ONE of the most striking agricultural developments of recent times is the rapid rise of the soybean within the last few years from the position of a substitute and emergency crop to a place of considerable economic importance in American agriculture and industry. First introduced into this country in 1804, it was grown for many years only in gardens as a curious plant from the Far East. Its culture has now spread over much of the territory east of the Mississippi River, and it has become well established in the cropping systems of this area as well as in the States bordering the west bank of the Mississippi.

The high nutritive value of the plant and its seeds has made it particularly valuable as a livestock feed. The seed, with its by-products, oil and oil meal, have great commercial possibilities as a food and for industrial purposes. In spite of the extensive investigations that have been conducted, the work of developing this versatile plant to its fullest possibilities is still in its infancy. While much has been done in determining the genetic relations of many seed and plant characters, the plant breeder has many problems of a complex nature ahead in the development of new and better varieties for the various purposes for which the crop is now being used.

HISTORY OF THE SOYBEAN

The early history of the soybean is lost in obscurity. Ancient Chinese literature, however, reveals that it was extensively cultivated and highly valued as a food centuries before written records were kept. It was one of the grains planted by Hou Tsi, a god of agriculture. The first record of the plant is contained in a materia medica describing the plants of China, written by Emperor Sheng Nung in 2838 B.C. The crop is repeatedly mentioned in later records, and it was considered the most important cultivated legume and one of the five sacred grains essential to the existence of Chinese civilization. Seed of the plant was sown yearly with great ceremony by the Emperors of China, and poets extolled its virtues. The records of methods of culture, varieties for different purposes, and numerous uses indicate that the soybean was perhaps one of the oldest crops grown by man.

Botanically the soybean usually has been referred to in literature as Glycine hispida (Moench) Maxim. In an extensive botanical
study Piper (fig. 1) came to the conclusion that the soybean must be
named *Soja max* (L.) Piper. Other botanists, however, consider
*Glycine javanica* L. the type species of *Glycine* and call the soybean
*Glycine max* (L.) Merrill.

The cultivated soybean is thought by many investigators to have
been derived from *Glycine ussuriensis* Regel and Maack, which
grows wild throughout much of
eastern Asia. This species is
prostrate in habit of growth,
has long fine twining stems,
small narrow leaves, appressed
hairs, purple flowers, small com-
pressed pods, and small oblong
seeds of a sooty-black color.

Karasawa (9), on the basis of
genetic data, believes the cul-
tivated soybean might have been
derived from this wild species
through the qualitative and
quantitative changes due to
gene mutation, unaccompanied
by any change in chromosomes.
A plant with characters be-
tween the wild and the culti-
vated species has been described
by Skvortzov (33) as *G. gracilis*
Skvortzov.

Europeans knew of soybeans
in the seventeenth century, and
they were tried in Germany,
England, France, and Hungary
but did not become commer-
cially established in any part
of Europe until in recent years.

The first mention of the soybean in American literature was in 1804,
when James Mease wrote: "The soybean is adapted to Pennsylvania
and should be cultivated." In 1889 W. P. Brooks, of the Massa-
chusetts Agricultural Experiment Station, brought a number of
varieties from Japan, and in 1890 C. C. Georgeon, of the Kansas
station, secured three lots from the same country. Undoubtedly
other early importations of seed from Asia were obtained through
missionaries, but no definite records have been found. Since 1890
most of our agricultural experiment stations have experimented with
soybeans and many bulletins have been published dealing wholly or
partly with the crop.

In 1898 the Department started to introduce large numbers of soy-
beans. Previous to this there were not more than eight varieties,
with limited adaptation to soil and climate, grown in the United States.³
Since that time the acreage of soybeans in the United States has in-

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1Italics in parentheses refer to Selected References on the Genetics of the Soybean, p. 1181.
2The eight varieties of soybeans grown in the United States were Ito San, Mammoth Yellow, Butterball,
Buckshot, Kingston, Guelph or Medium Green, Eda, and Ogemaw.
creased more than a hundredfold—from less than 50,000 acres in 1907 to nearly 5,500,000 acres in 1935. The increase in acreage and production in this country has been closely correlated with the introduction of varieties from the Orient and their development through selection.

WORLD DISTRIBUTION AND PRODUCTION

The soybean is grown to a greater extent in Manchuria, often called "The Land of Beans", than in any other country in the world (fig. 2). It occupies about 25 percent of the total cultivated area and is the cash crop of the Manchurian farmer (fig. 3). Chosen and Japan are large producers, and south of China the soybean is cultivated more or less in the Philippines, Siam, Cochin China, India, and the East Indies.

In the central part of the Union of Soviet Socialist Republics the districts of the Don and the southwest are said to be especially suited to the culture of this crop. In Czechoslovakia, in 1935, commercial beans were produced on a small scale. Rumania has also succeeded in growing soybeans of high quality, and the production of seed is rapidly increasing. In other parts of the world, particularly Germany, England, South Africa, British East Africa, Algeria, Egypt, New South Wales, and New Zealand, soybeans have been tried or are being grown in a small way.

In the Western Hemisphere the production of soybeans is concentrated chiefly in the Corn Belt region of the United States. In 1920,
14 States produced 3,000,000 bushels of seed, the leading States being North Carolina, Virginia, Alabama, Missouri, and Kentucky—North Carolina producing about 55 percent of the total. By 1931, seed production had increased to nearly 15,500,000 bushels, with Illinois, Indiana, North Carolina, and Missouri leading. In 1935, about 40,000,000 bushels of seed were produced, of which about 37,500,000 bushels (92 percent) were harvested in Illinois, Indiana, Iowa, Missouri, and Ohio, the first three States producing about 87 percent of the total. In Canada, production is confined chiefly to the Province of Ontario, where about 15,000 acres are planted to this crop. In other parts of the Western Hemisphere the acreage grown in any country is small.

Table 1 shows the increase in production of soybeans over an 11-year period, 1924-25 to 1935-36 inclusive, in the principal producing countries of the world.

**Table 1.—Increase in production of soybeans over an 11-year period, 1924-25 to 1935-36, inclusive, in the principal producing countries of the world**

<table>
<thead>
<tr>
<th>Country</th>
<th>Production in—</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1924-25</td>
<td>1935-36</td>
</tr>
<tr>
<td>Manchuria</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chosen</td>
<td>92,667,000</td>
<td>140,444,000</td>
</tr>
<tr>
<td>Japan</td>
<td>18,723,000</td>
<td>21,961,000</td>
</tr>
<tr>
<td>United States</td>
<td>15,367,000</td>
<td>13,907,000</td>
</tr>
<tr>
<td>Netherland India</td>
<td>5,190,000</td>
<td>39,637,000</td>
</tr>
<tr>
<td></td>
<td>3,536,000</td>
<td>6,676,000</td>
</tr>
</tbody>
</table>

1 From the following publication: U. S. Dept. Agr., Agricultural Statistics 1936.
2 1934-35. 3 1933-34 (decrease).
Figure 3.—The Manchurian farmer still harvests (A), threshes (B), and cleans (C) soybeans by hand methods inherited from his ancestors, whereas in the United States (D) modern machine methods are used.
UTILIZATION OF THE SOYBEAN

In the Orient the soybean is grown principally for the seed, which for centuries has been utilized in the preparation of a great variety of fresh, fermented, and dried food products indispensable in the diet of oriental people. Large quantities of beans are also crushed for oil, which is used for food and numerous industrial purposes; and the resulting cake or meal (fig. 4) is utilized chiefly as a fertilizer and to a small extent as feed for animals. European oil mills have for many years imported considerable quantities of soybeans from Manchuria (fig. 5) for crushing for oil and oil meal.

The soybean is used in the United States primarily for forage purposes, being either preserved as hay or silage or cut and fed green as standing. It is also pastured extensively with hogs and sheep, and is used to some extent as a green manure or cover crop. For many years the increasing supply of seed was matched by a steady demand for planting the expanding acreage and for use as a stock feed, but eventually other outlets had to be found. About 1920 the possibilities in home-grown soybeans attracted the attention of oil mills, and by 1929 they began to be a potent factor in the production of the crop for commercial purposes. In 1926 slightly more than 2,500,000 pounds of oil were produced in the United States, while more than 200,000,000 pounds were obtained from the 1935 crop.

Remarkable progress has been made in the last few years in developing food and industrial uses for the soybean, the oil, and meal. At present about 45 oil mills, including a few cottonseed oil mills, are crushing soybeans; more than 40 concerns are manufacturing soybean food products and soybean flour; and more than 75 factories are...
turning out various industrial products made from soybeans. Soybean oil has become an important product in many industries. In addition to the use of the meal in livestock feeds, considerable quantities are utilized in the manufacture of foods and industrial products. The high nutritional value of the soybean, known for many centuries in oriental countries, is becoming quite generally recognized in the United States. Many food concerns in various parts of the country are manufacturing numerous products wholly or in part from the soybean.

The following outline shows the diversity of uses to which the different products of the soybean are put:

**SOYBEAN UTILIZATION**

|---------|-------|-------|-----------|------|---------|----------|---------|-------|-----------|------|---------|----------|

IMPROVEMENT OF SOYBEAN VARIETIES

Soybean breeding is being conducted in the United States, Japan, Manchuria, China, India, Chosen, and the Union of Soviet Socialist Republics, and to some extent in a few European countries. As with other crops, the chief objective has been increased yield under local conditions. Within the last few years, however, with increased utilization of the soybean for industrial and food purposes, attention has also been given by plant breeders to the oil and protein content, the nutritive value, and the quality of beans.

