and that selection may be effective in isolating types from the same variety differing in resistance and susceptibility or in ability to transmit the disease.

Thus there is considerable evidence that varieties of soybeans differ greatly in relative resistance and susceptibility to certain diseases. Also sufficient information is available to show that selection of the variety or of the plants within the variety is an important factor in disease control.

#### YIELD OF SEED

Seed yield is probably the most sought-after character in soybeans at the present time. There are, of course, other characters that must be considered important; for example, ability to stand erect, early maturity, good seed quality, color of seed, resistance to disease, and the like. Extensive yield tests are being conducted at all experiment stations in states where soybeans are an important crop, for the purpose of determining the best yielding varieties. New strains developed by the plant breeder by selection or hybridization are carried thru a long series of nursery and field-plot tests, and their ranking with respect to yield determines whether they shall be distributed or not provided, of course, that no distinctly undesirable characters are present. Hence breeding for high yield of seed is a major problem in soybean improvement.

Seed yield is a very complex character. It is the end-result and sum total of the activities of the plant. Two main forces determine the amount of seed produced. These are growth conditions (environment) and heredity. Soil fertility, amount of space per plant, soil type, and moisture are examples of environmental influences. Heritable influences are concerned with the internal yield factors of the plants. They are responsible for yield differences between varieties produced under identical growth conditions. It is with the heritable factors that the plant breeder is most concerned.

The complexity of seed yield as a plant character makes it very difficult to study. The character must be broken down into its component parts and each studied separately as well as in combination with each other. Even with this simplification the problem is difficult because the component parts or attributes are also complex and do not lend themselves readily to genetic analysis. This is because they are quantitative in nature with a complicated mode of inheritance and are affected more or less by environmental influences. The complexity of each attribute of yield emphasizes the complexity of yield itself, which is the end result of all attributes working together.

The components or attributes which are thought to determine yield of seed in soybeans are as follows: number of nodes per plant, number of pods per node, number of seeds per pod, percentage of abortive seed, and size or average weight of seed. These attributes were studied for 26 different varieties at the Illinois Station in 1930. The results of this study are here presented.

One object of this study was to determine why one variety is a better yielder than another. To what yield component or components is the superiority of variety A due? Why is variety X at the bottom of the list? How do our standard varieties compare in the five yield attributes mentioned? Very little information is available which enables us to answer such questions as these. An attempt was therefore made to evaluate our varieties with respect to these internal yield factors in order to learn in what things they are superior and in what inferior and also to learn what varieties to use as parents in crosses in breeding for yield.

The common method of breeding for yield thru crossing has been to cross different varieties, grow the hybrids, select from among the  $F_2$ 's the plants that are apparently the best yielders, then test these in plant rows or rod rows and finally in drill plots for yield. The weight of seed produced per row or per plot is the criterion of superiority or inferiority. The original crosses were made without regard to the contribution of yield factors that each parent might make to the cross. This method appears rather haphazard, and founded on too little information of the parent types to justify the hope of securing improvement commensurate with the time and money expended. It would appear that if more information were available on the internal yield factors of our standard varieties, the selection of types to use as parents would be greatly facilitated and also the probability would be greater of producing types by hybridization that are superior to those we now have.

The same observations may be made with respect to selections for yield from ordinary varieties. The selection is based on appearance, and the plants selected are tested in plant and rod rows and later in drill plots, just as the hybrids are. A knowledge of the internal yield factors and their mode of inheritance should be helpful in making better selections and in judging their superiority or inferiority by progeny tests.

As a basis for comparing the 26 varieties of soybeans mentioned above, an attempt was made to secure a planting arrangement that would equalize growth conditions for all varieties. The following plan

was adopted. The rows were planted 2 feet 6 inches apart, and the plants stood 2 inches apart in the row. Two seeds were planted in each hill, and later the seedlings were thinned to one plant to a hill. Twelve hills of one variety were planted, then 12 hills of another, and so on till one planting of all varieties was completed. Then where the last variety left off, the second replication began and the same order was observed. This was continued till 15 replications had been completed. The rows were about 30 feet long, thus accommodating 13 varieties. Two full rows and 2 feet of the third row were thus required for each replication (starting with 27 varieties, one was discarded owing to poor stand). With this number of replications and this arrangement of varieties, the conditions of growth were fairly well equalized for each variety. This particular arrangement meant that successive replications of each variety were placed diagonally across the plot. The soil appeared to be quite uniform. Since it was planned to study individual plants, the plot was small as plots go (30 feet by 75 feet) and its very smallness resulted in lowered variability. There was practically a perfect stand, so that each plant of each variety can be considered to have had the same opportunity for development so far as plant environment was concerned. Finally, the first and twelfth plants of each replication were considered as border plants and not used in the study, thus eliminating the influences of end-to-end competition between varieties.

The individual plant was made the basis of yield determinations and of factors determining yield. Each plant was tagged and numbered. The plants in all replications of a particular variety were pulled when mature, tied together, and hung in a screen shed to dry. As soon as the plants were dry and before any pods shattered, the nodes were counted on each plant and the pods were picked off and placed in a numbered envelop on which was recorded also the number of nodes. Later the pods were classified and other data were taken and calculated, as will be described later. Because of the time and expense involved in taking the records on so many plants, only about 100 plants, or those in replications one to ten inclusive, were used in obtaining the results reported here.

An important phase of this study was that of evaluating the several varieties with respect to the measurable yield factors. This is shown by the means calculated for the following characters: number of nodes, number of pods per node, number of seeds per pod, percentage of abortive seed, and average weight of 100 seed. In Table 18, page 384, these means are given and also the probable errors of the means.

It is recognized that these data are for one year only, and that much more importance could be attached to them if they represented averages of studies extending over a period of three or more years. Data from another year's study may change the rankings of certain varieties with respect to one or more yield attributes. The writer's long experience and observations on soybeans, however, confirm him in the belief that the conclusions drawn from this study are, in the main, justified. Moreover, in the general problem of breeding for yield in soybeans the method of attack is important, and so far as the writer is aware, the method here described is new and untried for this crop and may have considerable promise for the future.

The varieties will be discussed further with respect to one character at a time.

### Number of Nodes per Plant

The mean node number for each variety as given in Table 18 is the mean total nodes for the plant, counting from the ground line to the tip. In soybeans, pods are usually borne at all the nodes except those nearest the ground. The particular node up from the ground at which the first pods are borne varies for different varieties, and for different plants in the same variety owing to a combination of hereditary and environmental factors. If plants have plenty of space the first pods are borne close to the ground, but if the plants are crowded the first pods are usually borne from one-half to a foot or more above the ground. This is an important factor in harvesting, for if pods are borne too close to the ground it is impossible to run the cutter bar low enough to get them and they are consequently left on the field. The measured yield is reduced below what is actually produced. Since pods are very seldom borne at the first few (2 to 4) nodes above the ground, it is perhaps not correct to include these in the total count, but it seemed simplest to use the node at the ground line as a starting point. Furthermore, on some plants branches arise on the main stem below the lowest pod, and if one counts only from the lowest pod he is omitting nodes that are more fruitful than if they bore a pod or two instead of branches. All things considered, it is believed that the total nodes, counted from the ground line to the tip, including also those on the branches, is fairest for all plants, and that method of counting was used in this study.

