Soybean Seed Protein Electrophoresis Profiles from 15 Asian Countries or Regions: Hypotheses on Paths of Dissemination of Soybeans from China[1]

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Soybean [Glycine max *(L.) Merr.*] *seed protein extracts from 1,603 accessions obtained from 15 Asian countries or regions (not including Japan) were analyzed for the presence of alleles of 2 proteins. Three alleles of the Kunitz trypsin inhibitor or SBTI-A*$_2$ *designated as* Ti^a, Ti^b *and* Ti^c *are electrophoretically distinguishable from one another by their different Rf values of 0.79, 0.75 and 0.83, respectively. The* Sp_1 *seed protein or β-amylase has 2 alleles designated* Sp$_1^a$ *and* Sp$_1^b$ *which are electrophoretically distinguishable from one another by their Rf values 0.36 and 0.42.*

About 94 percent of the soybean accessions had the Ti^a *allele. Two accessions from Korea, P.I. 157440 and P.I. 196168, do not have the SBTI-A*$_2$ *protein* (ti). *Two accessions, one from Pakistan and the other from Korea, were identified as having the* Ti^c *allele. Only the Korean and central Indian soybean populations have a high frequency for the* Ti^b *allele. Within Korea, the soybeans from those districts that lie closest to Japan have a high frequency for the* Ti^b *allele whereas the soybeans from those districts that lie closest to China have a low frequency for the* Ti^b *allele. The* Ti^b *allele is not present in soybeans from the Philippines, Vietnam, Thailand, Malaysia, Burma, Nepal, Pakistan, and Afghanistan. Only 1 accession each from Taiwan and Indonesia have the* Ti^b *allele.*

The Sp$_1^a$ *allele is not present in soybeans from Taiwan, Vietnam, Thailand, Malaysia, Indonesia, Burma, Pakistan and Afghanistan. The highest frequency for the* Sp$_1^a$ *allele occurs in soybean germ plasm from northern India and Nepal.*

The soybeans from Asia (including Japan) were divided into 3 gene centers—primary, secondary, and tertiary—containing 7 germ plasm pools. Paths of dissemination of the soybean from China to the rest of Asia were developed based upon a combination of electrophoretic data and available historical, agronomic, and biogeographical literature.

In a previous paper, we (Hymowitz and Kaizuma, 1979) demonstrated that seed protein electrophoresis is a powerful technique by use of which the paths of dissemination of soybeans [*Glycine max* (L.) Merrill] to and within Japan may be elucidated. We used as markers the banding patterns of Sp$_1$, an uncharacterized seed protein (Larsen, 1967), and the soybean trypsin inhibitor A$_2$ (SBTI-A$_2$) (Rackis et al., 1962). The Sp$_1$ locus has 2 codominant alleles—$Sp_1{}^a$ and $Sp_1{}^b$ (Larsen and Caldwell, 1968). The $Sp_1{}^a$ seed protein band occurs at Rf 0.36 and the $Sp_1{}^b$ seed protein band occurs at Rf 0.42 (Fig. 1) (Rf is the mobility relative to a bromophenol blue dye front in a 10% polyacrylamide gel anodic system in which a tris-glycine buffer, pH 8.3, is used) (Orf and Hymowitz, 1976a). Recently,

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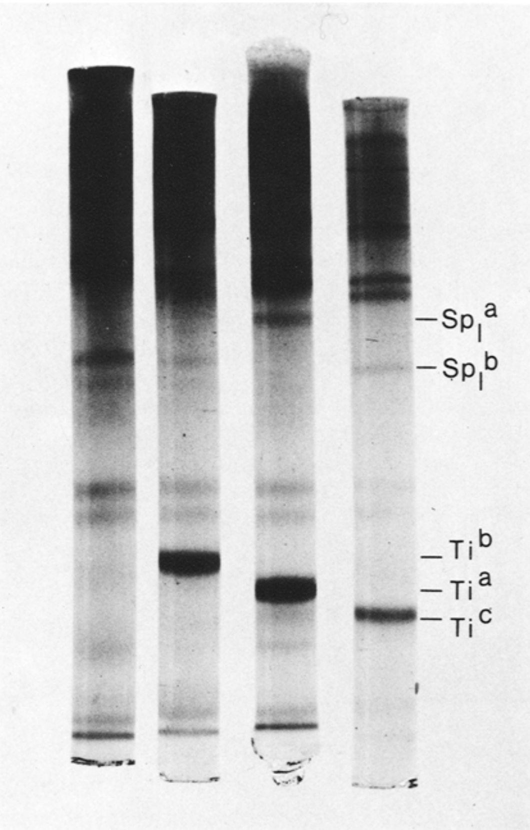

Fig. 1. Photograph of 10% polyacrylamide gel electrophoretic banding patterns of proteins in soybean seed extracts. Left to right: $tiSp_1^b$, $Ti^bSp_1^b$, $Ti^aSp_1^a$, and $Ti^cSp_1^b$.

Hildebrand and Hymowitz (1980) established that the Sp_1 seed protein is the enzyme β-amylase. Three types of SBTI-A_2 protein have been identified in soybean germ plasm. The types designated Ti^a, Ti^b and Ti^c are electrophoretically distinguishable from one another by their different Rf values of 0.79, 0.75 and 0.83, respectively (Fig. 1). The types are inherited as codominant alleles in a multiple allelic system at a single locus (Singh et al., 1969; Hymowitz and Hadley, 1972; Orf and Hymowitz, 1976b).