In the United States, more than 50 percent of the acreage devoted to soybeans is used for forage and pasture; breeding work, therefore, has tended largely toward the development of varieties for hay, silage, and pasture. The development of such varieties as Virginia, Laredo, Ootutan, Wisconsin Black, Manchu, Wilson-Five, Kingwa, Peking, and Ebony by selection from introductions has been the principal factor in the increased use and acreage.

Beginning with 1929, the use of soybean seed by oil mills has led to a demand for yellow-seeded varieties of high oil content. Agronomists and plant breeders have attempted to meet this demand by making large numbers of selections from foreign introductions and locally grown varieties and by analyzing these for oil content. This has brought about the development of several superior oil varieties and has resulted in a large increase in production of beans for milling purposes. The most popular of these varieties are Illini, Dunfield, Mukden, Mandell, Scioto, Mansoy, Manchu, Mamredo, Delsta, and Mandarin. Results of analyses with more than 1,000 selections and varieties have shown a range of from 12 to 26 percent in oil content. From studies of the oil content of varieties grown in a given locality,
it seems possible, from the breeding standpoint, to produce varieties high or low in oil, at least within the known ranges of variation exhibited by common varieties.\(^4\)

Quality, which may include several characters, the most important of which are the iodine number and the lecithin value, is the chief factor in the use of soybean oil. The drying property of an oil is measured by the iodine number, that of linseed being about 180. In a large number of tests with varieties and selections of soybeans, the iodine number ranged from 118 to 141. The iodine number of the wild soybean was found to be 155. To give soybean oil a better drying quality for paint purposes, its number must be raised. On the other hand, it is stated that oil with a low iodine number is more suitable for food purposes. Lecithin, a phosphatic compound, of which egg yolk was the chief source of supply, is now being extracted from soybean oil on a commercial scale. It is used extensively in the baking and confectionery trades, and also in textile and leather industries. Varietal studies show a range of 1½ to 3 percent, according to variety. The development of varieties high in lecithin and high and low in iodine number offers a most promising problem to the plant breeder. The best procedure in breeding for quantity and quality

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\(^4\)The Agricultural Experiment Station of the South Manchuria Railway at Kungchuling, Manchuria, has conducted experiments for several years toward the selection of varieties for high oil content. One variety, the Kungchuling, with seed uniform in size and shape and an oil content of more than 20 percent, has been widely distributed. To encourage the growing of this variety in regions to which it has been found adapted, the Experiment Station holds an annual soybean fair at which prizes are given to the farmers having the highest quality of seed (fig. 6).
of oil in the soybean is without doubt to analyze adapted varieties and then to isolate the best line from the best variety.

The development of new industrial uses for protein from the soybean and the value of this constituent in foods and feeds has led investigators to give more attention to varietal differences in the amount and quality of protein. Extensive analytical tests show a range of from 28 to 56 percent of protein (moisture-free basis), depending on variety and locality. Investigations of the nutritive value of soybean protein have shown that it contains all the essential amino acids. Studies by the Bureau of Chemistry and Soils of the United States Department of Agriculture with several standard varieties show a wide range in percentage of three amino acids—cystine, tryptophane, and tyrosine—which indicates the possibility of developing varieties of high nutritive value for animal feeds and human foods.

In the Orient, soybean foods to a very considerable extent supply the protein that is furnished largely by meats in the diet of western people. Oriental varieties of soybeans are distinguished not only according to seed and plant characters but also according to use, as for bean curd, bean sprouts, confections, and other food products. Increased recognition of the nutritional value of the soybean in the United States has created a demand for varieties more suitable for this purpose, since the varieties generally grown for commercial uses are not desirable for food. The principal drawbacks to the use of dried beans have been the length of time necessary for cooking and the flavor. Experiments with a large number of selections and varieties used in the Orient showed considerable variation. Some were of excellent flavor and became soft in less than 2 hours of cooking, while others remained hard and had little flavor or a pronounced bean flavor. Several of the most promising have been tested in various sections and the Easycook, Bansei, Rokusun, Jogun, Chusei, and Sousei are now in the hands of growers and seedsmen. Experiments by commercial firms have shown that these varieties are superior to commercial varieties for the manufacture of food products, such as bean flour, roasted beans, bean milk, and bean curd.

In Japan, certain varieties of soybeans were found that were used solely as green shelled beans. Ranging in maturity from 75 to 170 days, many of these introductions, and selections from them, have been found especially promising for various sections in the United States. The vegetable soybean offers an excellent food of high nutritional value, especially in the fall when other green beans are lacking and in sections where the Mexican bean beetle prohibits the growing of garden beans. As a result of selection, cooking tests, and adaptation studies, eight green vegetable varieties—Hahto, Kura, Kanro, Hokkaido, Higan, Chusei, Sousei, and Jogun—have been introduced in various sections of the country.

Although the major objective of soybean breeding has been to increase acreage yields, increasing utilization for food and industrial purposes demands improvement in quality as well as yield. With the vast number of introductions now under test by the Department and State experiment stations, there appears to be no reason why it should not be possible, by selection and hybridization, to develop varieties that possess all, or nearly all, the important characters desired by oil processors and by manufacturers of food and industrial products.
ADAPTATION

The soybean seems to be peculiarly sensitive to changes of soil and climate. Differences in behavior of the same pure-line variety in different localities are often very striking, so much so that it is often difficult to believe the variety is the same. Obviously, this adaptation explains why practically every locality in the soybean regions of the Orient has its own local varieties. Of the many varieties introduced into the United States, the same variety has rarely been secured a second time unless it was obtained from the same locality. In the Orient, limited areas appear to have varieties adapted to their own soil and climatic conditions. For the most part, Japanese varieties are unsuited to Manchuria and Chosen (Korea), and on the other hand, few Manchurian and Korean varieties are suited to Japan. Very few Korean varieties are adapted to the soil and climate of Manchuria. In these countries centuries of experience, aided by natural crossing and natural selection, have brought about the development of varieties adapted to special purposes. In China, Japan, Manchuria, and Chosen varieties are found especially suited for bean curd, bean milk, bean sprouts, green vegetable beans, bean flour, bean confections, oil and oil meal, and fermented products. Different regions in these countries have their own different varieties for these purposes.

One of the outstanding results of soybean improvement work in the United States has been the realization of the importance of varietal adaptation. Early investigators noted that introductions from various localities in the Orient differed widely in their adaptation to various regions or localities in this country. This led to the conclusion that by introduction and local selection strains adapted to all localities, conditions, and purposes could be developed. With the increase in the number of introductions and the development of new varieties from these for a greater range of soil and climatic conditions, the acreage in commercial plantings has increased.

In many regions of the United States adaptation experiments comparing standard varieties with newly developed sorts or new introductions indicate that the new types are better adapted than the commonly grown varieties, and it seems likely that varieties for different uses that suit requirements in nearly all our farming regions will be found. At present about 100 named varieties (see appendix, table 4) are generally grown or are being increased for greater distribution in this country. Although it would be highly desirable to limit the number of varieties in the trade, unfortunately each region must have locally adapted varieties suitable for different purposes in order to obtain the best results.

METHODS IN BREEDING

The soybean is normally a self-fertilized plant, the flowers being perfect, producing both pollen grains and ovules. The flowers are completely self-fertile, as shown by experiments carried on by Piper and Morse (30) at the Arlington Experiment Farm, Arlington, Va. (near Washington, D. C.), in 1909. Screened or bagged plants set pods and seeds as perfectly as plants in the open. Similar experiments by Woodhouse and Taylor (54) in India gave identical results. As
pollination occurs about as soon as the flower opens or a little before, there is little opportunity for cross-pollination to take place. However, natural crossing does occur. Since the plant is self-fertilized, the same general principles of breeding that apply to other self-fertilized crops may be applied to the improvement of the soybean.

Selection within self-fertilized plants is effective in purifying existing strains and makes some improvement possible, but variations are essential for any great improvement within a crop, and the only practical means the plant breeder has of inducing variations is by hybridization. By this method he may combine desirable characters from different varieties in one type and obtain plants that express a character to a greater or lesser extent than it was expressed in either parent. As with other crops, the major problem in the improvement of the soybean is to bring together into one type all the characters that are considered desirable for a certain set of conditions. From this standpoint, hybridization holds much promise for the development of special varieties of soybeans. This involves close study of wild and domestic species, varieties, and strains and their reactions to environment, as well as quantitative and qualitative analysis of oil, protein, and other constituents of the seed.

After varieties are selected or developed the grower faces the problem of maintaining them as pure strains. Commercial varieties of soybeans are in general relatively pure because the plant is self-fertilized. However, in a field of a single variety one often finds more or less off-type plants. Such mixtures may be brought about by careless methods of planting and threshing, by natural crossing, and by mutation. No natural crossing will result if mechanical mixtures are avoided. Mutations rarely occur and therefore are not an important factor. A variety can be kept relatively pure by careful methods of planting and threshing and by roguing out off-type plants.