Comparing the varieties with respect to node number, we find that there are very significant differences between certain of them. The hay types Wilson 5, Peking, and Ebony have the highest number of nodes; and the seed types Illini, A.K. 114, and Manchu have the

lowest number per plant. However, the seed types S.P.I. 54592, Morse, and W. Virginia 8 were also high, higher than the hay-type varieties Ilsoy, Virginia, and S.P.I. 65388. It is also interesting to compare the varieties in variability of number of nodes as indicated by the value of the probable error. Some varieties, A.K. 114, Illini, Mandarin, and Mansoy, were quite low (about .33); whereas other varieties, S.P.I. 54592, Wilson 5, Peking, and Ebony, were high (about 1.0). This point is clear when one compares the frequency distributions of the varieties for this character. In some the plants are grouped rather close together within a narrow range, while in others the plants are spread over a wide range. The highly variable varieties may be a mixture of types with respect to node number. This, however, can be determined only by a careful study of the progeny of selected plants within each variety.

### Number of Pods per Node

The number of pods per node was calculated for each plant by dividing the total number of pods by the number of nodes. The plants of each variety were then classified for this character and the mean for all plants determined. The results are given in Table 18.

Two main plant characters affect the number of pods per node; namely, number of nodes and pod-bearing habit. The first has already been discussed. Pod-bearing habit is determined largely by the growth habit of the plant. The two general types of growth in plants are called determinate and indeterminate. The distinction between these is concerned mostly with the kind and location of the inflorescence. Growth may be said to be indeterminate when there is no terminal inflorescence formed, when flower clusters are formed in the axils of the leaves from the base to the top of the plant, and when in the same flower cluster the lower flowers bloom first, followed by the next higher in regular order. In the determinate type there is a terminal inflorescence and the older flowers are at the center or top of the inflorescence and the younger flowers appear in order toward the outside. Strictly speaking then, growth habit in all soybeans is indeterminate.

However, many soybean varieties show certain features that usually belong to the determinate habit. While in the flower cluster the older flowers are at the base and the younger at the top, the stems of such varieties are terminated by a flower cluster (Fig. 26), and this of course stops further stem growth in length. In such types the axial as well as the terminal flower cluster contains many flowers, and the flower stalk may be and often is an inch or more in length. This

results in a plant which is rather short and stocky with comparatively few nodes but having a proportionately large number of flowers per node.

In contrast to this there are soybean varieties that more nearly approach the indeterminate type. They have no terminal inflorescence. When the stem reaches the height of the determinate-like type just described, it does not terminate in a flower stalk but continues as a stem, bearing a leaf at the next node and flower buds between the leaf

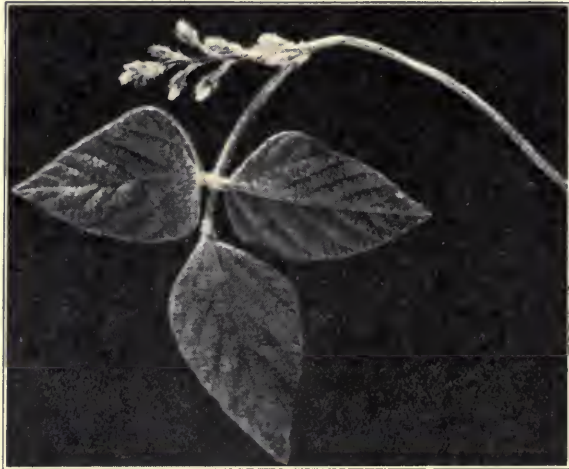


FIG. 26.—TERMINAL INFLORESCENCE OF A SOYBEAN PLANT AS GROWN IN THE GREENHOUSE

This is characteristic of many soybean types. In the field the terminal flower stalk or peduncle may bear as many as 20 flowers, but many flowers may drop off and never develop pods. The determinate type of inflorescence prevents further extension in length of the stem.

and the stem, and thus the stem continues to extend itself. This type of growth is characteristic of most hay-type soybeans. The stem often becomes fine and twiney toward the tip, and the internode length usually increases as the stem lengthens. Thus this type may have more nodes than the determinate-like type, is often taller, and the flower stalks are often shorter with fewer flowers, the number diminishing rapidly toward the tip of the stem, which usually bears a single pod. Fig. 14 brings out the important features of these two habits of growth, and Fig. 26 shows the long terminal flower stalk of the determinate-like type.



The growth habit and hence the flower-bearing habit in soybeans is worthy of more study than has hitherto been given to it. As stated above, some types are characterized by long flower stalks or peduncles at each node. In 1930 counts were made of the number of flowers on the terminal flower stalk of several plants of each of two strains. The results were as follows:

Plant No.....	1	2	3	4	5	6	7	8	9	10	Average
Strain A.....	15	16	23	17	15	23	19	14	17	16	17.5
Strain B.....	10	17	10	17	17	24	13	9	14	..	14.55

Tho no counts were made it was observed that the axial flower clusters of these plants appeared to be about as long and large as the terminal ones, and therefore to contain approximately as many flowers. Other strains have very short flower stalks and sometimes, especially toward the end of the stem, there is no flower stalk at all but simply a pedicel bearing a single flower at its tip.

Unfortunately for seed yield, the pod number of a plant seldom or never equals the flower number; it may be only half as much or even less, owing to dropping of flowers and small pods soon after fertilization occurs. For this reason it is a common sight to see long flower stalks, which bore 15 to 20 flowers, bearing only 2 to 5 pods at the base, all the flowers above having dropped off. Probably the plants started out to produce much more than they could properly nourish, and the curtailment was an adjustment to growth conditions. The interesting point is that the potential capacity for production was much greater than the realization. This is an important problem from the yield standpoint and merits careful study.

A comparison of soybean varieties with respect to number of pods per node may be made from results given in Table 18. The averages are not so high as might be expected from the appearance of the soybean plant itself. This is due to the fact that many nodes at the base of the plant were included in the total, for reasons explained above, tho normally they bore no pods at all. Also in many varieties, as pointed out above, the set of pods per node is rather sparse, especially toward the tip of the stem. However, there are numerous significant differences between varieties in this character. Peking, the variety with the highest average, 1.503, is a type which has large, many-flowered, many-podded peduncles (determinate-like habit). The Manchu, on the other hand, with a low average, .84, has small short flower stalks (indeterminate habit). The pod-bearing habit is probably the most important factor influencing the number of pods per node, but the rating of a variety on the basis of this character is

