13. AGRO-GENECEOLOGICAL APPROACHES TO THE VARIETY DIFFERENTIATION IN SOYBEANS, *Glycine max* (L.) MERRILL

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Origin and Dissemination of Cultivated Soybeans

As noted by many botanists and agronomists, the soybean, *Glycine max* (L.) Merrill has been believed to be a cultigen derived from the related wild species, *G. soja* Sieb. et Zucc. (syn. *G. ussuriensis* Reg. et Maack) which was classified into the subgenus *Soja* together with *G. max*, and both were determined to be distinct from the other species in the genus *Glycine* by Hermann (1962).

By domesticating the soybean plant under the human cultivation from the assumed progenitor *G. soja*, widespread distribution of soybeans as a crop is now seen over the world. However, the center of origin and paths of dissemination remain obscure in detail.

Leppik (1971) presented a view of distribution of plants belonging to the genus *Glycine*, and assumed that the central area of the distribution of the genus is in the tropical southern Asia where the greatest number of endemic species still live. He also said that from this area, the group of the plants has migrated to Central Africa and Oceania, and now forms an extensive pattern of distribution in the tropics, and that the milder coastal areas of Southeast Asia enabled one branch to move northward until it reached present-day Formosa, China, Korea and Japan where some wild species are still found. In spite of the unique opinion on the origin of the genus *Glycine*, he noted only the center of origin of cultivated soybeans in the area of the habitat of *G. soja*, where all akin to the Chinese center by Vavilov.

Within the territory of China including so-called Manchuria, region of Northeast China, the origin of cultivated soybeans has been considered in two regions, namely in Northeast China and in North China by some botanists, though they did not prove the systematic evidence.

A Russian botanist, Skvortzow (1927) found semi-cultivated soybeans named *G. gracilis* Skvortzow in the region near Harbin. Though there is a little doubt to classify the plants into a distinct species from *G. max*, the species appeared to be of intermediate type between *G. soja* and *G. max*. Following the discovery of the plants by Skvortzow, Fukuda (1933) presumed the origin of cultivated soybeans in Northeast China (Manchuria), since such plants of intermediate type had not been found in the other lands in Asia than Northeast China.

The author (Nagata 1959, 1960a) dealt with the problem of the origin in the final discussion of the studies on agronomic and geneecological differentiation of soybean varieties in Japan and in the world, and then settled the origin of cultivated soybeans in North and Central China, especially in North China, since there were found more various ecological races different in the characters explained in following chapters in the paper than in Northeast China. He has also made a figure showing the paths of dissemination to the countries or regions where soybeans are now or were cultivated.

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Pattern of the Cultivation Type of Soybeans, as a Basis for Considering Variety Differentiation

Though the process of development is not so clarified at present, soybean plants are now found throughout the world, and the variety is differentiating in the characters adaptable to lands of cultivation.

All of the crop plants including soybean are of product of ecological and agronomic adaptation, hence the variety should be considered agro-ecologically or agro-genecologically. Then the cultivation system in each of the cultivated lands is of significance to be discussed here first, since the pattern of variety distribution is affected mostly by the system.

In Japan and other countries in Asia, such a cultivation system is observed as well in regular arrangement as in paddy rice, *Oryza sativa* L., because the cultivation is old and wide in both.

In a general view of agronomy, the cultivation of soybeans is divided into two kinds; one is of full season crop type, and another of short season crop type. Full season crop type is named for the cultivation system harvested near the first frost time in autumn, and short season crop type for the system sown after the final frost and harvested before the first frost will come, namely in summer. In the latter, another crop is planted usually till the first frost. A medium type is often seen in the harvest at the time between both types. Such a concept of cultivation system is shown schematically in Fig. 2.

In North Japan, soybeans are cultivated only as a full season crop during the relatively short period of free frost, and harvesting is carried out earlier than in the central and south parts of Japan. The harvesting time become late in succession of the cul-

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Fig. 1.
tivated land towards the south. In the warm regions such as Kyushu, Okinawa and some prefectures in the Pacific coast, the cultivation as a short season crop is seen in parallel with full season cultivation. There is a distinct seasonal isolation, and the former is named the summer soybean (*natsu-daizu* in Japanese) in contrast to the latter named the autumn soybean (*aki-daizu*).

Such a cultivation system is seen in general in rice and other summer crops in Japan, and then similar nomination is used in adzuki-beans, Italian millet, buckwheat and others, but not in rice.