Natural and Artificial Crossing

Previous to 1907 it was quite generally assumed that natural crossing in the soybean did not occur. In that year oddly colored seeds were noted in the variety rows and plots at the Arlington Experiment Farm, and were selected by Piper and Morse (30). The progeny of these seeds in 1908 showed segregation for various seed and plant characters. In that year more than 100 single plants of supposed hybrid origin were selected and most of these broke up in the following year in simple Mendelian proportions, indicating that they were natural hybrids. It is often easy to detect hybrids by the peculiar coloration of the seeds (fig. 7). Among the more striking colors are yellow or green with narrow streaks or bands of black or brown beginning usually at the hilum and extending over half or more of the seed, or mainly centered about the hilum. Hybrid plants are also often distinguished by the unusual form of the pods near the tips of the branches. They are more swollen and the seeds are more crowded than normal; the pods are often thinner walled and much less pubescent, sometimes being nearly smooth.

Natural crossing in soybeans has been studied to some extent by various investigators and it is quite generally agreed that a limited amount does occur, but that it is much less than 1 percent.
Figure 7.—Seeds of a natural soybean hybrid showing peculiar types of coloration.
Even this small amount of natural crossing undoubtedly is responsible for many of the mixtures now occurring in our standard varieties. The crossing is made possible by the mechanical mixing of seed through careless methods of planting and harvesting. After finishing with one variety, the planters or harvesters are not thoroughly cleaned before starting on another, so that the two varieties are mixed in the same field. An excellent illustration of this is afforded by the Mammoth Yellow variety now produced in eastern North Carolina. For many years this was the only variety grown in that section and it remained pure. As other varieties were introduced, the Mammoth Yellow seed became more or less mixed and it is now difficult to find fields without offtypes.

Natural crossing in soybeans is undoubtedly brought about by small insects. Thrips have been observed to be very common in the soybean flowers at the Arlington Experiment Farm. Bees and other insects have also been observed working on soybean flowers. Studies by many investigators at various places indicate that soybean plants growing in contact with one another are more likely to be crossed than plants separated by a few feet.

Because the flower is very small and easily injured, the work of making artificial crosses with the soybean is a difficult and tedious operation. Under field conditions at the Arlington Experiment Farm, Piper and Morse (51) made successful crosses in about 20 percent of the operations. In the greenhouse, where it is difficult to secure normal behavior in the soybean plant in winter, no success has thus far attended efforts to produce hybrids. Under winter conditions, the plants are small and bear few flowers, which do not develop and open normally and which apparently become fertilized in the very early bud stage. Woodworth (63), in crossing studies, found that soybean crosses can be made in the greenhouse as well as in the field provided artificial light is used. Light from 500-watt bulbs was used in the early stages of plant growth to induce good vegetative development, and then the light was shut off to induce flowering. The percentage of successful crosses is said to compare favorably with that ordinarily obtained under field conditions.

Crossing the flowers in the afternoon from 3 to 7 o'clock has given the best results, and it also has been found best to emasculate and pollinate a flower the same afternoon. Experience has shown that emasculation is the most difficult part of the operation and must be performed before the soybean flower has fully opened. All of the flower buds should be removed from the raceme except those to be crossed, and in these the purple or white of the corolla must have appeared above the calyx. At this stage, the 10 anthers surrounding the stigma (fig. 8) are immature and may easily be removed without bursting the pollen sacs. After emasculation, pollination is a relatively simple process, the pollen being applied to the stigma at once. In collecting the pollen for crossing, it is advisable to select well-developed flowers just before they open or fresh-looking flowers that have just opened. After the pollen has been applied, the raceme should be enclosed in a small paper or cloth bag, or a leaf may be pinned around it to protect the parts from excessive evaporation.
Mutations

The origin of new varieties of soybeans without hybridization has apparently occurred in several instances that have come under the observation of investigators. Piper and Morse (30) cite a case in which a brown-seeded type, the Trenton, arose as a mutation from a yellow-seeded variety, the Mammoth Yellow. Grown side by side at the Arlington Experiment Farm, these varieties were indistinguishable by any character other than the seed color. Woodworth (63) explains this by assuming that the gene designated as $ii$, carried by the Mammoth Yellow variety, mutated to the gene designated as $i$, and that this permitted the brown pigment of the Mammoth Yellow hilum to extend over the whole seed coat to produce a brown bean.

A more recent mutation gave rise to the Avoyelles variety. This variety with medium-sized black seed was selected in Louisiana from a field of Otootan, a small black-seeded type, and it gave uniform progeny that in many characters is superior to Otootan. Stewart and Wentz (36) discovered a recessive glabrous type which they designated by the symbol $p_2$ and assumed that it arose as a mutation. Woodworth (63) notes the following mutations that have come under his observation: Dark to light pod, normal plant size to dwarf, normal green plant to variegated, and black hilum to brown hilum. In addition to these he has noted a few mutations in vegetative cells that resulted in "chimeras" of various kinds.
HYBRID VIGOR

The phenomenon of heterosis, or hybrid vigor, in soybeans was first reported by Wentz and Stewart (50), who found in the first-generation hybrid of some crosses considerable increases in height of plant over the average of the parents. 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. Studies on hybrid vigor involving a greater number of crosses and more characters were made by Veatch (46). In 16 crosses 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 stems and branch length, number of nodes, days from planting to flowering, seed weight or yield, and number of seed. Considerable variation, however, was found among the hybrids in the extent of hybrid vigor. Although the average of all the hybrids was higher in all characters studied than the average of all the parents, the average of all the better parents exceeded the average of the hybrids in average seed weight, number of seeds per pod, ratio of straw to grain, and average internode length.

Nagai (22) also reports that the individual of the first hybrid progeny is extremely prolific in comparison with its parents. In a cross between the Akazaya (seed yield per plant 34.18 grams) and the Hashikawa Yellow (seed yield per plant 34.18 grams) varieties, the first-generation hybrid yielded 52.97 grams and the first generation of the reciprocal cross 54.84 grams. In two other crosses similar evidences of hybrid vigor were shown in yield of seed over the parents. The problem of utilizing this hybrid vigor for increased production is rather complicated, and in order to make any definite progress more extensive investigations are essential.

INHERITANCE STUDIES AND CYTOLOGY

The many strains differing widely in plant and seed characters and the almost complete self-fertility of the soybean make it an excellent plant for genetic study. The tediousness and difficulty of artificial crossing undoubtedly have been the chief reasons why more extensive genetic analysis of the plant has not been undertaken. Woodworth (63) and Nagai (22) have perhaps made the most substantial contributions. Considerable information has been collected on the behavior of progeny of natural and artificial hybrids, the most important features of which are presented herein under discussions of various plant and seed characters.

PLANT CHARACTERS

Flower, stem, pubescence, and foliage

Soybean flowers occur in two colors, purple and white. While variations in intensity and grade of color occur in the purple-flowered varieties, no attempt has been made to differentiate them except by Nagai (22) and Takahashi and Fukuyama (42). Skvortzov (33)
mentions a wild species of soybean with yellow flowers in Manchuria. This is perhaps an error, as there has been no hint of yellow flowers in the 10,000 or more introductions of cultivated and wild varieties and strains from all parts of the world, studied by the Department and numerous State experiment stations. In crosses, Woodworth (58) found purple (W) dominant to white (w), with a simple ratio of 3 purple to 1 white in F₂. A dihybrid ratio of 9 purple, 3 purplish red, and 4 white was obtained in an F₂ generation by Takahashi and Fukuyama (42). Nagai (22) reports purple dominant to white in a simple segregation ratio, or the segregations may be observed in three colors, purple, purplish blue, and white in a 9:3:4 ratio, the purple in the case evidently being determined by two factors. Piper and Morse (31), in both artificial and natural hybridization, found flower color to separate in simple Mendelian ratio, the purple flowers being dominant.

The stems of soybean seedlings are either purple or green, the purple color being most abundant just below the cotyledons. Purple-stemmed plants bear purple flowers and green-stemmed plants bear white flowers. In extensive tests at the Arlington Experiment Farm no exception was found to this relationship. Woodworth (63) reports similar results and states that the same gene probably is responsible for both characters. Stem color is undoubtedly a reliable indication of the flower color to be shown later by the plant.

According to Nagai (22), many Japanese varieties of edible soybeans have a special character known as fasciation (fig. 9). In crosses of such plants with normal plants, Woodworth (63), Takagi (39), and Nagai (22) found fasciation to be recessive, and in F₂ a ratio of 3 normal to 1 fasciated was obtained.

Nearly all varieties of soybeans are pubescent, that is, the stems, leaves, and pods are covered with fine tawny (brown) or gray hairs. In most cases there is no difficulty in distinguishing the two colors, but in some instances in selection from natural hybrids the pubescence color often is intermediate between gray and tawny, and sometimes both colors appear on the same plant. With artificial hybrids, the colors of pubescence have behaved in the same way as with natural hybrids. Tawny pubescence (T) is dominant to gray (t), and in F₂ a simple ratio of 3:1 is obtained.