TABLE 18.—AVERAGE VALUES OF YIELD COMPONENTS FOR 26 SOYBEAN VARIETIES, 1930

Variety name or No.	Average number nodes per plant	Average number pods per node	Average number seeds per pod <sup>a</sup>	Abortive seed per cent.	Average weight 100 seeds grams	Average yield per plant grams
Mandarin.....	22.33 ± .344	1.12 ± .018	2.12 ± .015	31.60 ± .128	14.01 ± .138	4.84 ± .140
Brown Type 30.....	21.95 ± .368	1.24 ± .015	2.46 ± .016	30.39 ± .106	12.23 ± .104	5.77 ± .151
A.K. 114.....	19.67 ± .283	1.19 ± .018	2.50 ± .011	17.33 ± .507	16.11 ± .103	8.22 ± .204
Ito San.....	27.62 ± .636	1.13 ± .014	2.11 ± .013	17.35 ± .442	15.23 ± .107	8.30 ± .219
Illini.....	21.09 ± .393	1.33 ± .024	2.73 ± .008	16.96 ± .523	14.88 ± .096	9.82 ± .144
Manchu.....	23.31 ± .487	.84 ± .021	2.52 ± .015	17.56 ± .604	18.04 ± .093	7.04 ± .223
Wea.....	22.37 ± .494	1.25 ± .023	2.42 ± .015	24.25 ± .652	14.82 ± .015	7.46 ± .224
Black Eyebrow.....	24.67 ± .513	.97 ± .016	2.13 ± .016	21.36 ± .081	18.21 ± .177	7.79 ± .249
Mansoy.....	23.54 ± .340	.99 ± .024	2.19 ± .011	18.42 ± .573	17.54 ± .100	7.72 ± .267
Harbinsoy.....	26.31 ± .458	1.04 ± .026	2.08 ± .013	14.94 ± .465	14.56 ± .098	7.55 ± .250
Ebony.....	36.69 ± .407	.93 ± .026	2.07 ± .024	26.09 ± .662	10.84 ± .125	6.48 ± .248
S.P.I. 65394.....	19.43 ± .345	1.27 ± .018	2.65 ± .009	18.61 ± .594	13.35 ± .085	7.72 ± .270
Ohio 13-177.....	20.22 ± .612	1.08 ± .022	2.37 ± .012	25.07 ± .694	15.37 ± .131	8.91 ± .237
West Virginia 8.....	33.93 ± .645	1.17 ± .025	2.22 ± .009	25.24 ± .659	11.47 ± .094	7.46 ± .256
Peking.....	42.47 ± .369	1.50 ± .034	2.22 ± .009	24.31 ± .535	7.64 ± .074	8.29 ± .256
Virginia.....	28.53 ± .594	1.25 ± .032	2.00 ± .018	21.54 ± .627	11.84 ± .075	7.11 ± .210
Isoy.....	28.90 ± .506	1.27 ± .018	2.19 ± .011	22.09 ± .357	12.18 ± .100	8.09 ± .210
S.P.I. 04002-B.....	25.38 ± .578	.99 ± .022	2.68 ± .009	18.16 ± .538	15.54 ± .126	8.91 ± .243
S.P.I. 54610-3.....	24.97 ± .418	1.04 ± .020	2.71 ± .009	20.69 ± .482	13.23 ± .111	7.80 ± .235
S.P.I. 65388.....	30.14 ± .018	1.04 ± .020	2.77 ± .008	23.90 ± .590	4.94 ± .049	3.30 ± .103
S.P.I. 54592.....	36.22 ± .376	.86 ± .025	2.70 ± .013	20.56 ± .477	14.75 ± .100	10.22 ± .375
Aksarben.....	23.31 ± .500	1.14 ± .025	2.36 ± .014	18.56 ± .013	15.87 ± .148	8.49 ± .277
Norse.....	34.07 ± .248	1.32 ± .020	2.14 ± .024	19.62 ± .619	16.59 ± .146	7.62 ± .290
S.P.I. 65345.....	21.42 ± .426	1.32 ± .020	2.07 ± .007	16.94 ± .466	14.91 ± .115	7.22 ± .229
Dunfield.....	22.94 ± .641	.88 ± .022	2.35 ± .016	18.84 ± .660	16.95 ± .146	7.02 ± .250
Wilson 5.....	44.83 ± .274	1.02 ± .018	2.16 ± .011	26.49 ± .525	7.91 ± .073	5.98 ± .163

<sup>a</sup>Including abortive seed.

affected also by (1) the height above the ground at which the lowest pods are borne, and (2) the relative number of flowers dropping off and therefore not developing into pods.

### Number of Seeds per Pod

Soybean pods contain 1 to 4 seeds. The majority of pods produced by a plant contain 2 or 3 seeds. Whether the 2's are more numerous than the 3's, or vice versa, depends on the variety (Fig. 27). So much is this a varietal characteristic that one can generally refer to a variety as a 2-seeded or as a 3-seeded type, as the case may be. This is clear from Table 19, which shows the proportions of 1-seeded, 2-seeded, 3-seeded, and 4-seeded pods for all varieties under study. There can be no question that seed number per pod is a varietal characteristic (Fig. 28).

TABLE 19.—COMPARISON OF 26 SOYBEAN VARIETIES IN PERCENTAGE OF 1-SEEDED, 2-SEEDED, 3-SEEDED, AND 4-SEEDED PODS

Variety name or No.	Total number pods classified	1-seeded pods	2-seeded pods	3-seeded pods	4-seeded pods
		<i>perct.</i>	<i>perct.</i>	<i>perct.</i>	<i>perct.</i>
Mandarin.....	2495	16.2	53.3	30.1	.2
Brown T30.....	2805	7.4	37.2	55.0	.1
A.K. 114.....	2402	5.7	38.5	55.7	.4
Ito San.....	3476	12.7	64.0	22.9	.3
Illini.....	2899	1.8	21.5	76.4	.1
Manchu.....	1884	4.4	36.7	58.7	.1
Wea.....	2896	6.2	47.4	46.1	.1
Black Eyebrow.....	2505	12.0	64.4	23.4	.1
Mansoy.....	2451	7.9	64.7	27.2	.1
Harbinsoy.....	2906	12.5	64.2	23.1	.0
Ebony.....	3970	14.9	54.6	30.2	.2
S.P.I. 65394.....	2557	2.3	30.8	66.1	.6
Ohio 13-177.....	2993	6.2	50.2	43.5	.0
West Virginia 8.....	4003	15.8	52.2	31.9	.1
Peking.....	6701	8.4	60.4	30.9	.1
Virginia.....	3362	24.2	49.5	26.2	.0
Ilsoy.....	4029	12.3	53.8	33.8	.0
S.P.I. 04002 B.....	2434	2.9	24.8	72.1	.0
S.P.I. 54610-3.....	2754	2.9	22.7	74.3	.0
S.P.I. 65388.....	3116	2.4	20.3	74.5	2.5
S.P.I. 54592.....	2692	3.3	21.9	74.7	.0
Aksarben.....	2591	8.2	49.9	41.8	.0
Morse.....	2577	17.0	52.3	30.5	.1
65345.....	2910	8.3	75.8	15.7	.0
Dunfield.....	2243	7.5	47.4	44.9	.0
Wilson S.....	5038	14.4	52.4	33.1	.0

The 26 varieties examined ranged from 2.00 to 2.77 seeds per pod, including abortive seed (Table 18). Those that had an average of approximately 2, or a little above, were predominantly 2-seeded; those with an average of 2.65 to 2.80 were predominantly 3-seeded; and those ranging from 2.35 to 2.52 had about as many 2's as 3's (Table 19). Thus soybean varieties can be placed roughly in one or another of those three classes. Illini, S.P.I. 65394, S.P.I. 04002-B, S.P.I.

54610-3, S.P.I. 65388, and S.P.I. 54592 stand at the top in number of seeds per pod, being predominantly 3-seeded types. Ito San, Mandarin, Black Eyebrow, Mansoy, and others are predominantly 2-seeded types.