In more southern regions such as Formosa and South China, there are more than three times of soybean cultivation; the first is seeded in January to March, the second in May to June, and the third in October to November. This cultivation system is understood as succeeding series from the summer vs. autumn soybeans in South Japan as presented in Fig. 2.

However, such series are not found so significantly in the other continents, since there are differences in the history of cultivation and in other agronomic conditions from Asia. In the United States of America where is a wide region from north to south for soybean cultivation, there is a full season crop system, and no difference in summer vs. autumn soybeans.

**Agro-Genecological Conception as to the Variety Differentiation in Soybeans**

In Japan, more than four hundred varieties or strains were supposed to be grown, and then more than thousand entities could be estimated to being differentiated over the world. In handling numerous varieties for breeding and cultivation, grouping or classification in ecological regards and in agronomic dealing is of necessity and of importance. However, the method adopted and the trait dealt with are somewhat different by the country and researchers, and have been affected by the spread of region applied and the number of varieties used remarkably.

In the United States of America where only full season crop is adopted, a grouping system by maturity from 0 or 00 to VIII; 0 is of the earliest maturity and adaptable to the north, VIII of the latest to the south, is being practiced as an official standard (Morse and Carter 1949).

In Japan, the intention of grouping soybeans into summer-vs. autumn-soybean types has been prevailing from the time before scientific investigation had begun. As an early
agronomic research, Matsumoto (1942) grouped many varieties in Japan into three types; the summer soybean, intermediate, and autumn soybean types, by practical cultivation in Kyushu. Ariga (1948) carried out more detailed classification into the same three types and eight subgroups by the seeding time of each variety showing the standard number of days to flowering—40 days.

Both of the classifications of soybean varieties are available, but no distinction between the varieties in the north and the south in Japan and other countries in the world was attempted.

Fukui and Arai (1951) grouped soybeans by the number of days to flowering and the number of days of seed forming period from flowering to maturity (Table 1). The result shows that the early flowering varieties from Kyushu and Kanto districts have rather short seed forming period (IIa) in comparison with those from Tohoku district (IIc).

Table 1. Grouping soybean varieties by one lengths of the period to flowering and the seed forming period
(after Fukui and Arai 1951)

<table>
<thead>
<tr>
<th>Seed forming period</th>
<th>Period to flowering</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
</tr>
<tr>
<td>a</td>
<td>9</td>
</tr>
<tr>
<td>b</td>
<td>18</td>
</tr>
</tbody>
</table>

Period to flowering; I : very short to V : very long, Seed forming period; a : short to c : long

The author (Nagata 1950, 1959, 1960a, b, c) carried out many experiments to make the distribution pattern of soybeans in Japan and in the world clearer with special regards to the summer vs. autumn soybean habit and the plant habit.

The summer vs. autumn soybean habit was dealt with grouping the varieties in summer soybean type (SI, SII), intermediate type (MIII, MIV), autumn soybean type (AV, AVI, AVII) and the tropical soybean type. The degree of the habit was expressed by the reduced rate of the period of flowering by delayed seeding time exactly, and estimated roughly by the number of days of period to flowering at normal seeding time (see Table 4). In parallel with the grouping, the relative flowering period and relative growing period which were calculated as the ratios of each of flowering period and growing period to the period to flowering were used as the properties of varieties separating the others from the true summer soybeans cultivated as the short season crop.

In the result of investigations of the two relative periods, the varieties from Manchuria and the United States were ascertained to be long in both of the relative periods, and then grouped separately as a special summer soybean type (SIp) by reason of their fairly distinct properties from others. Moreover, some of the varieties from Hokkaido and Tohoku district have been found to have long relative growing period in spite of the short relative flowering period, and then the varieties from Kyushu and Okinawa cultivated as a short season crop were short in both of the two relative periods. The difference in the relative growing period between the soybeans mentioned is shown in Table 2, but was not used for making a separate type, since there was a continuous change and no distinct limit. The relative growing period can be taken as the properties of varieties responsible to the seed size, and also the relative growing period and
Table 2. Regional distribution of soybeans with respect to their relative growing period in the varieties of summer soybean type and of intermediate type (Nagata 1960)