Several yellow-seeded Japanese varieties, such as the Hadaka and Mizukuguri, are entirely glabrous, that is, lack pubescence or hairiness. These glabrous varieties of early, medium, and late maturity have been found by Japanese investigators to be highly resistant to attack by the pod borer (Laspeyresia glycinivorella Mats.), while pubescent varieties are highly susceptible to injury from this pest. In the United States, Johnson and Hollowell (8) found glabrous varieties subject to considerable injury from the leafhopper (Empoasca fabae (Harris)), while pubescent varieties were immune. According to Woodworth (63), glabrous soybeans fall into two distinct types. When crossed with pubescent varieties, one type behaves as a dominant while the other type behaves as a recessive. In each case the ratio is 3:1, indicating that a single factor pair is involved. Nagai and Saito (23) discovered the dominant type and Stewart and Wentz (36) the recessive. Glabrous soybean plants are smaller, shorter, and
Figure 9.—A, Stems and pods of fasciated soybean plants; B, determinate pod-bearing type; C, indeterminate pod-bearing type.
yield less than most pubescent plants, according to Nagai and Saito (23) and Owen (25). Nagai (22) had one case in which strictly glabrous plants occurred in the F3 generation in a cross of pubescent parents. The occurrence of this glabrous progeny was attributed to mutation.

In a study of the differences in amount of pubescence in American and Indian varieties, Woodhouse and Taylor (54) noted that the leaves of the Bengal "types I-V" differ from those of the Nepali "type VI" and the American varieties in being covered with soft upright hairs on their upper surfaces, whereas, the upper surfaces of the latter are covered with closely appressed hairs. In a cross between the cultivated and the wild soybean (Glycine ussuriensis), Karasawa (9) found appressed pubescence in the wild soybean dominant to erect in the cultivated soybean, the segregation occurring in accordance with the monohybrid ratio.

A wide variation occurs in the leaves of soybeans, involving shape, size, color, and degree of persistence. These characters merge by insensible degrees so that they are useful in differentiating varieties only in extreme cases. In shape the leaflets in some cases are ovate-lanceolate or almost linear; in others, nearly orbicular. In color they are usually a pale green but in some varieties dark green. In nearly all varieties the leaves commence to turn yellow as the pods begin to ripen and commonly all have fallen when the pods are mature. A few varieties, however, like the Medium Green, Old Dominion, Kingwa, and Wisconsin Black, retain their leaves until all or nearly all of the pods are mature. It has been quite generally observed that varieties with yellow cotyledons have leaves that turn yellow as they mature, whereas some varieties with green cotyledons have leaves that remain green and persist until maturity. It is believed that the retention of green in the leaves is associated or tied up with the green cotyledon color and is separate and distinct from the simple retention of leaves by the plant. Additional leaflets occur not uncommonly in several varieties. This seems to be especially true with the linear-leaved form and with several early green-vegetable varieties from Japan, which frequently have leaves with four or five leaflets.

According to Nagai (22) there are two kinds of yellow leaves. One is greenish yellow from the beginning of growth and has little chlorophyll. The other has a normal or nearly normal amount of chlorophyll when young, but the leaves turn yellow as the plant grows. It was found that when either kind is crossed with a green-leaved variety, yellow leaves are recessive to green leaves, segregating in a 3:1 ratio in the former and in a 15:1 ratio in the latter.

Takahashi and Fukuyama (42), in studies of hybrids between normal and narrow-leaflet forms, found the F1 generation to be intermediate, and in the F2 a ratio of 1:2:1 was obtained. Woodworth (68) found essentially similar results in crosses between normal and narrow-leaflet forms, except that the broad shape was partially dominant and the F2 generation was made up of two main forms, broad and narrow, in a 3:1 ratio. There were a few F2 plants, however, that seemed to be intermediate in leaflet shape between the two parents.
In a cross made by Takahaslii and Fukuyama (42) between a variety showing 73 percent of the compound leaves with extra leaflets and a normal variety the hybrid showed 52 percent of the compound leaves with extra leaflets. In the F₂, however, a ratio of 3 plants with extra leaflets to 1 normal plant was obtained.

Woodworth (63) found in the F₂ generation of a hybrid a single plant with variegated leaves. As neither parent possessed this character, it was supposed that the variegation arose as a mutation. In crosses with normal and variegated plants, variegation proved to be recessive. While the deviation from the expected 3:1 ratio was rather large, it was believed that variegation \((v₁)\) is a simple recessive to normal in inheritance. Takagi (39) has reported a type with greenish-yellow leaves that appeared in one-sixteenth of the F₂ progeny of a cross between two normal, green-leaved plants.

**Height of Plant and Maturity**

Two cases of inheritance of size in the soybean plant have been reported in which definite segregation in plant height was observed. Woodworth (58) describes a natural hybrid that segregated in the ratio of 3 tall-growing plants to 1 short, stocky, early-maturing plant. Stewart (34) reports a dwarf form that behaved in inheritance as a simple recessive to the normal.

In soybeans there is a complete series of varieties ranging from very early (about 75 days) to very late (200 days or more). With very few exceptions earliness is correlated with size, the tallest varieties being latest. The maturity character usually has a complicated mode of inheritance because it is determined by numerous genes. Woodworth (58), however, describes a progeny of plants that segregated for two plant sizes, tall and short, in a 3:1 ratio. Coupled with plant size was a difference in maturity. The tall variety matured usually about 2 weeks later than the short variety. In this case, late maturity was dominant. Studies by Veatch (46) tended to confirm this, but Owen (25) found the F₁ of crosses between early and late varieties to resemble the early in time of maturity more than the late, and in F₂ the range in maturity due to segregation covered the entire parental range.

**Pod-Bearing Habit and Pod Characters**

In a classification of soybean varieties Etheridge, Helm, and King (5) placed 100 or more varieties into classes with respect to pod-bearing habit as determinate and indeterminate (fig. 9). The determinate class has a dense array of pods on the central stem, terminating in a blunt apex, with a thin dispersal on the lateral branches. The indeterminate class has a sparse and comparatively even distribution of pods over all branches and stems, a diminishing frequency toward the top of the central stem being notable. Woodworth (63) obtained a segregation for pod-bearing habit of 69 indeterminate plants to 19 determinate plants, a single-factor difference appearing to be involved.

The pods of the soybean exhibit a wide variation in color, ranging from very light straw yellow through numerous shades of gray and brown to black. As yet very little work has been done in classifying varieties as to pod color or in studying pod-color inheritance; however, pods usually have been divided into two groups—dark pods, which are
mostly black or nearly so, and light pods, ranging from a very light tan to light brown. In inheritance studies, Woodworth (58) and Piper and Morse (31) found dark pods dominant to light and in the F<sub>2</sub> obtained a ratio of 3 dark to 1 light.

While the pods in most varieties of soybeans are distinctly compressed, some are cylindric, and all possible intermediate forms exist. Nagai (22) places pods into two general classes, flat and bulky. In crosses he found the segregation of these two characters quite distinct, the flat (compressed) being dominant to the bulky (cylindric).

Soybean pods in most varieties contain two to three seeds, rarely one or four. The linear-leaf soybeans from Manchuria possess a large percentage of four-seeded pods, although a few five-seeded pods have been found. Without doubt, seed number per pod is a hereditary character, although in some instances it is quite unstable, depending upon method of culture, season, and fertility of the soil. Nagai (22), in a cross between two-seeded and three-seeded varieties, found that about 70 percent of the pods that segregated in the F<sub>2</sub> generation were two-seeded.

Under changeable weather conditions most soybean varieties tend to shatter their seeds readily. Some varieties, however, such as the Biloxi and Manchu, have been noted that hold their seeds better than others. The wild soybean shatters very easily and the Medium Green begins to shatter with the first mature pods. Piper and Morse (31), in a cross between the Medium Green and a glabrous nonshattering variety (F. P. I. No. 22876) from Japan, found the nonshattering character to be dominant to the shattering character of the Medium Green. Nagai (22) found in hybrid progeny of cultivated and wild soybeans that the shattering character was dominant to nonshattering, the segregation ratio in the F<sub>2</sub> being 3 shattering to 1 nonshattering.

**Sterility, Growth Habit**

As early as 1908, Piper and Morse (31) found small dwarflike plants, bearing few or no pods, in the different hybrid selections at the Arlington Experiment Farm. These plants were sterile or nearly so. Owen (28) describes a sterile strain in which both ovules and pollen grains were nonfunctional. This strain was found in a progeny of Manchu soybeans that segregated into 3 normal to 1 sterile, apparently a single-gene mutation being responsible.