FIG. 27.—SOYBEAN PODS ARRANGED ACCORDING TO NUMBER OF SEED CONTAINED

Soybean varieties differ in the proportion of the kinds of pods they bear with respect to number of seeds. A, C, and E represent pods from one plant of Illini: (A) 3-seeded pods; (C) 2-seeded pods; and (E) 1-seeded pods. B, D, and F represent pods from two plants of Ito San; (B) 3-seeded pods; (D) 2-seeded pods; and (F) 1-seeded pods. This is only one of the important components influencing yield of seed in the soybean.

### Percentage of Abortive Seed

The occurrence of abortive or undeveloped seeds in soybeans was studied many years ago by Halsted,<sup>11, 12\*</sup> who classified pods of three varieties, namely, Early Brown, Wilson, and Ito San. Of 4,382 pods containing 9,584 seeds, 1,259 seeds or 13.14 percent were abortive. The percentage of abortiveness in Early Brown was 15; in Wilson, 6.75; and in Ito San, 14.2.

Also in these early studies Halsted gave attention to the relation of abortiveness to position in the pod. A very interesting fact discovered by Halsted was that the basal seed (that nearest the point of attachment of the pod to the plant) showed by far the highest proportion of abortiveness. He states, "Twenty-six and two-tenths percent of 4,382 pods have one or more abortive ovules, and of these 1,149 pods, 71.5 percent have an abortive basal ovule, and 31.9 percent are with aborts at the tip."

In an extensive study of abortiveness in soybeans conducted re-

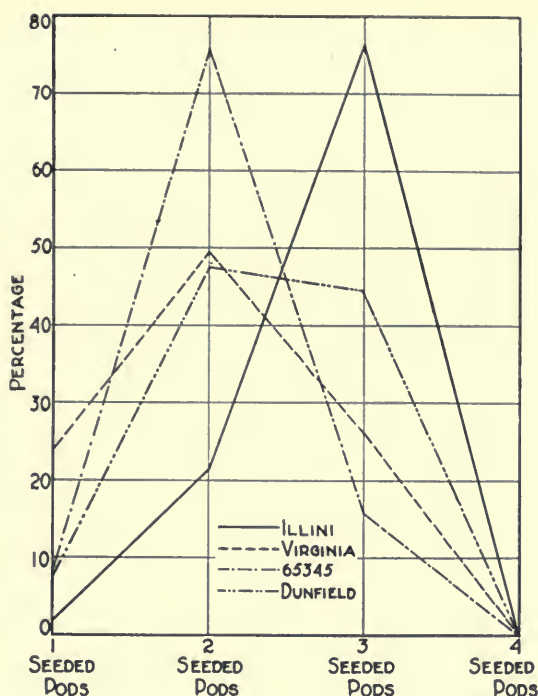


FIG. 28.—COMPARISON OF SOYBEAN VARIETIES IN NUMBER OF SEEDS PER POD

Varieties of soybeans differ greatly in the proportion of 1-seeded, 2-seeded, 3-seeded, and 4-seeded pods. In this diagram four varieties are represented. About 75 percent of the pods borne by the Illini variety were 3-seeded, while about 75 percent of the pods borne by the strain S.P.I. 65345 were 2-seeded. Fifty percent of the Virginia pods were 2-seeded, about 25 percent 1-seeded, and 25 percent 3-seeded. The importance of this character in seed yield is obvious.

cently at the Illinois Station (Woodworth<sup>55\*</sup>) the above findings were in large measure confirmed. In a study of eight different varieties, most of which were selected strains from the A.K. variety, there was a range in mean percentage of abortive seeds of 9.4 for A.K. 114 to 22.2 for Illini. Many of these strain differences were large enough to be significant. Hence there appeared to be varietal differences in amount of abortiveness. Also, the author's data on the relation of abortive seeds to their position in the pod were substantially in agreement with those of Halsted. With respect to counts on the Illini variety it was stated that "of 115 two-seeded pods having abortive seeds, 87, or 75.65 percent, are in the basal position; 16, or 13.9 percent, in the tip position, and 12, or 10.45 percent, had both seeds abortive. Similarly, of

the 569 three-seeded pods having one seed abortive, 498, or 87.52 percent, are abortive in the basal position; 39, or 6.85 percent, in the middle position; and 32, or 5.63 percent, in the tip position. Also certain combinations of positions are more favored for abortiveness than others. Thus, of 118 three-seeded pods with two abortive seeds, 82, or 69.49 percent, are abortive in base and middle positions; 26, or 22.03 percent, are abortive in base and tip positions; and only 10, or 8.48 percent, in the middle and tip positions" (Fig. 29).

There were certain other interesting facts gleaned from this study. No relation was apparent between the number of seeds per pod and the amount of abortiveness. That is to say, 2-seeded pods had about the same percentage of abortion as 1-seeded or 3-seeded pods. There was considerable difference in the size or degree of development of the aborts with reference to their position in the pod. Thus the abort in the tip of the pod was found to be the least developed of all, both in 2-seeded and 3-seeded pods, and the abort in the basal position was the larger in 2-seeded pods and only slightly below the size of the middle abort in 3-seeded pods. Comparisons between normally developed seeds in pods containing one or more abortive seeds and in pods containing no abortive seeds revealed the fact that the latter class of pods contained the heavier seeds. Finally a relation was found between the amount of abortiveness and position on the plant. Halsted<sup>11\*</sup> found that the percentages of abortive seeds increased from the lower to the upper parts of the plant. Results at this Station differed somewhat from those of Halsted in that the lower part of the plant showed only slightly less abortiveness than the tip, and the middle of the plant showed the least amount.

In the present study the mean percentage of abortive seeds was calculated for each of the 26 varieties in the following manner: After the pods were classified, and the potential number of seeds determined for each plant, the pods were threshed and the "good" or normally developed seeds were counted. The number of good seeds divided by the potential number and the quotient multiplied by 100 gave the percentage of good seeds. This percentage subtracted from 100 gave the percentage of abortive seed. In Table 18 the mean percentage for each variety is given, together with the probable error.