<table>
<thead>
<tr>
<th>District</th>
<th>Relative growing period</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2.3 2.5 2.7 2.9 3.1 3.3</td>
<td></td>
</tr>
<tr>
<td>Hokkaido</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tohoku</td>
<td>1 1 1 4 1</td>
<td>11</td>
</tr>
<tr>
<td>Kanto</td>
<td>2 3 2 1 2</td>
<td>11</td>
</tr>
<tr>
<td>Chubu</td>
<td>1 2 1 1</td>
<td>5</td>
</tr>
<tr>
<td>Kinki</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chugoku</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shikoku</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kyushu</td>
<td>1 4 2 5 4 1 1</td>
<td>20</td>
</tr>
<tr>
<td>Okinawa</td>
<td>1 1</td>
<td>2</td>
</tr>
</tbody>
</table>

The relative flowering period should be considered as the products of the comparative effects of photoperiodism on the varieties before and after the flower primordia initiation (Nagata 1960a, b, d).

The plant habit was studied on the vining habit first, and four types, namely, consistent vining, variable vining, special non-vining, and normal types were noticed and used for grouping the varieties. Among four types, the consistent and special non-vining types are of indeterminate growth, but the variable and normal types are of determinate growth. The variable vining type is of ecological appearance characterized by limited vining prevailing in very early planting, and of importance for practical cultivation, but difficult to find the attribute in normal cultivation, and then no difference is detected from the normal type. The consistent vining type is of late flowering and vining normal cultivation, and the special non-vining type of early flowering and non-vining in general view, though both are in common with each other in their indeterminate growth habit. The special non-vining type has a intimate relationship to the special summer soybean type, and the long-relative flowering period of the type is especially seen as direct result of indeterminate growth. The appearance of determinate vs. indeterminate growth is illustrated in Fig. 3, and relationship among the charc-
ters mentioned above are explained schematically in Figs. 4 and 5.

When settled the found on the habits, the author made the consideration on the geographic distribution of soybean varieties.

The summer vs. autumn soybean habit including the tropical soybean type was seen in succession from north to south, especially in the varieties grown as full season crops. The soybeans cultivated as short season crops in Kyushu, Okinawa, and other warm regions in Japan were classified as summer soybean or intermediate type. The varieties in Formosa where are three cultivation systems should be understood as the succeeding series to the distribution of soybeans in Japan, and were arranged in the habit as shown in Table 3, and the soybeans from Southeast Asia were observed to be different in the habit and the most were classified as the tropical soybean type later in flowering than AVII (Table 4). Then, the distribution is illustrated diagramatically in Fig. 6.

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**Fig. 4.**

**Fig. 5.**

**Fig. 6.**
Table 3. Summer vs. autumn soybean habits of soybeans in Formosa differing with their practical seeding time (Nagata 1960a)

<table>
<thead>
<tr>
<th>Seeding time</th>
<th>Type of the habit</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Summer</td>
<td>Interm.</td>
</tr>
<tr>
<td>Jan. to Mar.</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>May to June</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Oct. to Nov.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>3</td>
<td>7</td>
</tr>
</tbody>
</table>

Table 4. Comparison of the soybeans in Southeast Asia to representative varieties of seven classes of summer vs. autumn soybean habit (Nagata 1960)

<table>
<thead>
<tr>
<th>Country or region</th>
<th>Date of flowering</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>July 10</td>
</tr>
<tr>
<td>Formosa</td>
<td>3</td>
</tr>
<tr>
<td>Philippine</td>
<td>1</td>
</tr>
<tr>
<td>Viet Nam</td>
<td></td>
</tr>
<tr>
<td>Thailand</td>
<td></td>
</tr>
<tr>
<td>Malaya</td>
<td></td>
</tr>
<tr>
<td>Burma</td>
<td>1</td>
</tr>
<tr>
<td>Pakistan</td>
<td></td>
</tr>
<tr>
<td>India</td>
<td></td>
</tr>
<tr>
<td>Indonesia</td>
<td>1</td>
</tr>
<tr>
<td>Control</td>
<td>SI</td>
</tr>
<tr>
<td></td>
<td>SIII</td>
</tr>
</tbody>
</table>

The distribution in the habit in the world are shown in Fig. 7. In China, the pattern of distribution is similar to that in Japan since there are soybeans in different cultivation systems. However, there is a simple north to south succession in the United States and in Europe because of simple cultivation system.