All soybeans are strictly determinate as to growth, that is, the plants reach a definite size according to environment and then mature and die. The great majority of varieties are erect and branching with a well-defined main stem. The branches may be all short, or the lower ones elongated, either spreading or ascending. In other varieties the stems and branches, especially the elongated terminals, are more or less twining and usually weak, so that the plants are only suberect or even procumbent. The latter kind is represented by varieties from India and certain Siberian varieties of *Glycine gracilis*. The stem of the wild soybean (*G. ussuriensis*) is long and twining with a procumbent habit. Karasawa (9) in crossing experiments with the wild and cultivated soybeans found the F<sub>1</sub> hybrid of a twining nature. All of the plants of the F<sub>2</sub> and F<sub>3</sub> generations were more or less twining.
SOYBEANS

SEED CHARACTERS

Color of Seed Coat, Hilum, and Cotyledon

Most varieties of soybeans have unicolored seeds of straw yellow, olive yellow (greenish yellow), green, brown, or black. In some varieties straw-yellow seeds are very pale, especially when old, and they are sometimes erroneously called white, but no truly white seeds are known in soybeans. In straw-yellow varieties, the seeds have a greenish tinge if harvested before they are fully mature, which sometimes makes it difficult to distinguish them from varieties whose fully mature seeds are greenish yellow. Bicolored seed occurs in several varieties such as Black Eyebrow, Meyer, Taha, and Kura. The most common of the bicolored patterns is green or yellow with a saddle of black or brown, the latter not being sharply delineated. Some varieties have their seeds brindled brown and black, the two colors somewhat concentrically arranged. One variety has black seeds faintly marked with minute brown specks. On heterozygous plants the seeds are often irregularly bicolored and in some cases tricolored. Several black and a few brown varieties, with the outer layer of the testa broken by numerous cracks so as to expose the inner white layer, have been introduced from Chosen. In the case of the black-seeded and one or two brown-seeded introductions, this splitting has a net-like appearance that gives the beans a black-and-white or brown-and-white color.

Individual selections of natural hybrids by Piper and Morse (31) at the Arlington Experiment Farm gave some rather interesting results in the breaking up of the various seed colors. The selections with a single seed color, as straw yellow, black, or brown, broke up in simple Mendelian proportions, while those with more than one color presented a different ratio in the progeny.

Nagai (20) makes the following classification of soybeans according to color of seed coat:

1. Beans producing no anthocyanin pigment in the seed coat.
2. Beans producing anthocyanin pigment in the seed coat.

Owen (27) found the following classification of seed-coat color in soybeans most useful for the purpose of interpreting Mendelian characters:

1. Self-color type.
2. Bicolor type.
3. Eyebrow pattern with green or yellow background.
4. Green or yellow seed coat with dark hilum.
5. Green or yellow seed coat with light hilum.

The genetic relationships of seed-coat colors and the effect of other genes on the colors have been studied extensively by Woodworth (55), Nagai (22), Owen (27), Terao (43), and Stewart (35). The inheritance of seed-coat color in soybeans differs somewhat from that of other members of the legume family. In soybeans, those seed-coat colors producing no plastid pigments as a rule mask those producing plastid pigment. The black pigment, according to Owen (29), is a very intense purple belonging to the general class of anthocyanins. The brown pigment is closely related to quercetin, and the green and yellow are plastid pigments.
According to Woodworth (55), the black and brown pigments are genetically independent of green and yellow in inheritance. Black is dominant to brown, and in F2 a ratio of 3 black to 1 brown is obtained. Green is dominant over yellow, and in F2 a ratio of 3 green to 1 yellow is obtained. When black or brown is crossed with green or yellow, the results are influenced by genes for inhibition of black and brown pigments over the seed coat. Owen (27) cites a case of incomplete dominance over brown. A natural hybrid was accidentally found that segregated according to a ratio of 3 black to 1 brown in the progeny that was grown, but all heterozygous plants bore seed slightly speckled with brown. It is believed that this brown speckling or flecking on the black seed coat is different from that symbolized by Woodworth (see table 2, symbol Fl.).

Varieties of soybeans exhibit a wide range of color types in the hilum, ranging from a pale-yellow or colorless hilum through various shades of brown to black. Two complementary genes for black pigment formation in the seed coat and hilum have been affirmed by Nagai (22), Woodworth (55), and Owen (27). The symbols for these genes were designated C and L by Nagai, B and H by Woodworth, and R and R2 by Owen, the symbolism given by Owen appearing to be preferable according to Woodworth (65). In some early experiments which led to the suggestion of complementary factors for black hilum, Woodworth (55) obtained, in a cross between a strain with a black hilum and a strain with colorless hilum, black- and brown-hilum plants in the ratio of 9:7. He pointed out, however, that the ratio probably was 9 black:6 brown:1 colorless, because, on account of mottling of the seed coat, the plants having seed with brown hilums could not be easily distinguished from plants having seed with colorless hilums, and consequently they were classed together. Nagai (22) found in a cross between a plant having seed with a light-brown hilum and a plant having seed with a dark-brown hilum that the F1 plants have slightly brownish seed and the F2 may be dark brown, brown, and light brown in a 1:2:1 ratio. Woodworth (63), in crosses with parents of dark-brown hilum and light-brown hilum, found that the difference in the intensity of hilum color is due to the genes T, t, for tawny v. gray pubescence. Plants with T have dark-brown hilums, and plants with t have light-brown hilums. The genes for purple and white flowers (W1W1) have also been found to influence black and brown seed coat or hilum colors.

The cotyledons in the soybean are of two colors, yellow and green. When young the cotyledons are green, but in most varieties they turn to yellow toward maturity, while some varieties retain the original green. The behavior of the green and yellow cotyledons in natural and artificial hybrids has given some very interesting results. In 1909 Piper and Morse (31) noted in hybrid selection work that, with many plants having straw-colored to greenish-yellow seeds, seeds with green cotyledons and seeds with yellow cotyledons occurred on the same plant and sometimes in the same pod. These plants produced three kinds of progeny—those bearing only yellow-cotyledon seeds, those bearing only green-cotyledon seeds, and those bearing both kinds. The ratio was approximately 1:1:2, respectively, indicating that yellow was a simple Mendelian dominant to green. This
segregation in cotyledon color has been confirmed by Woodworth (55), who found evidence for two (duplicate) genes for yellow cotyledon. Terao (43) found in crosses that the cotyledon color of the hybrid progeny was the same as that of the female parent in every case and that there was no evidence of segregation in succeeding generations, indicating that cotyledon color in soybeans is maternal in inheritance. Maternal inheritance of cotyledon color in the soybean has been substantiated by Piper and Morse (31) and by Owen (24).

At least two kinds of transmission of the colors of the cotyledon are known. One is transmission through the maternal plant—that is, if the female parent is yellow the cotyledon of F₁ becomes yellow, and if it is green F₁ shows green cotyledons. Terao (43) suggests that there are two factors, G and Y, representing chlorophyll in two cotyledon colors. G is the one that always remains green and Y is the one that changes to yellow. In the other case of the inheritance of the cotyledon color, a simple Mendelian ratio has been obtained in F₂ in which yellow- and green-cotyledon seeds occur in a 3:1 or 15:1 ratio according as the parents differ by one or more genes.

Other Seed Characters

Defective or cracked seed coats have been observed by several investigators in black-, brown-, and yellow-seeded varieties and rarely in those having green seed. In some yellow and green seeds mottled with brown, the defects, or cracking, are found to occur mostly in brown areas. The character is undesirable, for in the defective or cracked areas the very thin inner coat cannot furnish the protection against unfavorable weather and disease organisms that is afforded normal soybeans in which the seed coat completely covers the seed. Stewart and Wentz (37), in a cross between the Wisconsin Black and Mandarin varieties, obtained in the F₂ 51 normal to 5 defective or cracked, suggesting a 15:1 ratio. Nagai (22), in a cross between plants with normal and defective seed coats, found the defective or cracking character to be partially dominant. In F₂ a large number of individuals were produced showing different degrees of cracking, a rough estimate giving a ratio of 9 defective or cracked to 7 normal.

Nearly all varieties of soybeans have a comparatively smooth seed coat but differ more or less in the degree of smoothness. In some varieties the seed coat is rather dull in appearance, while in others it is bright and glossy. In the variety Sooty, some black and brown Siberian varieties of Glycine gracilis, and the wild soybean there is a distinct bloom covering the entire seed coat. The bloom can easily be scraped off, exposing the comparatively smooth seed coat underneath. In a cross between the Sooty and Manchu varieties, Woodworth (63) obtained a 3:1 ratio in the F₂ generation, while in another cross a 27:37 ratio was found in the F₂. In interpreting these ratios, he assumes that three genes, B₁, B₂, and B₃, are involved and that all three must be present together to manifest the bloom. If any one of these genes is not present, the character does not develop.

The range in size of soybean seed varies according to the variety, each variety having its own typical seed size. Varieties and introductions tested at the Arlington Experiment Farm ranged in average weight of 100 seeds from about 4 grams for the smallest to about
40 grams for the largest. Although seed size is mentioned in numerous published descriptions of soybean varieties, Nagai (22) and Takagi (39) are apparently the only investigators who have made studies of the inheritance of this character, the same results being obtained by both. In a cross of small seed (100 seeds = 10.2 grams) × large seed (100 seeds = 25.5 grams) Nagai obtained from the F₁ generation seed intermediate in size (100 seeds = 14.2 grams). The segregation in the F₂ plants gave a wide range of variation between the seed sizes of the parent. Nagai states that it is very difficult to find plants bearing seeds of the same size as those of the larger plant and believes that many factors are involved in the inheritance of size of seed.