In general it can be said that the percentage of abortiveness in soybeans is higher than would appear to be the case on casual observation of the plants as they are approaching maturity in the field. The lowest mean percentage in Table 18 is 14.94 for the Harbinsoy variety and the highest is 31.6 for the Mandarin. In the case of the Mandarin,

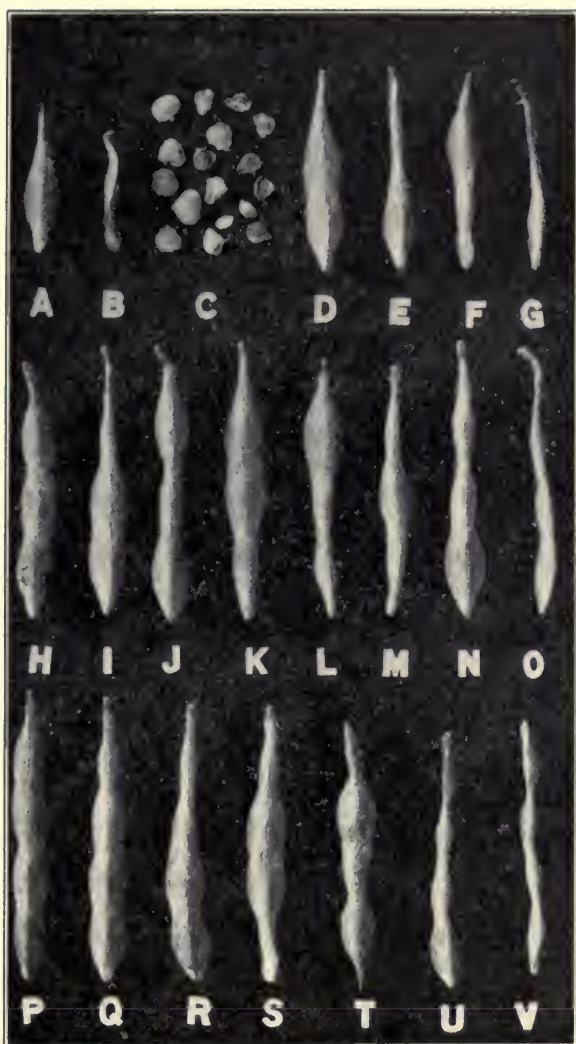


FIG. 29.—APPEARANCE OF ABORTIVE SEEDS OF THE SOYBEAN AND THEIR LOCATION WITHIN THE PODS

(A, B) One-seeded pods: (A) nonabortive, (B) abortive. (C) Abortive seeds ranging from small shriveled masses to half-grown seeds. (D-G) Two-seeded pods: (D) nonabortive, (E) basal, (F) tip, abortive, (G) both seeds abortive. (H-O) Three-seeded pods: (H) nonabortive, (I) basal, (J) middle, (K) tip, (L) middle and tip, (M) basal and tip, (N) basal and middle, abortive, (O) all three seeds abortive. (P-V) Four-seeded pods: (P) nonabortive, (Q) basal, (R) basal and second, (S) basal and tip, (T) basal and third, (U) basal, second, and third, abortive, (V) all four seeds abortive.

therefore, almost a third of the seeds were abortive or undeveloped. A majority of the varieties, that is, 16 of the 26, were 20 percent or above. Tho the probable errors are fairly high, many of these means show differences great enough to be significant. It is believed therefore that while growth and seasonal conditions may, and probably do, affect the amount of abortiveness, the character may be expressed to different degrees in different varieties owing in part at least to genetic factors.

### Size of Seed

A glance at the seed of different soybean varieties reveals the fact that they vary in size as well as in shape. Each variety has its own typical seed size (Fig. 30). Some varieties, such as Black Eyebrow, are large-seeded and others, such as S.P.I. 65388, Peking, or Wilson 5, are small-seeded. Growth conditions, such as soil fertility, inoculation, and the like, modify the seed-size, increasing it if favorable, decreasing it if unfavorable; but if these conditions are the same for all varieties, as they should be if comparisons are to be made, distinct and significant differences in seed size will be shown by different varieties.

For purposes of the present study the average weight of 100 seeds was calculated for each plant of each variety. This was obtained in the following manner: The seeds of each plant were weighed to tenths of a gram. The number of seeds per plant was counted and this number divided into 100. The factor thus obtained was multiplied by the weight of seeds for the plant to give the weight of 100 seeds. The plants of each variety were then classified on the basis of this character, and the mean weight of 100 seeds of each variety, together with its probable error, was obtained. The results are given in Table 18.

The varieties range in average weight of 100 seeds from about 5 grams for S.P.I. 65388 to a little over 18 grams for Black Eyebrow and Manchu. Most of them, however, range from about 12 to 18 grams. Strains of soybeans are known which bear seeds much larger than those of any variety in this experiment, and there are seeds of wild types of soybeans that are much smaller than the smallest used in this study.

Seed size is mentioned in numerous published descriptions of soybean varieties and it has even been used as a part of the key in classifying varieties. The relative size of soybean seed is often expressed as so many in a pound or bushel. Many farmers seem to prefer small-seeded types because they go farther in seeding and hence the seed-cost per acre is smaller. The large seed contains more food material, however, and thus is able to give the seedling a better start than is the small seed.



### Correlation Between Yield Components and Yield

One would naturally expect that the yield components that have been discussed would show a direct and important relation to yield of seed. This would be true of each yield component in turn if all other yield factors were kept constant. For instance, if number of pods per node, number of seeds per pod, percentage of abortive seed, and size

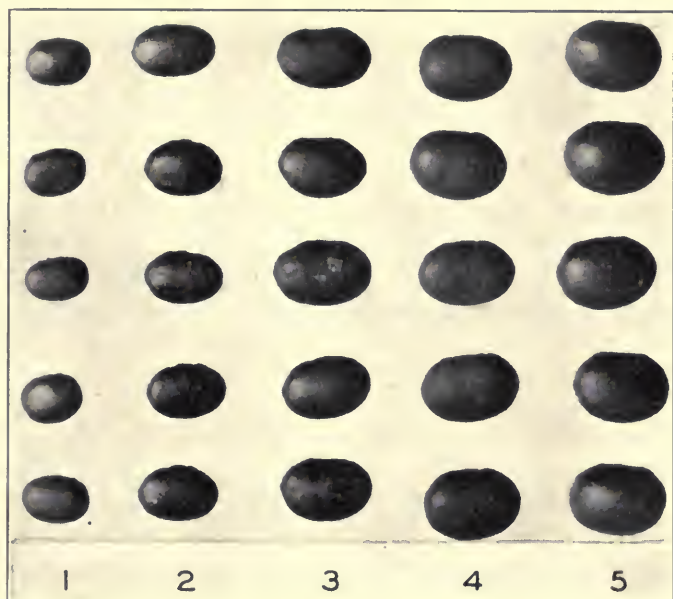


FIG. 30.—SOYBEANS OF DIFFERENT SIZES

Seeds of soybean varieties differ greatly in size and hence in weight. The seeds here pictured represent in general the five groups into which the varieties used in an analysis of yield could be classified for this character. (1) S.P.I. 65388, 4.94 grams per hundred seeds; (2) Peking, 7.64 grams; (3) West Virginia, No. 8, 11.47 grams; (4) S.P.I. 65345, 14.91 grams; and (5) Black Eyebrow, 18.21 grams.

of seed were the same for all varieties and the varieties differed only in number of nodes, then of course there would be a very close relationship between yield and number of nodes. But the true situation is quite different from this. There is involved the problem of the relationship between the yield components themselves, which will be discussed later.