With regards to the relative flowering period and the relative growing period, some aspects of variety distribution in Japan and in the world were expressed already in the chapter, and a summarized picture is submitted to Fig. 8. Among the soybeans in summer soybean and intermediate types, the special summer soybean type which is long in both of the relative periods is surely the property of the soybeans in Northeast China, North America, and Europe; the type of long relative growing period and of short relative flowering period is seen to be prevailing in the north of Japan; the type short in both of two relative periods is found in the south of the country. In China Proper, all of the types are found in the figure.

Distribution of the soybean varieties was also considered in their plant habit as shown in Fig. 9. Special non-vining type is found in Northeast China, North America, and Europe since the type is closely intimate with the special summer soybean type. The consistent vining type is found in the south of the temperate zone and towards the tropic zone, because the vining is expressed with the autumn- and tropical-soybean habit having long growing period. The soybeans in Japan and Korea are of normal
Fig. 7.

Fig. 8.
type in most of all. In China Proper, all of the types are found in the same trend as in the other habit. It is interesting to notice that the type all the same as that in the north of Japan is found in Sweden. This is a result of introduction of materials from Japan (Holmberg 1955).

After the development of genealogy or experimental taxonomy, ecotype has been considered as the distinct entity in meaning the subspecies order of morphological taxonomy. Then, the ecotype is being used in many crops for nomination of ecologically differentiated cultivars, especially in Japan. Ecological races are, however, being
ever distributed continuously in parallel with the change of items conditioning the environment, making the cline suggested by Huxley (1938, 1940) as an auxiliary taxonomic unit. Common is now the opinion that is limiting the use of the world ecotype in a special case of distinct ecological isolation in biologists.

In the distribution of soybean varieties, some kinds of cline were found. The summer vs. autumn soybean habit is the attribute of the variety making the typical climatic cline from north to south named N-S cline. The relative flowering period and relative growing period are the attributes of the variety modifying the N-S cline as shown in Fig. 10. The plant habit is also the factor arranging the varieties in another cline, as presented in Fig. 11. Putting the clines above mentioned together, the author settled four clines in Fig. 12. Then, in terminal part of each cline, the characterized

![Fig. 12.](image_url)

![Fig. 13.](image_url)
genetic entity was observed respectively, and the name *ecotype* was given to such genetic communities including representative varieties in the regions: 1. *ecotype manchuriensis* (Manchurian ecotype), 2. *ecotype japonicus borealis* (north Japanese ecotype), 3. *ecotype japonicus australis* (south Japanese ecotype), 4. *ecotype indo-chinensis* (Indo-Chinese ecotype). Distribution of four ecotypes is explained schematically in Fig. 13.

The author has assumed the origin of soybean cultivation and paths of dissemination as the result of such clinal and ecotypic conceptions of soybeans in the world as already shown in Fig. 1.

**Introduction of Soybeans Basing Upon the Agro-Geneecological Differentiation**

Such agro-genecological concepts should be of worth for introducing the soybean varieties for cultivation and breeding. There is, however, a little space for the problem, so that brief discussion will be made herein.

Generally speaking, China, especially North and South China, where are many kinds of soybean varieties or strains, and is a pool of available genes, should be noticed as the place to search the breeding materials. In the ecological principle of introducing plants next, the materials should be favorably gathered from the habits similar at the phenological and agronomic conditions. We can see the result of such a principle in the introduction from Northeast China to the United States of America. In the United States, great number of soybeans have been gathered from Asia, especially from Japan but present varieties grown in corn belt are of Northeast China ecotype and of origin from Northeast China (Manchuria), and Japanese origin soybeans are only cultivated for vegetable use (Nagata 1960c, see Fig. 1). Both of the United States and Northeast China are similar in the continental climate in contrast with the marine climate in Japan, and also in rather extensive cultivation for oil production against intensive cultivation for vegetables and fermented products in our country. On the contrary, success was made in the introduction to Sweden from North Japan where are similar in marine climate as already mentioned in the late chapter (Holmberg 1955). The author had seen an interesting fact in the Republic of Yugoslavia where been as an expert of ETAP of FAO more than ten years ago (Nagata 1962). There was superior in the performance with early introduced varieties from Northeast China (Manchuria) to the United States such as Wisconsin-, Hudson-, and Montreal-Manchu to the newly bred varieties in the United States. That is considered as the result of nearly locality of Yugoslavia to Northeast China than the United States.