The objectives of this investigation were: 1) to determine the distribution of the electrophoretic types of SBTI-A_2 and Sp_1 seed proteins in soybean populations from 15 Asian countries or regions; and 2) to combine electrophoretic data with the findings of the available historical, agronomic and biogeographical literature to suggest possible paths of dissemination of the soybean from China to certain countries or regions within Asia.

MATERIALS AND METHODS

The 1,603 soybean accessions investigated herein were introduced into the United States (U.S.) as plant introductions (P.I.) over a period of time from the following 15 countries or regions in Asia: Korea (417); U.S.S.R. (16); northeast

TABLE 1. DISTRIBUTION OF ALLELES OF THE TI AND SP_1 LOCI IN SOYBEAN ACCESSIONS FROM 15 ASIAN COUNTRIES OR REGIONS.

Country or region	No. plant introductions tested	Plant introductions in each category					Plant introductions in each category		
		Ti^a	Ti^b	Ti^c	ti	% Ti^b	$Sp_1{}^a$	$Sp_1{}^b$	% $Sp_1{}^a$
Korea	417	366	48	1	2	11.5	83	334	19.9
U.S.S.R.	16	16	0	0	0	0	2	14	12.5
Northeast China	661	656	5	0	0	0.8	66	595	10.0
Central and south China	142	138	4	0	0	2.8	12	130	8.4
Taiwan	18	17	1	0	0	5.6	0	18	0.0
Philippines	20	20	0	0	0	0	1	19	5.0
Vietnam	5	5	0	0	0	0	0	5	0.0
Thailand	34	34	0	0	0	0	0	34	0.0
Malaysia	13	13	0	0	0	0	0	13	0.0
Indonesia	33	32	1	0	0	3.0	0	33	0.0
Burma	2	2	0	0	0	0.0	0	2	0.0
Nepal	14	14	0	0	0	0.0	5	9	35.7
India	219	184	35	0	0	16.0	52	167	23.7
Pakistan	4	3	0	1	0	0.0	0	4	0.0
Afghanistan	5	5	0	0	0	0.0	0	5	0.0

China (661), south and central China (142); Taiwan (18); Philippines (20); Indonesia (33); Vietnam (5); Thailand (34); Malaysia (13); Burma (2); Nepal (14); India (219); Pakistan (4); and Afghanistan (5).

The procedure for extraction of the 2 seed proteins, i.e., SBTI-A_2 and Sp_1 from raw mature soybeans, and for determination of the electrophoretic banding patterns of their alleles was published elsewhere (Hymowitz and Hadley, 1972; Orf and Hymowitz, 1976a). Alleles of both seed proteins were identified simultaneously on 10% polyacrylamide gels in an anodic system in which a tris-glycine buffer, pH 8.3, was used.

RESULTS

In North America, soybeans are classified into 12 maturity groups (MG) based upon day-length response. Soybeans grown in Canada and in the northern parts of the U.S. are classified as MG 00 and 0, respectively. In central U.S., soybeans belonging to MG II through V are grown. Soybeans adapted to the subtropical and tropical zones are classified in MG IX and X.

Of the soybean population from the Far East, that is Korea, U.S.S.R., northeast China, central and south China, and Taiwan, only the Korean soybeans had an appreciably high frequency of the Ti^b allele (12%) (Table 1). Most of the soybeans in the Far Eastern population belong to MG II through V. One plant introduction (P.I. 196172) from Korea had the Ti^c allele. The seed has a black seed coat and the $Sp_1{}^a$ allele. This accession is different from the 6 sources of Ti^c from Japan (P.I. 86064, 227557, 246367, 304217, 342004, 360844) which have yellow seed coats and the $Sp_1{}^b$ allele (Hymowitz and Kaizuma, 1979).

Two accessions from Korea, P.I. 157440 and P.I. 196168, do not have the SBTI-A_2 protein (Fig. 1). Plant Introduction 157440 was introduced into the U.S. in 1947 under the name *Kin du* (Russell, 1954). Possibly *Kin du* is the same as *Kum du* which in English means golden bean. Plant Introduction 196168 was

TABLE 2. DISTRIBUTION OF ALLELES OF THE TI LOCUS ACCORDING TO MATURITY GROUPS IN ACCESSIONS FROM DIFFERENT GEOGRAPHICAL DISTRICTS OF KOREA.

District	Ti allele	Maturity group							Subtotal	% Ti^b
		I	II	III	IV	V	VI	VII		
Hamkyeong	Ti^a	1	3	8	8	1	2		23	
	Ti^b	0	0	1	1	1	0		3	11.5
Pyeongan	Ti^a		1	7	16	5	2	1	32	
	Ti^b		0	1	1	1	0	0	3	8.6
Hwanghae	Ti^a				10	4	3	2	19	
	Ti^b				0	1	0	0	1	5.0
Kyeonggi	Ti^a	3	12	16	42	28	8	2	111	
	Ti^b	0	2	1	4	3	0	0	10	8.3
Kangwon	Ti^a				8	21	4	0	33	
	Ti^b				1	5	1	1	8	19.5
Choongcheong	Ti^a			2	3	34	17		56	
	Ti^b			0	1	5	3		9	13.8
Kyeongsang	*ti*					1			1	
	Ti^a			1	8	6	5		20	
	Ti^b			0	6	2	0		8	27.6
Cheonla	Ti^a			1	3	20	5		29	
	Ti^b			0	0	2	1		3	9.4
Cheju	Ti^a					1	1		2	0