That a variety may rank high in one yield component, such as number of nodes, and may be low, intermediate, or high in one or more of

the other yield components, such as number of seeds per pod, is shown in Fig. 31, which is built from the data in Table 18. The figures at the bottom of the columns in this graph indicate the following varieties:

1.....	S.P.I. 54592.	14.....	Morse
2.....	Illini	15.....	Harbinsoy
3.....	Ohio 13-177	16.....	West Virginia 8
4.....	S.P.I. 04002 B	17.....	Wea
5.....	Aksarben	18.....	S.P.I. 65345
6.....	Ito San	19.....	Manchu
7.....	Peking	20.....	Dunfield
8.....	A.K. 114	21.....	Ebony
9.....	Ilsoy	22.....	Wilson 5
10.....	S.P.I. 54610-3	23.....	Brown Type 30
11.....	Black Eyebrow	24.....	Virginia
12.....	S.P.I. 65394	25.....	Mandarin
13.....	Mansoy	26.....	S.P.I. 65388

It is apparent from this study that inferiority in one yield component may entirely counterbalance superiority in another in the case of a single variety. S.P.I. 65388, for example, ranked first in number of seeds per pod but was lowest in yield of seed on a plant basis. Furthermore the variety that ranked highest in yield, S.P.I. 54592, did not rank highest in any single yield component; indeed in average number of pods per node it was one of the lowest. The lower yielding varieties appear to have higher percentages of abortive seed and smaller seed, in general, than the higher yielding varieties; however, the other yield components appear to show little if any relation to yield. These facts are also evident from the correlation coefficients.

These relationships will probably be better understood if we bear in mind that we are concerned here with genetic, not nongenetic, correlations. All the varieties were so planted and so grown that the growth conditions were very much the same for each. Since this is so, we can leave the environmental or nongenetic influences out of consideration. If we were to correlate number of nodes, for example, with yield of seed for plants within the variety, we should no doubt obtain a correlation coefficient high enough to be significant. This would be so because both number of nodes and yield are influenced by the same cause, namely, growth conditions; consequently the two characters would tend to vary together. A condition that increases the number of nodes likewise increases yield, and a condition that decreases the number of nodes decreases yield. Now these environmental effects are not inherited and therefore are of no importance to the plant breeder except as they modify the results obtained. He is vitally concerned, however, with genetic correlations, that is, with correlations that tend to cause two characters to be inherited together

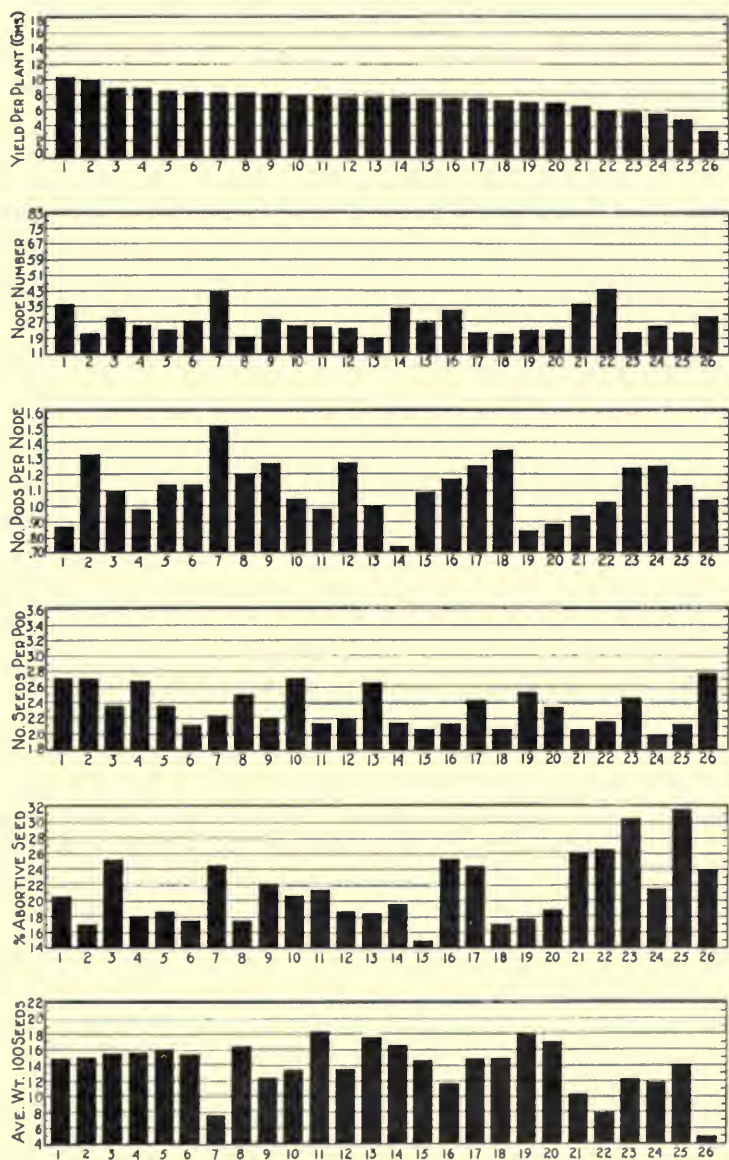


FIG. 31.—RELATION OF YIELD COMPONENTS TO YIELD OF SEED

In the top diagram 26 different varieties of soybeans are ranked according to yield. In the other diagrams each variety maintains the same relative position. From these figures a good idea of the relation between yield components and yield may be obtained.

because they are determined by the same genes in the germplasm or by different genes located near together on the chromosomes, thus preventing random assortment to the gametes.

There are two methods of determining genetic correlations. One is by the method followed in this study; namely, that of growing and testing as many different types as possible under comparable growth conditions, calculating the means for the various characters on a plant basis, and using these means as separate items in calculating the correlation coefficients. The plant breeder wishes to know how important these separate yield components are in producing high yield. Do all types, for example, with a high number of nodes give high yields, and all types with a low number of nodes give low yields? If this question can be answered in the affirmative, then the breeder knows that to get high yields he must have types with a high number of nodes. He knows what plants to select and what to reject, and he knows what types to use as parents in crosses and what types not to use for this purpose. A similar line of reasoning could be used with respect to all the other yield components studied.

The second method of determining whether genetic correlations exist is by the method of hybridization. Crosses can be made between strains in which the characters are expressed to different degrees and the  $F_2$  plants studied and classified with respect to these characters. For example, S.P.I. 65388 has the highest average number of seeds per pod, 2.765, and also the lowest yield, 3.304 grams per plant (Table 18). Ito San, on the other hand, has a low number of seeds per pod, 2.113, and yields 8.3 grams a plant, more than twice as much as S.P.I. 65388. These facts in themselves might suggest that there is no genetic relation between this yield attribute and yield. If now a cross be made between these varieties, will there be a tendency for these characters to stay together in the hybrids, thus maintaining the same combinations as existed in the parents, or will there be segregation and recombination according to chance? That is to say, by recombination will the nonparental types having (1) a high number of seeds per pod and high yield, and (2) a low number of seeds per pod and low yield be obtained in the  $F_2$  generation, in addition to the parental types; and if so, will they be obtained in proportions which suggest independence or partial linkage? If these new combinations are obtained, the linkage, if any exists, cannot be complete; and if they are obtained in proportions expected on a chance basis, then it can only be concluded that no linkage at all exists.

Data are not now available which will enable us by a study of

hybrids to get at the genetic relationship between these yield components and yield tho some hybrid material is on hand which it is hoped will furnish data for this study in the near future. Hence we must confine ourselves for the present to the first method; namely, that of correlation using the varietal means. Accordingly correlation coefficients have been calculated, using the means of the varieties as separate items and the formula commonly employed when the data are ungrouped. The results are given in Table 20.