However, the agronomic circumstances are always variable in the course of progress, and then a new genesource becomes of necessity to improve native varieties. There is another principle of introduction that has to be carried out for gathering available exotic genes. In this purpose, different agro-ecotypic soybeans from abroad have to be taken in. We are making the works using the indeterminate growth habit of Manchurian ecotype, and some varieties were bred in Hokkaido (Nagata 1966), and also interesting new strains are being performed in Kumamoto in Kyushu and in Nagano in Central Japan.

The ecotype is defined as a community conditioned by many endemic genes in the habitat, hence the varieties belonging to a given ecotype have unfavorable genes with an useful characteristic in the introduced lands. Moreover, it is an important fact that the unfavorable genes are never seen on the phenotype in the native land. In the breeding of indeterminate growth type soybeans adaptable to Japan, we have many problems. The newly bred soybeans have useful characteristics such as tall stems and high resistance to lodging adaptable to solid planting and machinery cultivation, and high yielding ability to some extent, but they are less resistant against the damage in
cool summer in Hokkaido, and susceptible to the diseases occurred in hot and wet weather at harvesting time in Kyushu, which do not appear in Manchuria and the United States.

Thus the agro-geneecological view of differentiation of soybeans should be useful for introducing the materials for cultivation and breeding, if it is practiced in accordance with the step of progress of agronomy, and most efficient techniques to the materials are applied.

**Discussion**

H. K. Jain, India: Has any one made a diallel series of crosses between the different agro-ecological types? If so, what types of gene interactions are observed?

**Answer:** As suggested in your comment, genetic analyses of different agro-ecotypes are surely most important considering the significance of varietal differentiation for the cultivation and breeding. But, such complete series of diallel crosses as commented here has not been attempted, and also gene analysis on many characters including interaction between them are not yet completed, because the experiments are very laborious.

We have made some crosses between the representative varieties of agro-ecotypes, and have analysed genetic behaviors of indeterminate vs. determinate growth habit as well as some agronomic characters associated with the growth habit. We are not doing any crossing experiments among the north and south Japanese ecotypes and Manchurian ecotype in order to contribute to the breeding of indeterminate type varieties adaptable to Japan.

T. Sanbuichi, Japan: Determinate and indeterminate soybeans were originally distinguished by the morphological types of varieties. But when we make the hybrid between two types, we can see much variation among indeterminate types. So, I have tried to deal with the indeterminate type of growth as a quantitative character. Will you give me any good idea about the definition of this character?

**Answer:** As suggested in your comment, determinate vs. indeterminate growth habit should be dealt with as a quantitative character, I think. It seems to be many minor genes, perhaps, in a series of poly-genes other than the major genes $Dt$, $dt$ which were already clarified.

In dealing with the growth habit as a quantitative character, I have suggested using the number of stem nodes after flower primordia initiation, and made some crossing experiments, but it has been difficult to make clearer the minor genes governing the habit. Please, see the literature cited (Nagata 1960c).

K. Hanada, Japan: I heard some plants are sensitive to a little difference of day length, such as of 15 minutes, and also some tropical rice varieties respond to the little difference of day length in the tropics. I don't know, if they need this kind of soybean varieties in some tropical regions, but are there this kind of soybean varieties in the tropical area?

**Answer:** Your question seems to be concerning with the critical or threshold hour of daylength, which determines the beginning of flower primordia initiation under succeedingly different photoperiods.

In this meaning, all the tropical type soybeans and some of the autumn ones are of the kind of varieties you suggested. Because those varieties of soybean respond well to photoperiod and initiate flower primordia formation under the short photoperiod such as 12 to 13 hours. Those varieties open the flower fairly and produce much of the seed under the day-length shorter than the critical one, but do not develop flower primordia under a little longer day-length than the critical one. As mentioned in your
comment, such a little difference as fifteen minutes in the critical day-length has much effect on the flower primordia initiation.

In agro-geneecological sense, such varieties sensitive to short day-length are surely adaptable to the cultivation in the tropical regions where the day-length is short and less of seasonal change, especially to the cultivation in which the plant emerges under the day-length a little longer than the critical one and grows vegetatively till the day when the day-length becomes shorter and flowering begins.

Comparing with rice, such a characteristic of variety should be more useful for soybean, because no variety having the long basic vegetative period independent to the day-length was found in soybean in our researches but in rice in the tropics.

References