introduced into the U.S. in 1951 under the name *Baik tae* (Russell, 1957). Attempts to locate the specific area from which the accessions came were not successful. Apparently the agricultural records of the Central Experiment Station, Suwon, were destroyed during the Korean War. Standard trypsin inhibitor assays conducted on extracts from sliced gels by the method of Singh et al. (1969) confirmed the reduction of trypsin inhibitor activity in the gel regions where Ti^a, Ti^b, and Ti^c bands are located. The symbol *ti* was assigned to the two accessions without the SBTI-A$_2$ protein (Orf and Hymowitz, 1979).

All 16 soybean accessions from the U.S.S.R. had the Ti^a allele, while only 5 out of 661 accessions from northeast China had the Ti^b allele (Table 1). Curiously, P.I. 54608-3 had the Ti^b allele but sublines P.I. 54608-1, P.I. 54608-2, and P.I. 54608-5 had the Ti^a allele. Similarly, P.I. 91108-2 had the Ti^b allele while subline P.I. 91108-1 had the Ti^a allele. The 3 other accessions (P.I. 91100, 91734, 92718-2) from northeast China containing the Ti^b allele were collected in Kungchuling, Kirin Province (Ryerson, 1932, 1933).

One plant introduction (P.I. 368037) from Taiwan had the Ti^b allele. The accession was introduced into the U.S. as 'Nungshih 64-91' from the Agricultural Research Institute, Taipei. The cultivar was selected from the cross between 'Nungshih H-11' and P.I. 200492 (Hyland, 1974). Plant Introduction 200492 is the Japanese cultivar 'Komata' which is adapted to Kyushu Island and has the Ti^b allele (Hymowitz and Kaizuma, 1979). Two other cultivars derived from the same cross (P.I. 368038, 368039) have the Ti^a allele. Therefore, the second parent of the cross, Nungshih H-11, should have the Ti^a allele. Most probably, all Tai-

TABLE 3. DISTRIBUTION OF ALLELES OF THE SP_1 LOCUS ACCORDING TO MATURITY GROUPS IN ACCESSIONS FROM DIFFERENT GEOGRAPHICAL DISTRICTS OF KOREA.

District	Allele	Maturity group							Subtotal	% Sp_1^a
		I	II	III	IV	V	VI	VII		
Hamkyeong	Sp_1^a	0	0	0	1	2	1		4	15.4
	Sp_1^b	1	3	9	8	0	1		22	
Pyeongan	Sp_1^a		0	1	4	1	1	0	7	20.0
	Sp_1^b		1	7	13	5	1	1	28	
Hwanghae	Sp_1^a				0	1	0	0	2	10.0
	Sp_1^b				10	4	3	1	18	
Kyeonggi	Sp_1^a	0	0	2	9	7	1	0	20	16.5
	Sp_1^b	3	13	15	37	24	7	2	101	
Kangwon	Sp_1^a				1	9	1	0	11	26.8
	Sp_1^b				8	17	4	1	30	
Choongcheong	Sp_1^a			0	0	8	10		18	27.7
	Sp_1^b			2	4	31	10		47	
Kyeongsang	Sp_1^a			1	4	2	1		8	27.6
	Sp_1^b			0	10	7	4		31	
Cheonla	Sp_1^a			0	0	1	0		1	3.1
	Sp_1^b			1	3	21	6		31	
Cheju	Sp_1^a					1	1		2	0.0

wanese soybean cultivars except those recently introduced from Japan carry the Ti^a allele.

Four accession from central and south China had the Ti^b allele. Three out of the 4 accessions (P.I. 62204, 103088, 123577) were introduced from central China, i.e., Shantung, Honan, and Hopeh Provinces, respectively. The collection site of the remaining accession (P.I. 55089) is unknown.

Twenty percent of the soybean population from Korea had Sp_1^a allele. This is about 4 times the percentage of Sp_1^a alleles found in Japanese soybean cultivars (Hymowitz and Kaizuma, 1979). Soybean populations from the U.S.S.R., northeast China, and central and south China had about the same percentage (10%) of the Sp_1^a allele. All soybeans from Taiwan have the Sp_1^b allele.

Of the 417 soybean introductions from Korea analyzed, we were able to identify the area of adaptation for 371 accessions. The soybean accessions from Kyeongsang, the region closest to Kyushu Island, Japan, had the highest frequency for Ti^b and Sp_1^a alleles (Table 2, 3, Fig. 2). The soybeans identified as adapted to Choongcheong and Kangwon Districts, the districts adjacent to Kyeongsang, had the next highest frequencies for the Ti^b and Sp_1^a alleles. Kyeonggi is the only district having soybeans classified in MG I through VII.