TABLE 20.—CORRELATION COEFFICIENTS BETWEEN YIELD COMPONENTS AND YIELD, AND BETWEEN THE COMPONENTS THEMSELVES

Characters correlated	Pearson (r)
Number of nodes and plant yield.....	.019 ± .132
Number of pods per node and plant yield.....	.191 ± .127
Number of seeds per pod and plant yield.....	.200 ± .127
Percentage of abortive seed and plant yield.....	-.521 ± .096
Average weight of 100 seeds and plant yield.....	.519 ± .096
Number of nodes and number of pods per node.....	-.184 ± .128
Number of nodes and number of seeds per pod.....	-.193 ± .127
Number of nodes and percentage of abortive seed.....	.347 ± .116
Number of nodes and average weight of 100 seeds.....	-.592 ± .086
Number of pods per node and number of seeds per pod.....	-.101 ± .131
Number of pods per node and percentage of abortive seed.....	.159 ± .128
Number of pods per node and average weight of 100 seeds.....	-.382 ± .112
Number of seeds per pod and percentage of abortive seed.....	-.238 ± .125
Number of seeds per pod and average weight of 100 seeds.....	-.047 ± .103
Percentage of abortive seed and average weight of 100 seeds.....	-.520 ± .096

It is recognized that certain limitations obtain in the interpretation of these coefficients. The numbers are small, there being only 26 varieties and therefore 26 pairs of items to correlate. Statisticians are wary of correlations calculated on so small a number. One reason is that when the numbers are small, the items might become grouped by chance in such a way as to appear to indicate correlation even when none is to be expected. As the number of items increases, the probability of occurrence of correlation by chance decreases. If we take this into account, and apply Fisher's criterion,<sup>7\*</sup> with a level of significance of  $P = .01$ , the correlations between yield and average weight of 100 seeds and between yield and percentage of abortive seed are the only ones high enough to indicate with reasonable certainty that correlation exists. Correlations between the other yield components and yield are too low to indicate relationship.

Furthermore, even tho most of the correlations were too low to indicate relationship, it should not be concluded that such yield components have nothing to do with yield, but rather that their individual

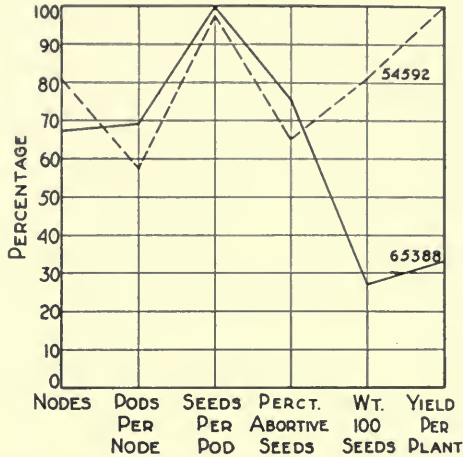


FIG. 32.—COMPARISON OF HIGHEST AND LOWEST YIELDING STRAINS OF SOYBEANS IN THE YIELD STUDY, WITH RESPECT TO THE COMPONENTS OF YIELD OF SEED

Each yield component for each strain is expressed as a percentage of the highest value in the test. These two strains were quite similar in all components except in weight of seed as expressed in grams per hundred seeds. This diagram illustrates the important influence of seed weight on plant yield, other things being approximately the same.

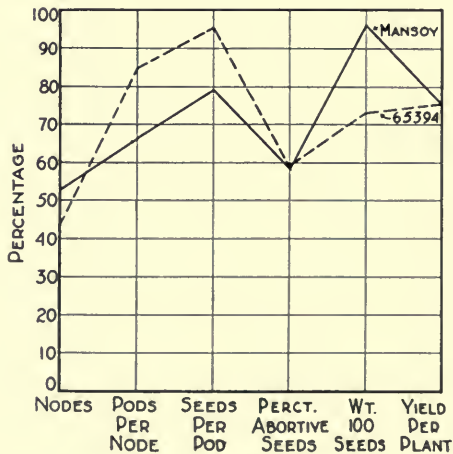


FIG. 33.—TWO VARIETIES OF SOYBEANS WITH THE SAME YIELD PER PLANT BUT DIFFERING GREATLY IN THE SEVERAL COMPONENTS THAT MAKE UP YIELD

Each yield component for each strain is expressed as a percentage of the highest value in the test. The superiority of S.P.I. 65394 over Mansoy in number of pods per node and number of seeds per pod is counterbalanced by Mansoy's superiority in seed size. Thus the same yield is attained by two different varieties by different routes.

effects may have been counterbalanced by the influence of others. For example, S.P.I. 65388 is the highest in average number of seeds per pod, but it is lowest in plant yield. If we seek for the cause of its extremely low yield we find it in the very small seed which it produces (Fig. 32). Numerous other cases may be cited. If each yield component could vary in turn while all the other components were held

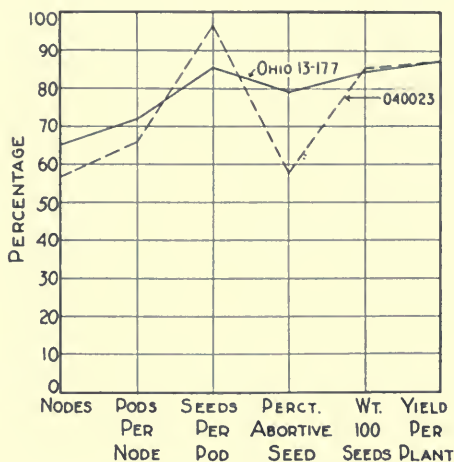


FIG. 34.—TWO VARIETIES OF SOYBEANS THAT PRODUCED THE SAME YIELD PER PLANT BUT ATTAINED THEIR YIELDS IN DIFFERENT WAYS

Each yield component for each strain is expressed as a percentage of the highest value in the test. This diagram shows the importance of number of seeds per pod in producing high yield. Thus superiority in one component may compensate for inferiority in one or more other components. In breeding for high yield, therefore, a promising method would be to attempt to combine into one type, by cross-breeding, all components expressed to the highest degree possible.

constant, yield of seed per plant would vary also and in the same direction, and hence a close relationship would be shown. But this does not happen in nature. Other yield components are also varying at the same time, being expressed to different degrees in different varieties. Thus it is difficult to get at the relative influence of each component on the resulting yield—to find which has the strongest influence, which the least. A variety may be thought of as a biotype exhibiting a certain characteristic yield capacity which is due to a particular combination of the various yield attributes. These combinations admit of almost endless diversity, and probably no two varieties have the same combination tho they may give the same yield (Figs. 33 and 34).

Finally, there is evidence for a slight negative relationship between percentage of abortive seed and actual yield per plant in grams ( $r = -.521 \pm .096$ ). That is to say, varieties with high percentage of abortive seed tend to be low yielders of good seed, and varieties with low percentage of abortive seed tend to be high seed yielders. This appears reasonable, but there are many exceptions. A high-yielding plant may have a high percentage of abortion, and a low-yielding plant a low percentage. That is, high percentage abortion does not always accompany low yields, and low percentage does not always accompany high yields. This is evident from a comparison of varieties with respect to these characters in Table 18.

Percentage of abortive seed is an important character in a given variety from a yield standpoint. This is illustrated by the fact that if, in a given variety with 30 percent abortion, something could be done to lower the abortion to 15 percent without affecting the other yield components at all, the yield would be increased 20 percent.