A considerable mottling of the seed of many yellow- and green-seeded varieties occupied the attention of plant breeders more than a decade ago. This 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. Seeds with black hilums were mottled with black, and seeds with brown or colorless hilums were mottled with brown. In 1924 Woodworth and Cole (66) described the character and believed the cause to be physiological rather than genetical. After further studies, Woodworth states that the problem of mottling has some genetic aspects and also that a strain may be developed by selection that lacks the objectionable feature of mottling exhibited by the original variety. This is substantiated by selection of nonmottling plants from the Dixie variety, resulting in a pure yellow-seeded strain. Owen (26) concluded after an extensive investigation of this subject that mottling is due both to hereditary and environmental factors. In artificial hybrids the pubescence color was found in one instance to influence the extent of mottling, tawny pubescence increasing it, gray pubescence decreasing it. Owen, however, could not designate any particular factor as being the most important in causing mottling. The problem had certain genetic aspects, but the environmental effects were also quite evident. In recent years, mottling has not appeared to any great extent and it has been suggested that perhaps the wider use of varieties not subject to mottling has been an important factor.

Yield of Seed

In considering the most desirable character in varieties of soybeans, the most valuable single desideratum, as with other crops, is high yield of seed. Other characters of course are important, such as habit of growth, seed quality, color of seed, ease of shattering, etc., but extensive tests are being conducted at experiment stations in States where soybeans are an important crop to determine the best yielding varieties.

From the standpoint of inheritance, seed yield is a very complex character. The amount of seed produced is determined by heredity and environment (soil fertility, soil type, method of culture, and seasonal conditions). Woodworth (63), in studies of the yield character, has analyzed yield of seed into its component parts—number of nodes, number of pods per node, number of seeds per pod, percentage of abortive seed, and size of seed—and attempted to evaluate each variety studied 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 or medium in others. No variety was found to rank highest in all. The conclusion reached was that the method of cross-breeding 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.

**Disease Resistance**

Although the soybean is attacked by a number of bacterial and fungus diseases, none of which reach serious proportions in oriental countries, no one disease as yet has caused serious injury to the crop in the United States. As cultivation continues, however, diseases undoubtedly will increase and assume more serious proportions. Breeding for disease resistance, therefore, may become an important factor in the improvement of the soybean. Studies of the various diseases of the soybean already found in this country indicate that varieties differ markedly in relative resistance to certain bacterial and fungus diseases.

Woodworth and Brown (65), in studies on varietal resistance and susceptibility to bacterial blight (*Bacterium glycineum* Coerper), found that field experiments indicated that soybean varieties vary greatly in their relative susceptibility to the bacterial blight. Of 48 varieties studied, about half were completely resistant, and the other half ranged from complete susceptibility to partial resistance.

A bacterial blight (*Bacterium sojae* Wolf) of soybeans was found on a number of varieties in North Carolina by Wolf (52). Studies failed to disclose any evidence of varietal resistance or susceptibility in any of the varieties.

Lehman and Woodside (16) made a very extensive study on resistance and susceptibility of soybean varieties to the bacterial pustule disease (*Bacterium phaseoli sojense* Hedges). After field observations and inoculations in greenhouse plantings, they were able to classify 56 varieties with respect to their resistance and susceptibility to the disease.

Extensive studies and experiments have been made on the mosaic disease of soybeans by Kendrick and Gardner (13). Results indicated quite clearly that varieties differ greatly in relative resistance and susceptibility.

“Brown spot” (*Septoria glycines* Hemmi), a fungus disease attacking the foliage of the soybean, has been studied by Wolf and Lehman (53), who noted differences among soybean varieties in relative resistance and susceptibility.

Another fungus disease, fusarium blight (*Fusarium bulbigenum* Cke. and Mass. var. *tracheiphilum* (E. F. Sm.) Wr.), was observed in North Carolina by Cromwell (3). In extensive variety tests, all varieties were found susceptible with the exception of the Black Eyebrow, which in two tests showed considerable resistance.

Lehman (15), in a study of another disease, frogeye leaf spot (*Cercospora daizu* Miura), attacking the foliage of the soybean, found that the early-maturing varieties in a certain group escaped serious injury while the late-maturing sorts suffered most.
Identification of Genes and Chromosomes

Several synonymic difficulties were encountered in establishing the identity of genes that different investigators have studied and designated differently. In cooperation with Woodworth and Williams, of the Illinois Agricultural Experiment Station, literature on the genetics of the soybean was reviewed thoroughly as to the genes of the soybean, and symbols were designated for each by the various geneticists. Liberty was taken in some cases to assign symbols to genes that have been studied but not named and certain symbols have been changed to bring them into line with current usage.

Every effort has been made to make the list given in table 2 of the appendix as complete as possible, and it is hoped that the list given here will help to establish greater conformity in the designation of soybean genes in the future.

According to counts made by Karpetschenko, Kawami, Fukuda (Karasawa, 9), and Veatch (48), the chromosome number in soybeans is given as 20 for the haploid and 40 for the diploid condition. The same number has also been counted in the wild soybean by Tschechow and Kartaschowa (45), as well as Fukuda (6). In F₁ hybrids between the wild and cultivated species of soybeans, Karasawa (9) found the same somatic chromosome number as in the parents. No abnormalities were found in the pollen mother cell in the course of sporogenesis, and the pollen therefrom was normal. Moreover, the fertility of the F₁ and its progeny was quite normal, indicating that the two species contain on the whole the same kind of genom.

Linkage studies in the soybean have not been very extensive, due largely, perhaps, to the difficulty of making artificial crosses. Woodworth, Nagai and Saito, Owen, and Stewart and Wentz have been the chief contributors to our meager knowledge of the association of genes in inheritance in the soybean. In table 3 of the appendix are shown the linkage groups reported up to the present time.

A provisional chromosome map of soybeans showing linkage relations of a few factors is given in figure 10. In chromosome 1, the gene order may not be as represented, since E and D₂ have not been studied together. In chromosomes 3 and 4, the order may be as represented or reversed.
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(45) Tschechow, W., and Kartaschowa, N.

(46) Veatch, C.

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(62) **Woodworth, C. M.**

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(65) ——— and **Brown, F. C.**

(66) ——— and **Cole, L. J.**

(67) ——— and **Veatch, C.**

**APPENDIX**

**Workers Identified With Soybean Improvement**

**United States**

United States Department of Agriculture, Bureau of Plant Industry, Division of Forage Crops and Diseases:
- W. J. Morse, Washington, D. C.
- W. M. Stuart, Jr., and C. H. Binkley, Arlington Experiment Farm, Arlington, Va.
- J. L. Carter, Urbana, Ill.
- M. G. Weiss, Ames, Iowa.
- J. L. Stephens, Tifton, Ga.
- T. F. Akers, West Point, Miss.
- R. E. Stitt, Statesville, N. C.
- H. A. Schoth, Corvallis, Oreg.

State agricultural experiment stations:
- California, Berkeley: W. W. Mackie.
- Delaware, Newark: G. L. Schuster.
- Iowa, Ames: H. D. Hughes, J. B. Wentz.
- Maryland, College Park: J. E. Metzger, R. G. Rothgeb.
- Minnesota, St. Paul: A. C. Arny, W. M. Myers.
- Missouri, Columbia: W. C. Etheridge, C. A. Helm, B. M. King.
- New Jersey, New Brunswick: H. B. Sprague.
- North Dakota, Fargo: A. F. Yeager.
- Oklahoma, Stillwater: B. F. Kiltz.
SOYBEANS

South Carolina, Florence: E. E. Hall.
Tennessee, Knoxville: H. P. Ogden.
Texas, College Station: E. B. Reynolds.
West Virginia, Morgantown: J. A. Rigney.

Foreign Countries

Australia:
Department of Agriculture, New South Wales:
  Glenn Innes: S. L. Macindoe.
  Trafotor: W. H. Darragh.
  Richmond: N. S. Shirlow.
  Sydney: H. Wenholz.

Canada:
  Central Experimental Farm, Ottawa: F. Dimmock.
  Dominion Experiment Station, Harrow: C. W. Owen.
  Agricultural College, Guelph: O. McConkey.

England:

Germany:
  Kaiser Wilhelm Institute, Manchberg: W. Rudorf.
  Südd. Soya-Institut, München: K. Baumeister.
  Soya-Institut, Mannheim: L. Müller.

Japan:
  Imperial Agricultural Experiment Station, Tokyo: H. Terao.
  Hokkaido Imperial Agricultural Experiment Station, Kotoni: V. Fujine, T. Hoshino.
  Saitama Agricultural Experiment Station, Ageo: T. Hasegawa.
  Central Agricultural Experiment Station, Suigen (Chosen): I. Nagai.
  Central Agricultural Experiment Branch Station, Shariin (Chosen): Y. Takahashi.
  Akita Agricultural Experiment Station, Akita: K. Adachi.

Manchuria:
  South Manchuria Railway Agricultural Experiment Stations:
    Hsiungyocheng: K. Hisatake.
    Kaiyuan: S. Kofuku.