All 105 soybean accessions from southeast Asia, that is, the Philippines, Vietnam, Thailand, Malaysia and Indonesia, had the Ti^a allele (Table 1), with one exception. This was P.I. 181699 which was introduced into the U.S. as the cultivar 'Ringgit' from Surinam via Indonesia (Russell, 1956). The cultivar 'Ringgit' is a selection from the cross No. 27 by No. 69 (Departemen Pertanian, n.d.). No. 27 was selected from No. 16 which was introduced into Indonesia from Taiwan. No. 69 was collected at Tjirebon, Indonesia; however, its origin or pedigree is

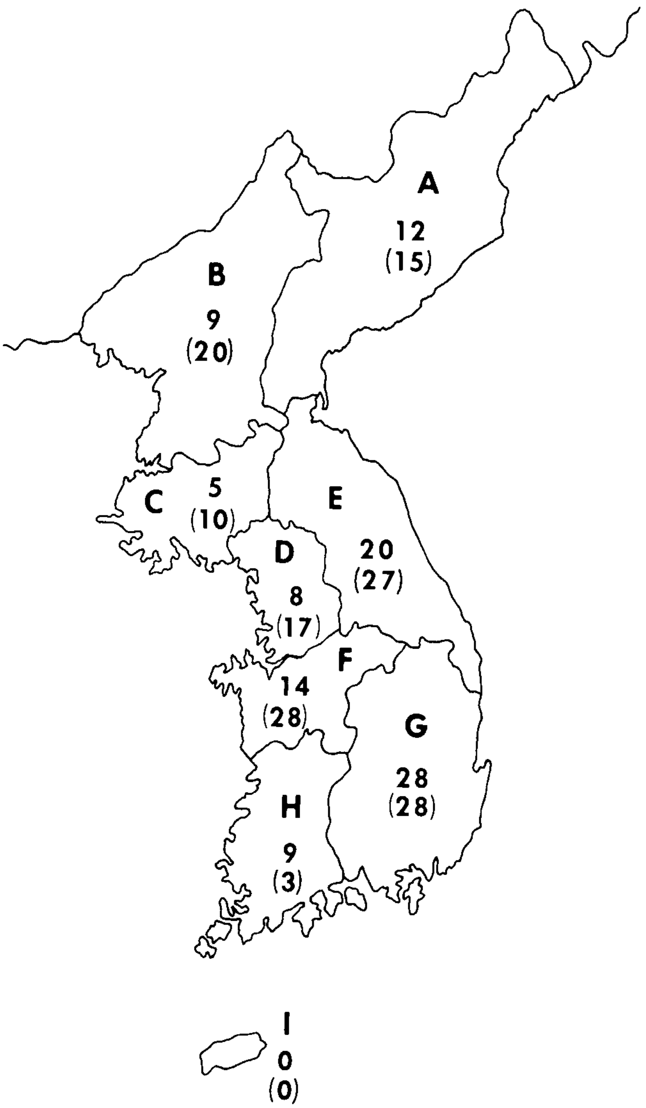

Fig. 2. Geographical distribution of alleles of the Ti and Sp_1 loci by districts within the Korean peninsula. A—Hamkyeong; B—Pyeongan; C—Hwanghae; D—Kyeonggi; E—Kangwon; F—Choongcheong; G—Kyeongsang; H—Cheonla; and I—Cheju. Figures in parentheses are % of Sp_1^a, the others % of Ti^b. The values are rounded out to the nearest whole number.

unknown. Most accessions in the southeast population belong to MG VII through X.

All 105 soybean accessions from southeast Asia except 1 had the Sp_1^a allele (Table 1). The only exception was P.I. 206258 which was introduced into the U.S. from the Philippines in 1953 under the cultivar name 'Headgreen' (Russell, 1958). Nothing else is known about the history of the plant introduction.

Of the 244 soybean accessions from southcentral Asia, that is, Burma, Nepal, India, Pakistan and Afghanistan, only the Indian population had the Ti^b allele (Table 1). Sixteen percent of the Indian soybean accessions had the Ti^b allele and

TABLE 4. DISTRIBUTION OF ALLELES OF THE TI LOCUS ACCORDING TO MATURITY GROUPS IN ACCESSIONS FROM DIFFERENT INDIAN STATES.

		Maturity group							
State	Allele	V	VI	VII	VIII	IX	X	Subtotal	% Ti^b
Assam	Ti^a	0	0	3	1	0	0	4	0.0
Uttar Pradesh	Ti^a	0	12	39	22	6	0	79	0.0
New Delhi	Ti^a	4	1	6	2	3	1	17	
	Ti^b	0	0	0	1	0	0	1	5.6
Punjab	Ti^a	0	0	3	0	0	1	4	0.0
Madhya Pradesh	Ti^a	0	0	0	34	3	43	80	
	Ti^b	0	0	0	2	0	32	34	29.8

most of these were classified in MG VII, VIII, and X (Table 4). One plant introduction (P.I. 205384) from Pakistan had the Ti^c allele. The accession was introduced into the U.S. in 1953 via the American Embassy, Karachi (Russell, 1958). It has a yellow seed coat, yellow hilum and erect habit of growth. In contrast, the other soybean introductions from Pakistan have a procumbent growth habit. Possibly, the accession was introduced into Pakistan from Japan.

The soybeans from Burma, Pakistan and Afghanistan only had the Sp_1^b allele (Table 1). On the other hand, the frequency of the Sp_1^a was very high in the soybean populations from Nepal (36%) and India (24%).