### Correlation Between Yield Components Themselves

In breeding for yield it is desirable not only to be able to evaluate varieties with respect to the several yield components, but also to know whether the components themselves are related. To what extent, for example, do number of nodes and number of seeds per pod go together in inheritance? Can high number of pods per node be combined with low percentage of abortive seed?

The present study on yield attributes in soybeans involving many varieties has demonstrated that no variety ranks first in all yield components. A variety that ranks well in one or more attribute may rank low or medium in others. Manchu soybeans, for example, rank high in average weight of seed but low in number of pods per node. On the other hand, Peking soybeans rank high in number of pods per node and low in seed size or average weight. What are the chances of isolating from a cross between these two varieties a type that is high in both characters? If these yield attributes are independent in inheritance, the chances should be good of securing this recombination type if sufficient numbers of plants are grown. But if the characters are genetically associated so that they tend to stay combined in the same way they are in the parents rather than be distributed to the hybrid plants independently, then the probability is lessened of securing types carrying the desired combination of these characters.

As in the case of the genetic relationship of yield attributes with yield, there are two methods of getting at the genetic association of the yield attributes with each other. One is to calculate the correlation



coefficients between each component and every other component using the varietal means as separate items. This was done and the results are given in Table 20.

Without placing too much reliance on these coefficients because of the small number of items used (only 26), we may be justified in making the following statements: Varieties with a low number of nodes tend to have large seed and a low percentage of abortive seed, and varieties with a high number of nodes tend to bear small seed but to have a high percentage of abortive seed. High number of pods per node appears to go with small seed, and small number with large seed. Finally, varieties with a high percentage of abortive seed tend to bear small seeds, and those with a low percentage, tend to bear large seeds. This last-mentioned relationship is of interest in the light of a statement made above in the discussion of the occurrence of abortive seeds in soybeans. When the average weight of good seeds in pods containing no abortive seeds was compared with the average weight of good seeds in pods containing one or more abortive seeds, it was found that the former were the heavier. Thus absence of abortion seemed to accompany better seed development. Whether there is any connection between these two instances of relationship, the future will determine.

It does not appear from these coefficients that the yield components are strongly associated. While there seemed to be certain tendencies, as was pointed out, yet there were many exceptions in the case of individual varieties, and almost any combination of degrees of development of two components appeared possible. If this is the true situation, it is just what the plant breeder desires, for it means that there is high probability that he will be able to build up a type which is superior in more attributes than any type he now has.

The other method of determining the genetic relationship between the yield attributes is by crossing. This method is theoretically sound, but there are serious practical difficulties in its use, such as the confusing effects of growth conditions and the complexity of inheritance of yield components, which are themselves quantitative in nature. Data are not now available which can be used for this study, but the  $F_2$  generation of certain crosses will be tested in the near future with this problem in mind.

### SUMMARY

Soybeans are normally self-fertilized. Natural crosses rarely occur, usually fewer than 1 percent. Hence the same principles of breeding

apply to the soybean as to other self-fertilized crops such as wheat, oats, and barley.

Considerable work has been done on the genetics of the soybean. Cotyledon color exhibits both maternal and Mendelian types of inheritance. Other seed and plant characters exhibit the Mendelian type only. Most of the characters so far studied are concerned with differences in color or structure, and very few have anything to do with yield or performance. The soybean has twenty pairs of chromosomes, and hence presumably, the possibility of twenty groups of independently inherited characters. To date only three groups of linked genes are known. Much, therefore, remains to be done, not only in identifying other linkage groups, but also in learning more about the inheritance and relationships of economically valuable characters such as pod-formation habit, yield of seed, and percentage of oil.

Variations are necessary for improvement. The only practicable means the plant breeder has of inducing variations is by hybridization. Treatment with X-rays has induced changes in other organisms, but these changes are detrimental for the most part. The occurrence of mutations and natural crosses at various times in the past has furnished the soybean breeder with an abundance of different types for use in an improvement program.

Mass selection is quite effective in purifying a variety that has become mixed mechanically or thru mutation and natural crossing. Pedigree selection may be resorted to, particularly for isolating the better yielding line or lines from a mixed variety. Thus Illini and Mansoy are pure-line selections from the A.K. and Manchu varieties respectively. Selection within pure lines of soybeans is ineffective. The progeny of artificial or natural crosses may be bulked in the  $F_2$  generation and carried along as an ordinary variety, with fair assurance that after six to ten years the majority of plants selected will be pure for their characters.

The advantages of hybridization consist in the possibility of combining desirable characters from different varieties into one type, in obtaining plants expressing a character to a greater or less extent than it was expressed in either parent (transgressive segregation), and in securing hybrid vigor which may be utilized for increased production in the soybean if  $F_2$  segregates can be isolated possessing more dominant growth factors in the homozygous condition than were possessed by either parent. While many crosses have been made in the soybean primarily for genetic studies, no varieties of commercial importance have yet been produced at the Illinois Station as a result of hybridiza-

tion. It is believed, however, that this method has promise for the future.

In breeding for quantity and quality of oil in the soybean, the best procedure appears to be to analyze adapted varieties and then to isolate the best line from the best variety. After the best line has been isolated, further selection is ineffective. Differences in oil content are believed to be inherited, but attempts to secure types with increased oil content by crossing lines from the same variety were unsuccessful. Crosses between varieties differing significantly in oil content may have more promise, particularly if large numbers of plants can be analyzed and tested in the  $F_2$  and later generations.

Varieties of soybeans differ greatly in relative resistance and susceptibility to plant diseases.

An attempt was made to analyze yield of seed into its component parts, that is, number of nodes, number of pods per node, number of seeds per pod, percentage of abortive seed, and size of seed, and to evaluate each variety with respect to these components. The general situation was that any particular variety was found to rank well in one or more components and low in others. No variety was found to rank highest in all. Significant negative correlation ( $r = -.521 \pm .096$ ) was obtained between percentage of abortive seed and yield, and significant positive correlation ( $r = .519 \pm .096$ ) between average weight of 100 seeds and yield. Hence varieties with a low percentage of abortive seed and large seed tend to give the better yield. With respect to the components themselves the following statistically significant correlations were found:

— Number of nodes and percentage of abortive seed.....	$r = .347 \pm .116$
Number of nodes and average weight of 100 seeds.....	$r = -.592 \pm .086$
Number of pods per node and average weight of 100 seeds.....	$r = -.382 \pm .112$
Percentage of abortive seed and average weight of 100 seeds.....	$r = -.520 \pm .096$

Hence varieties with small seeds tend to have a high number of nodes, a high number of pods per node, and a high percentage of abortive seed; and varieties with large seed tend to have a low number of nodes, a low number of pods per node, and a low percentage of abortive seed. Also, varieties with a low number of nodes tend to have a low percentage of abortive seed, and varieties with a high number of nodes tend to have a high percentage of abortive seed. These relationships, however, are not so close as to prevent the occurrence of recombination types as a result of crosses. Consequently the method of crossbreeding that has for its object the production of types with all yield components expressed to a higher degree than in the parents appears to be a promising method of breeding for increased seed yield in the soybean.

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