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<thead>
<tr>
<th>Symbol</th>
<th>Dominant-recessive characters</th>
<th>Authority</th>
<th>Date published, observed, or reported</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Appressed pubescence; a, erect pubescence.</td>
<td>Karasawa</td>
<td>1906</td>
</tr>
<tr>
<td>B, B₁, B₂</td>
<td>Complementary genes for bloom on seed coat.</td>
<td>Woodworth</td>
<td>1932</td>
</tr>
<tr>
<td>C₁, C₂</td>
<td>Complementary genes for cracking on seed-coat surface.</td>
<td>Nagai</td>
<td>1926</td>
</tr>
<tr>
<td>D₁, D₂</td>
<td>Duplicate genes for yellow cotyledons; d₁, green cotyledons.</td>
<td>Woodworth</td>
<td>1921</td>
</tr>
<tr>
<td>D₃₁</td>
<td>Normal seed coat; d₃₁, defective seed coat.</td>
<td>Stewart and Wentz</td>
<td>1930</td>
</tr>
<tr>
<td>D₃₂</td>
<td>Normal seed coat; d₃₂, defective seed coat.</td>
<td>Williams</td>
<td>1935</td>
</tr>
<tr>
<td>D₄</td>
<td>Normal type; d₄, dwarf type.</td>
<td>Stewart</td>
<td>1927</td>
</tr>
<tr>
<td>D₅</td>
<td>Indeterminate growth; d₅, determinate growth.</td>
<td>Woodworth</td>
<td>1923</td>
</tr>
<tr>
<td>E</td>
<td>Early maturity; e, late maturity.</td>
<td>Owen</td>
<td>1927</td>
</tr>
<tr>
<td>F</td>
<td>Normal stem development; f₁, fasciated or flattened stem.</td>
<td>Takagi, F</td>
<td>1929</td>
</tr>
<tr>
<td>F₁</td>
<td>Black seed coat flecked or speckled with brown; f₁, self or solid black.</td>
<td>Woodworth</td>
<td>1930</td>
</tr>
<tr>
<td>G</td>
<td>Green seed coat; g, yellow seed coat.</td>
<td>Nagai</td>
<td>1931</td>
</tr>
<tr>
<td>I, I₁, I₂, I₃</td>
<td>Multiple allelomorphic series responsible for inhibition of black or brown pigment in seed coat: I, Total inhibition; seeds show no black or brown pigment even in hilum. I₁, Partial inhibition; permits pigment only in hilum. I₂, Partial inhibition; responsible for Black Eyebrow pattern. I₃, No inhibition; seeds entirely black or brown.</td>
<td>Owen</td>
<td>1928</td>
</tr>
</tbody>
</table>
Table 2.—List of genes in soybeans—Continued

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Dominant-recessive characters</th>
<th>Authority</th>
<th>Date published, observed, or reported</th>
</tr>
</thead>
<tbody>
<tr>
<td>I, M</td>
<td>Dark-colored or black pods; 1, light-colored pods; ( m ), no motting.</td>
<td>Woodworth</td>
<td>1923</td>
</tr>
<tr>
<td>N</td>
<td>Broad leaflet of most varieties; ( na ), narrow leaflet.</td>
<td>Owen</td>
<td>1929</td>
</tr>
<tr>
<td>( N_A )</td>
<td>Broad leaflet of most varieties; ( na ), narrow leaflet.</td>
<td>Takashashi and Fukuyama</td>
<td>1919</td>
</tr>
<tr>
<td>( P_1 )</td>
<td>Inhibition of pubescence, causing glabrousness; ( p_1 ), no inhibition.</td>
<td>Stewart and Wenz.</td>
<td>1926</td>
</tr>
<tr>
<td>( P_2 )</td>
<td>Pubescence; ( p_2 ), no pubescence.</td>
<td>Nagai</td>
<td>1921</td>
</tr>
<tr>
<td>( R_i, r_i, r_i^* )</td>
<td>Multiple allelomorphic series for seed-coat color.</td>
<td>Nagai and Saito</td>
<td>1926</td>
</tr>
<tr>
<td>( R_e )</td>
<td>Complementary with ( R_i ) for black seed coat or hilum.</td>
<td>Nagai and Saito</td>
<td>1924</td>
</tr>
<tr>
<td>( r_e )</td>
<td>Complementary to ( r_i ) and ( R_i ) for buff coat or hilum.</td>
<td>Nagai and Saito</td>
<td>1923</td>
</tr>
<tr>
<td>( S )</td>
<td>Shattering of wild soybean, dominant to nonshattering of Kuradaizu.</td>
<td>Nagai</td>
<td>1926</td>
</tr>
<tr>
<td>( S_h )</td>
<td>Shattering of wild soybean, dominant to nonshattering of Kuradaizu.</td>
<td>Nagai</td>
<td>1926</td>
</tr>
<tr>
<td>( S_p )</td>
<td>Spreading or fan-shape habit of growth; ( S_p ), erect compact habit of growth.</td>
<td>Nagai</td>
<td>1926</td>
</tr>
<tr>
<td>( S_t )</td>
<td>Normal production of seed; ( s ), sterility.</td>
<td>Nagai</td>
<td>1926</td>
</tr>
<tr>
<td>( T )</td>
<td>Tawny or brown pubescence color; ( t ), gray pubescence color.</td>
<td>Nagai</td>
<td>1926</td>
</tr>
<tr>
<td>( T_i, T_r, T_r^* )</td>
<td>Multiple allelomorphic series for seed-coat color.</td>
<td>Nagai and Saito</td>
<td>1926</td>
</tr>
<tr>
<td>( T_e )</td>
<td>Complementary with ( T_i ) for black seed coat or hilum.</td>
<td>Nagai and Saito</td>
<td>1924</td>
</tr>
<tr>
<td>( t_e )</td>
<td>Complementary to ( t_i ) and ( T_i ) for buff coat or hilum.</td>
<td>Nagai and Saito</td>
<td>1923</td>
</tr>
<tr>
<td>( X )</td>
<td>Extra leaflets in compound leaf; ( x ), normal number, three.</td>
<td>Nagai</td>
<td>1926</td>
</tr>
<tr>
<td>( Y_b, Y_b^* )</td>
<td>Complementary for green plant; ( y_b ), leaves turn yellow as plant grows; vigor fair.</td>
<td>Nagai</td>
<td>1926</td>
</tr>
<tr>
<td>( Y_t )</td>
<td>Normal green plant; ( y_t ), greenish-yellow leaves; weak plant.</td>
<td>Nagai</td>
<td>1926</td>
</tr>
<tr>
<td>( Y_b )</td>
<td>Normal green plant; ( y_b ), yellowish leaves; mutant found in Wilson-V.</td>
<td>Nagai</td>
<td>1926</td>
</tr>
<tr>
<td>( Y_y )</td>
<td>Normal green plant; ( y_y ), yellow-green leaves; mutant found in F. P. I. 65838; plant low in vigor.</td>
<td>Nagai</td>
<td>1926</td>
</tr>
<tr>
<td>( Y_l )</td>
<td>Normal green plant; ( y_l ), pale-green leaves; mutant found in F. P. I. 65838; plant low in vigor.</td>
<td>Williams</td>
<td>1936</td>
</tr>
<tr>
<td>( Y_e )</td>
<td>Normal green plant; ( y_e ), leaves, stem, and pods become yellow as plant develops.</td>
<td>Nagai</td>
<td>1934</td>
</tr>
<tr>
<td>( Y_t )</td>
<td>Normal green plant; ( y_t ), yellow-green leaves in young plant, becoming green as plant develops.</td>
<td>Woodworth</td>
<td>1935</td>
</tr>
</tbody>
</table>