Within India, virtually all soybeans containing the Ti^b allele came from Madhya Pradesh and were classified in MG X (Table 4, Fig. 3). Morphologically, soybean seed from Madhya Pradesh can be divided into 2 groups, i.e., black oval and yellow round seed types. Within Madhya Pradesh, most of the soybeans with the Ti^b allele are in the black oval group and come from Seoni, Nagpur, and nearby areas (Table 5). On the other hand, the black oval soybeans from the Ujjain, Indore, Mhow, and Dewas areas have the Ti^a allele. The yellow round soybeans with the Ti^b allele only are found around the Jabalpur region.

Surprisingly, the frequency of the Sp_1^a allele was very high (62%) in the soybean population from Uttar Pradesh (Table 6). Except for 3 of 114 accessions from Madhya Pradesh having the Sp_1^a allele, the soybeans from the other states in India had the Sp_1^b allele. The soybeans from Uttar Pradesh introduced into the U.S. were collected in the Kumaon Hill region, just west of Nepal (Hymowitz, 1969). The accessions were classified into 4 categories based upon seed morphology (Table 7): a) black seed coat—flat seeded (56%); b) brown seed coat—flat seeded (22%); c) yellow seed coat—round seeded (10%); and d) chocolate seed coat—large round seeded (13%). Most soybeans with the Sp_1^a allele came from the black seed coat—flat seeded category.

DISCUSSION

1. Soybean germ plasm pools

By combining the results of our previous paper (Hymowitz and Kaizuma, 1979) which were concerned with the distribution of Ti and Sp_1 alleles within a population of Japanese soybean cultivars, with the data reported herein, we will at-

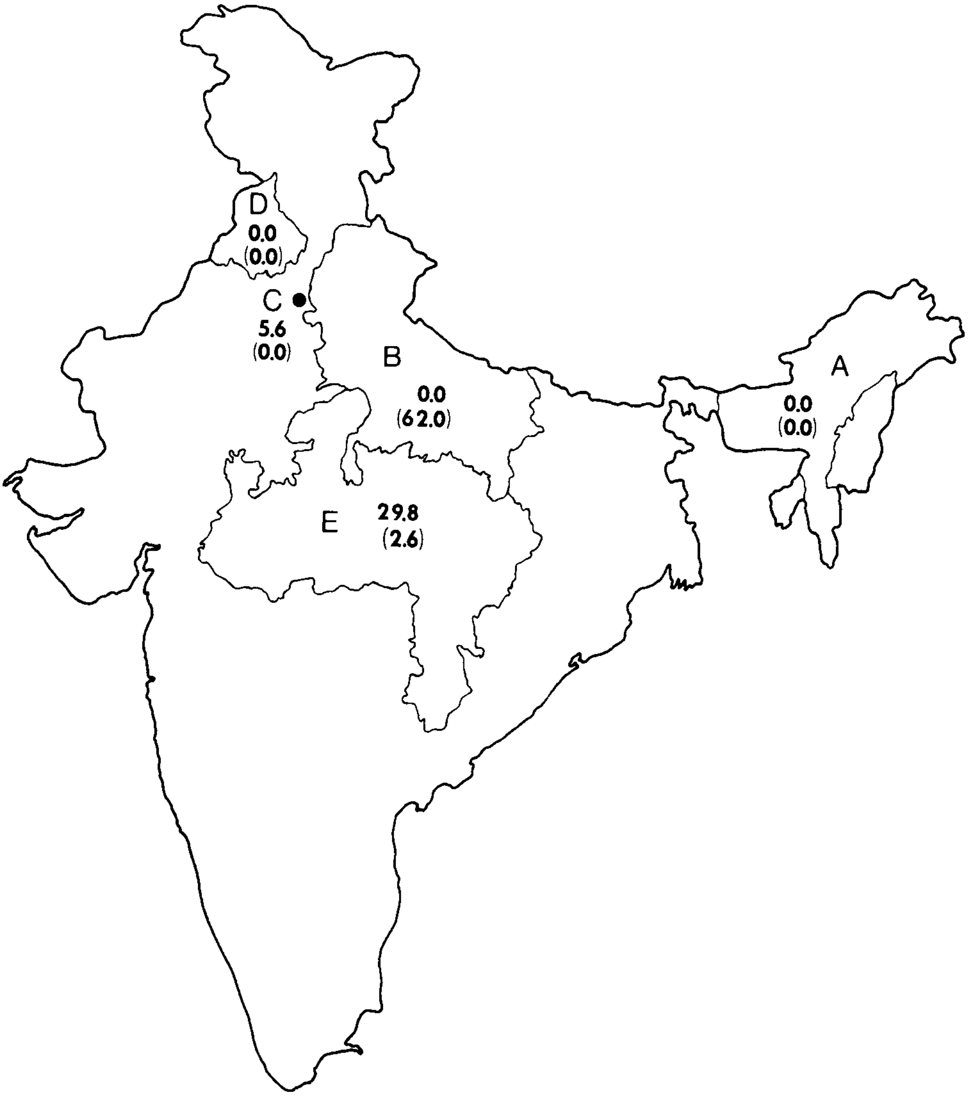

Fig. 3. Geographical distribution of alleles of the Ti and Sp_1 loci by states within India. A—Assam; B—Uttar Pradesh; C—New Delhi; D—Punjab; and E—Madhya Pradesh. Figures in parentheses are % of Sp_1^a, the others % of Ti^b.

tempt to group the soybeans grown in Asia into germ plasm pools and discuss the relationship among them. Also, we will suggest areas that need to be visited to collect additional soybean germ plasm.

At present we recognize 7 soybean pools (SGP) in Asia which are as follows: 1) northeast China and the U.S.S.R., 2) central and south China; 3) Korea; 4) Japan; 5) Taiwan and southeast Asia; 6) north India and Nepal; and 7) central India. The eastern half of north China where the soybean emerged as a domesticate around the 11th century B.C. is considered the most probable center for dissemination of germ plasm (Hymowitz, 1970).

The soybean population from northeast China and the U.S.S.R. (SGP1) pri-

Table 5. Distribution of alleles of the Ti locus according to seed morphology in soybean accessions from various districts within Madhya Pradesh, India.

		Seed morphology		
Districts	Ti allele	Black-oval	Yellow-round	Subtotal
Jabalpur	Ti^a	11	39	50
	Ti^b	6	5	11
Seoni, Nagpur, and nearby	Ti^a	1	0	1
	Ti^b	22	0	22
Ujjan, Indore, Mhow, and Dewas	Ti^a	29	0	29
	Ti^b	1	0	1
% Ti^b		44.4	11.4	

marily contains Ti^a (99%) and Sp_1^b (90%) (Table 8). The Ti^b allele is very rare in this germ plasm pool.

The soybean population from central and south China (SGP2) is very close to SGP1 with regards to the frequency of Ti^a (97%) and Sp_1^b (8%) (Table 8). The major differences between the populations are that the soybeans from SGP1 are adapted to long-day lengths, a shorter growing season and the cooler temperatures of the North Temperate Zone. In addition, the soybeans from SGP1 principally are grown as a field crop, whereas the soybeans in SGP2 are grown as a vegetable or market garden crop. Therefore, the soybeans in SGP1 tend to be more erect and not as viny as the soybeans in SGP2.

The soybean population from Korea (SGP3) differs from SGP1 and SGP2 in having higher frequencies of Ti^b (12%) and Sp_1^a (20%) (Table 8). Within the Korean soybean population, the soybeans from districts that lie closest to China have protein banding patterns and morphological characters that resemble SGP1. On the other hand, the soybeans from those districts that lie closest to Kyushu Island, Japan, have extremely high frequencies for Ti^b and Sp_1^a. Most probably the buildup of the Ti^b and Sp_1^a alleles in the Korean soybean population is due to the modern introduction of Japanese cultivars having the $Ti^bTi^bSp_1^aSp_1^a$ genotype.

Table 6. Distribution of alleles of the Sp_1 locus according to maturity group in accessions from different Indian states.

		Maturity group							
State	Sp_1 allele	V	VI	VII	VIII	IX	X	Subtotal	% Sp_1^a
Assam	Sp_1^b	0	0	3	1	0	0	4	0.0
Uttar Pradesh	Sp_1^a	0	6	21	19	3	0	49	62.0
	Sp_1^b	0	6	18	3	3	0	30	
New Delhi	Sp_1^b	4	1	6	3	3	1	18	0.0
Punjab	Sp_1^b	0	0	3	0	0	1	4	0.0
Madhya Pradesh	Sp_1^a	0	0	0	2	1	0	3	2.6
	Sp_1^b	0	0	0	34	2	75	111	

TABLE 7. DISTRIBUTION OF ALLELES OF THE SP_1 LOCUS ACCORDING TO SEED MORPHOLOGY IN SOYBEAN ACCESSIONS FROM NEPAL AND UTTAR PRADESH, INDIA.

		Seed morphology				
Area	Sp_1 allele	Black flat	Brown flat	Yellow round	Chocolate round	Subtotal
Nepal	Sp_1^a	5	0	0	0	5
	Sp_1^b	2	0	1	6	9
Uttar Pradesh	Sp_1^a	40	8	1	0	49
	Sp_1^b	5	12	7	6	30
% Sp_1^a		86.5	40.0	11.1	0.0	
% Subtotal		56	22	10	13	

The soybean population from Japan (SGP4) is distinct in having a high frequency of Ti^b (39%) and low frequency of Sp_1^a (6%) (Table 8). The population of present day Japanese soybean cultivars may have developed from the genetic intermingling of 2 sources (Hymowitz and Kaizuma, 1979). The first source may have been the early introduction of Korean germ plasm that carried Ti^a and Sp_1^b (including Sp_1^a) into Japan. The second source was the development of the summer season type cultivars adapted in Kyushu Island which are almost exclusively of the $Ti^bTi^bSp_1^bSp_1^b$ genotype and have the determinate growth habit (Nagata, 1960). Perhaps these summer season types were introduced directly from central China to southern Japan. The major difficulty with this assumption is that the Ti^b allele rarely is found in central China. On the other hand, summer season type soybeans are known to be grown in the Yangtze valley region (Shen, 1951). Nevertheless, the source of soybean germ plasm that developed into the Japanese summer season type cultivars remains to be determined.

The soybean population from Taiwan and southeast Asia (SGP5) is composed almost entirely of the $Ti^aSp_1^b$ alleles (Table 8). Unfortunately, the population from this region is poorly represented in the U.S. soybean germ plasm collection. Hence, seed collections need to be made in the region before any meaningful interpretations can be made concerning germ plasm pool relationships.