Table 3.—Linkage of soybean characters

<table>
<thead>
<tr>
<th>Characters associated</th>
<th>Symbols</th>
<th>Percent-age crossing over</th>
<th>Authority</th>
<th>Date published, observed, or reported</th>
</tr>
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<tbody>
<tr>
<td>Green seed coat and green cotyledons</td>
<td>( G, d_i )</td>
<td>13</td>
<td>Woodworth</td>
<td>1921</td>
</tr>
<tr>
<td>Tawny pubescence and black seed coat or hilum color.</td>
<td>( T, R_o )</td>
<td>0</td>
<td>Woodworth</td>
<td>1932</td>
</tr>
<tr>
<td>Early maturity and tawny pubescence</td>
<td>( E, T )</td>
<td>6</td>
<td>Owen</td>
<td>1927</td>
</tr>
<tr>
<td>Defective seed coat and gray pubescence</td>
<td>( d_e, t )</td>
<td>0</td>
<td>Stewart and Wenz.</td>
<td>1930</td>
</tr>
<tr>
<td>Inhibition of pubescence and brown seed coat or hilum.</td>
<td>( P_i, r_i )</td>
<td>12</td>
<td>Owen</td>
<td>1927</td>
</tr>
<tr>
<td>Inhibition of pubescence and black motting on a self-brown seed coat.</td>
<td>( P_i, M )</td>
<td>18</td>
<td>Nagai and Saito</td>
<td>1923</td>
</tr>
<tr>
<td>Pubescence color and cotyledon color</td>
<td>( T, d_i )</td>
<td>13</td>
<td>Williams</td>
<td>1932</td>
</tr>
<tr>
<td>Defective seed coat and pubescence</td>
<td>( d_e, p_i )</td>
<td>2</td>
<td>Williams</td>
<td>1935</td>
</tr>
<tr>
<td>Variety</td>
<td>Origin</td>
<td>Year</td>
<td>Days to mature</td>
<td>Flower color</td>
</tr>
<tr>
<td>--------------</td>
<td>--------------------------------</td>
<td>------</td>
<td>----------------</td>
<td>--------------</td>
</tr>
</tbody>
</table>
| Agate        | Introduction, Japan             | 1929 | 90             | p, w, t      | sy + br         | y, br                                                | 2-3 2,816, g
| A. K.        | Introduction, Manchuria         | 1912 | 110            | p, w, g, t   | sy              | y, y, pa to bl                                      | 2-3 2,650, f
| Arkansas      | Introduction, China             | 1913 | 105            | p, w, g      | sy              | y, y, g                                            | 2-3 2,693, f
| Arlington     | Introduction, China             | 1908 | 125            | p, w, g, t   | bl               | y, bl                                               | 2-3 2,750, f
| Arksoy        | Introduction, Chosen            | 1914 | 140            | p, g          | sy              | y, bl                                               | 2-3 3,136, f, gr
| Avoyelles     | Selection, Gray, Louisiana      | 1902 | 170            | p, t          | bl               | y, bl                                               | 2-3 3,138, f, gr
| Barsei        | Introduction, Japan             | 1929 | 110            | p, t          | sy              | y, y                                                | 2-3 1,936, de, gv
| Barchet       | Introduction, China             | 1908 | 150            | p, t          | br               | y, br                                               | 2-3 9,950, f
| Biloxi        | do                             | 1908 | 165            | p, t          | br               | y, br                                               | 2-3 1,875, f
| Black Eyehow  | Introduction, Manchuria         | 1911 | 105            | p, w, t       | bl, br          | y, bl                                               | 2-3 2,450, f
| Cayuga        | do                             | 1925 | 100            | w, t          | bl               | y, bl                                               | 2-3 3,632, f, gr
| Chame         | Introduction, Japan             | 1929 | 125            | w, t          | br               | y, br                                               | 2-3 1,904, g
| Chennie       | Introduction, Siberia           | 1906 | 100            | p, t          | br               | y, bl                                               | 2-3 4,675, f
| Chestnut      | Selection, Arlington Experiment Farm | 1907 | 105 | p, t | br | y, br | 2-3 3,275, f |
| Chiquita      | Introduction, China             | 1910 | 135            | p, w, g      | sy              | y, y                                                | 2-3 4,050, f, gr
| Chusel        | Introduction, Japan             | 1929 | 110            | w, g          | sy              | y, y                                                | 2-3 2,066, de, gv
| Columbia      | Introduction, China             | 1908 | 125            | p, w, g      | gr               | gr                                                  | 2-3 3,350, f
| Creole        | do                             | 1927 | 165            | p              | sy             | y, bl                                               | 2-3 5,120, f, gr
| Delnoshay     | Selection, York, Mississippi    | 1925 | 165            | w, p, g      | sy              | y, br                                               | 2-3 2,340, gra
| Delsta        | do                             | 1925 | 130            | w, p          | sy              | y, br                                               | 2-3 1,860, gra
| Dixie         | Selection, Arlington Experiment Farm | 1914 | 135 | p, g | sy | y | 2-3 3,825, f |
| Dunfield      | Introduction, Manchuria         | 1913 | 110            | p, w, g      | sy              | y, br                                               | 2-3 4,175, f
| Easycook      | Introduction, China             | 1894 | 133            | p, g          | sy              | y, br                                               | 2-3 2,700, de, gra
| Ebony         | Introduction, Chosen            | 1901 | 123            | p, w, t       | bl               | y, bl                                               | 2-3 5,750, f
| Elton         | Introduction, Siberia           | 1906 | 105            | p, g          | sy              | y, y                                                | 2-3 2,625, f
| Fuji          | Introduction, Japan             | 1929 | 115            | p, w, t       | oy              | y, bl                                               | 2-3 1,456, de, gra
| George Washington | Selection, Clapp, Virginia    | 1921 | 135            | p, t          | sy              | y, y, pa to bl                                      | 2-3 3,200, f, n,s
| Georgian      | Introduction, China             | 1927 | 165            | p, t          | sy              | y, br                                               | 2-3 3,968, gra, f
| Goku          | Introduction, Japan             | 1929 | 110            | w, p, g      | sy              | y, br                                               | 2-3 3,216, gra
| Habaro        | Introduction, Siberia           | 1906 | 105            | p, w, g, t   | sy              | y, br                                               | 2-3 3,100, gra
| Haberlandt    | Introduction, Chosen            | 1901 | 130            | p, w, t       | sy              | y, br                                               | 2-3 2,400, gra, de
| Hahko         | Introduction, Japan             | 1915 | 130            | p, t          | oy              | y, bl                                               | 2-3 1,290, gv, de
| Hakone        | do                             | 1929 | 115            | w, t          | oy              | y, br                                               | 2-3 1,440, gv, de
| Harbinsoy     | Selection, Arlington Experiment Farm | 1922 | 120 | w, t | sy | y | 2-3 2,950, f, gra
| Haysse        | Introduction, China             | 1927 | 160            | w, t          | sy              | y, br                                               | 2-3 4,176, f, gra
| Herman        | Selection, Herman, North Carolina | 1915 | 135 | p, t | sy | y | 2-3 2,450, gra
| Hiran         | Introduction, Japan             | 1929 | 135            | p, g          | sy              | y, br                                               | 2-3 1,984, gv, de
| Hiro          | do                             | 1930 | 115            | w, t          | bl               | y, bl                                               | 2-3 1,312, gv, de

1 bl = black; br = brown; de = dry edible beans; f = forage; g = gray; gr = green; gra = grain; gv = green vegetable beans; oy = olive or greenish yellow; p = purple; pa = pale; sy = straw yellow; t = tawny; w = white.
2 Name of breeder.
<table>
<thead>
<tr>
<th>Variety</th>
<th>Origin</th>
<th>Year</th>
<th>Days to mature</th>
<th>Flower color</th>
<th>Pubescence color</th>
<th>Coat color</th>
<th>Germ color</th>
<th>Hilum color</th>
<th>Seeds per pod</th>
<th>Use</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hokkaido</td>
<td>Introduction, Japan</td>
<td>1930</td>
<td>115</td>
<td>p, w</td>
<td>g</td>
<td>sy</td>
<td>y</td>
<td>y</td>
<td>2-3</td>
<td>1,232</td>
</tr>
<tr>
<td>Hollybrook</td>
<td>Selection, Wood, Virginia</td>
<td>1902</td>
<td>112</td>
<td>w</td>
<td>t</td>
<td>sy</td>
<td>y</td>
<td>y</td>
<td>2-3</td>
<td>2,130</td>
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<td>Introduction, China, Japan</td>
<td>1910</td>
<td>105</td>
<td>p</td>
<td>g</td>
<td>sy</td>
<td>y</td>
<td>y</td>
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<tr>
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<td>1900</td>
<td>105</td>
<td>p</td>
<td>t</td>
<td>sy</td>
<td>y</td>
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<td>Hurrelbrink</td>
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<td>1901</td>
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<td>p</td>
<td>t</td>
<td>sy</td>
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<td>y</td>
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<td>t</td>
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<td>g</td>
<td>bl</td>
<td>y</td>
<td>y</td>
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<td>g</td>
<td>bl+oy</td>
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<td>1914</td>
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<td>p</td>
<td>g</td>
<td>bl</td>
<td>y</td>
<td>y</td>
<td>2-3</td>
<td>7,453</td>
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<tr>
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<td>Selection, Arlington Experiment Farm</td>
<td>1907</td>
<td>120</td>
<td>p</td>
<td>w</td>
<td>g</td>
<td>y</td>
<td>br</td>
<td>2-3</td>
<td>3,585</td>
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<tr>
<td>Mammoth Brown</td>
<td>Selection, North Carolina</td>
<td>1907</td>
<td>120</td>
<td>p</td>
<td>w</td>
<td>g</td>
<td>y</td>
<td>br</td>
<td>2-3</td>
<td>3,585</td>
</tr>
<tr>
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<td>Introduction, origin unknown</td>
<td>1907</td>
<td>120</td>
<td>p</td>
<td>g</td>
<td>sy</td>
<td>y</td>
<td>bl</td>
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<td>2,150</td>
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<tr>
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<td>Selection, York, Mississippi</td>
<td>1910</td>
<td>120</td>
<td>p</td>
<td>g</td>
<td>sy</td>
<td>y</td>
<td>y</td>
<td>2-3</td>
<td>3,220</td>
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<tr>
<td>Manchu</td>
<td>Introduction, Manchuria</td>
<td>1910</td>
<td>120</td>
<td>p</td>
<td>g</td>
<td>sy</td>
<td>y</td>
<td>y</td>
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<td>1910</td>
<td>120</td>
<td>p</td>
<td>g</td>
<td>sy</td>
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<td>y</td>
<td>2-3</td>
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<td>1910</td>
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<td>p</td>
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<td>sy</td>
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<td>120</td>
<td>p</td>
<td>g</td>
<td>sy</td>
<td>y</td>
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<td>1889</td>
<td>120</td>
<td>p</td>
<td>gr</td>
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<td>br</td>
<td>2-3</td>
<td>2,485</td>
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<td>Merko</td>
<td>Introduction, Siberia</td>
<td>1900</td>
<td>115</td>
<td>p, w</td>
<td>t, g</td>
<td>br</td>
<td>y</td>
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<td>2-3</td>
<td>4,680</td>
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<td>Introduction, China</td>
<td>1901</td>
<td>115</td>
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