The soybean population from northern India and Nepal (SGP6) contains Ti^a (99%) and Sp_1^b (54.6%) (Table 8). The Ti^b allele is very rare in this germ plasm

TABLE 8. DISTRIBUTION OF ALLELES OF THE TI AND SP_1 LOCI IN ASIAN SOYBEAN GERM PLASM POOLS.

	Frequency distribution			
Region	Ti^a	Ti^b	Sp_1^a	Sp_1^b
1. Northeast China and U.S.S.R.	99.3	0.7	10.0	90.0
2. Central and south China	97.2	2.8	8.5	81.5
3. Korea	87.8	11.5	19.9	81.1
4. Japan[a]	59.5	39.2	5.5	94.5
5. Taiwan and southeast Asia	98.3	1.6	0.8	99.2
6. North India and Nepal	99.2	0.8	45.3	54.6
7. Central India	71.2	29.8	2.6	97.4

[a] Data taken from Hymowitz and Kaizuma, 1979

pool. Soybeans with black seed coats and procumbent growth habit, the prevailing soybean type in this region, overwhelmingly carry the $Sp_1{}^a$ allele (Table 7). Hymowitz (1969) found that the farmers of the Kumaon Hills of northern India prefer to grow black-seeded soybeans in the belief that these types were higher yielding and tastier than yellow-seeded types. Most probably, farmer preference for the black seed types resulted in the accumulation of the $Sp_1{}^a$ allele in the soybean germ plasm from northern India and Nepal. The soybean population from Burma, Pakistan and Afghanistan could not be evaluated since there were very few accessions from these countries in the U.S. soybean germ plasm collection.

The soybean population from central India (SGP7) is similar to the Japanese soybean germ plasm pool (SGP4) in having a high frequency of Ti^b (30%) and low frequency of $Sp_1{}^a$ (3%) (Table 8). However, unlike SGP4 where the Ti^b allele is distributed throughout Japan, in central India the Ti^b allele is concentrated in soybeans from Seoni, Nagpur, and nearby areas of Madhya Pradesh. These soybeans may have been introduced from Japan. On the other hand, the Ti^a allele is concentrated in soybeans from Jabalpur, Ujjan, Indore, Mhow, and Dewas areas of Madhya Pradesh. These soybeans may have been introduced from China and southeast Asia (Kale, 1937).

2. *Time and space*

The development of soybean germ plasm pools is connected intimately with the social, cultural, and political activities of man over periods of time and space. Soybean germ plasm pools were developed by human intervention in the natural selection process. "Fully domesticated plants," such as the soybean, "are artifacts produced by man as much as an arrowhead, a clay pot, or a stone ax" (Harlan, 1975).

The primary soybean germ plasm pool, or in Vavilov's terminology the primary gene center, is China (Vavilov, 1951). Surely the soybean reached northeast, central and south China as well as peninsular Korea by the first century A.D. (Kwon, 1972; Lo, 1961). The movement of the soybean within the primary gene center is associated with the development, consolidation of territories, and degeration of Chinese dynasties.

From the first century A.D. to the Age of Discovery, soybeans were introduced and land races were established in Japan, southeast Asia and southcentral Asia. These regions comprise the secondary gene center for soybeans. The movement of the soybean during this period of time was based upon the establishment of sea and land trading routes, for example, the silk road (Boulnois, 1966), the emigration of certain tribes from China (Prince Dhaninavat, 1961), and the rapid acceptance of the soybean as a staple food by certain cultures, for example, the Indonesians. Within the secondary gene center there are regions in which the soybean has been modified extensively by man, e.g., Japan, while in other areas the soybean has not been modified at all or at the most very slightly from the original introductions, e.g., northern India. Hence, Japan should be considered a very active microcenter and northern India a passive microcenter within the soybean secondary gene center.

Central India may be considered a recent or tertiary soybean gene center.

Fig. 4. Paths of dissemination of the soybean from China.

Another tertiary soybean gene center lies within the U.S., while incipient tertiary centers are being established in South America and Europe. In addition, the U.S. and Brazil are centers of soybean crop production.

The concept of primary, secondary and tertiary gene centers unifies time and space relationships with regard to the establishment of new genetic combinations within the species *Glycine max*. Another feature of this concept is that it establishes the foundation upon which future soybean germ plasm collection activities can be built.

3. *Paths of dissemination*

By combining seed protein banding data with available historical, agronomic and biogeographical literature, we have developed an hypothesis concerning the dissemination of the soybean from China to other countries or regions in Asia. Our ideas are based partly upon the pioneering studies of Nagata (1960) who primarily used physiological and morphological data to point out possible paths of dissemination of the soybean from China to the rest of the world.

In developing our hypothesis, we identified 2 major restraints concerning the movement of the soybean. One restraint is physiological and the other historical. Due to the fact that soybeans are day-length sensitive, they spread much easier between east and west than between north and south. Hence, in the dissemination process quantum latitudinal movement of soybeans was rare. Secondly, according to Ho (1975) the movement of the soybean out of its home area did not take place until the seventh century B.C. Therefore, the trial and error period for the adaptation, establishment and dissemination of the soybean from region to region within China, after the seventh century B.C., proceeded at a very rapid rate. As part of the dissemination process, the soybean was moved back and forth across geographical areas as a consequence of wars, famine, emigration, immigration, and trade.

The suggested paths of dissemination of the soybean from the eastern half of north China to other regions in Asia are shown in Fig. 4 and summarized below:

1. The soybeans grown in the U.S.S.R. (Asia) came from northeast China.
2. The soybeans grown in Korea are derived from 2 or 3 possible sources—northeast China, north China and the introduction of soybeans from Japan especially in the southern part of Korea.
3. The soybeans grown in Japan were derived from the intermingling of 2 possible sources of germ plasm—Korea and central China. Most probably the first points of contact were in Kyushu and then the soybean slowly moved northward to Hokkaido. In addition the soybean moved southward from Kyushu to the Ryukyu Islands where they came in contact with the soybeans moving northward from Taiwan.
4. The soybeans originally grown in Taiwan came from coastal China.
5. The germ plasm source for the soybeans grown in southeast Asia is central and south China.
6. The soybeans grown in the northern half of the Indo-Pakistan subcontinent came from central China.
7. The soybeans grown in central India were introduced from Japan, south China and southeast Asia.

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LITERATURE CITED

Boulnois, L. 1966. The Silk Road. (Trans. by D. Chamberlain.) Dutton, New York.

Departemen Pertanian. n.d. Silsilah Dan Varian, Berberapa Varitas Tanaman Pertanian, Lembaga Pusat Penelitian Pertanian, Bogor, Indonesia.

Harlan, J. R. 1975. Geographic patterns of variation in some cultivated plants. J. Heredity 66: 182–191.

Hildebrand, D. F., and T. Hymowitz. 1980. The Sp_1 locus in soybeans codes for β-amylase. Crop Sci. 20: 165–168.

Ho, P. T. 1975. The Cradle of the East. Chinese Univ. Hong Kong and Univ. Chicago Press, Hong Kong.

Hyland, H. L. 1974. Plant Inventory No. 179. USDA, Washington, D.C.

Hymowitz, T. 1969. The soybeans of the Kumaon Hills of India. Econ. Bot. 23: 50–54.

———. 1970. On the domestication of the soybean. Econ. Bot. 24: 408–421.

———, and H. H. Hadley. 1972. Inheritance of a trypsin inhibitor variant in seed protein of soybeans. Crop Sci. 12: 197–198.

———, and N. Kaizuma. 1979. Dissemination of soybeans (*Glycine max*): Seed protein electrophoresis profiles among Japanese cultivars. Econ. Bot. 33: 311–319.

Kale, F. S. 1937. Soya Bean. 2nd edit. F. Doctor., Baroda, India.

Kwon, S. H. 1972. History and the land races of Korean soybean. Sabrao Newslett. 4: 107–111.

Larsen, A. L. 1967. Electrophoretic differences in seed proteins among varieties of soybeans, *Glycine max* (L.) Merrill. Crop Sci. 7: 311–313.

———, and B. E. Caldwell. 1968. Inheritance of certain proteins in soybean seed. Crop Sci. 8: 474–476.

Lo, H. L. 1961. The southward expansion of Chinese civilization and the advancement of learning in Kwangtung Province. *In* Symposium on Historical, Archaeological and Linguistic Studies on Southern China, South-East Asia and the Hong Kong Region. F. S. Drake, general editor. Univ. Hong Kong Press, Hong Kong.

Nagata, T. 1960. Studies on the differentiation of soybeans in Japan and the world. Mem. Hyogo Univ. Agric. 3 (Agron. Series No. 4): 63–102.

Orf, J. H., and T. Hymowitz. 1976a. The gene symbols Sp_1^a and Sp_1^b assigned to Larsen and Caldwell's seed protein bands A and B. Soybean Genet. Newslett. 3: 27–28.

———, and ———. 1976b. Inheritance of a second trypsin inhibitor variant in seed protein of soybeans. Crop Sci. 17: 811–813.

———, and ———. 1979. Inheritance of the absence of the Kunitz trypsin inhibitor in seed protein of soybeans. Crop Sci. 19: 107–109.

Prince Dhaninavat. 1961. Thai migrations. *In* Symposium on Historical, Archaeological and Linguistic Studies on Southern China, South-East Asia and the Hong Kong Region. F. S. Drake, general editor. Univ. Hong Kong Press, Hong Kong.

Rackis, J. J., H. A. Sasame, R. K. Mann, R. L. Anderson, and A. K. Smith. 1962. Soybean trypsin inhibitors: Isolation, purification and physical properties. Arch. Biochem. Biophys. 98: 471–478.

Russell, P. G. 1954. Plant Inventory No. 155. USDA, Washington, D.C.

———. 1956. Plant Inventory No. 157. USDA, Washington, D.C.

———. 1957. Plant Inventory No. 159. USDA, Washington, D.C.

———. 1958. Plant Inventory No. 161. USDA, Washington, D.C.

Ryerson, K. A. 1932. Plant Inventory No. 106. USDA, Washington, D.C.

———. 1933. Plant Inventory No. 107. USDA, Washington, D.C.

Shen, T. H. 1951. Soybeans. *In* Agricultural Resources of China. Cornell Univ. Press, Ithaca, New York.

Singh, L., C. M. Wilson, and H. H. Hadley. 1969. Genetic differences in soybean trypsin inhibitors separated by disc electrophoresis. Crop Sci. 9: 489–491.

Vavilov, N. I. 1951. The Origin, Variation, Immunity, and Breeding of Cultivated Plants. (Trans. by K.S. Chester.) Chronica Botanica, Waltham, Massachusetts. Reprinted by Ronald Press, New York.