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The genetic diversity of cultivated soybean grown in China

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Abstract Cultivated soybean (*Glycine max*) is an economically important crop that is grown for its oil and protein products. A better knowledge of its genetic diversity will be valuable for the utilization, conservation, and management of germplasm collections. Using the database of the National Germplasm Evaluation Program of China (NGEPC), we studied the geographical distribution of accessions, the genetic diversity of 15 qualitative and quantitative characters, and the genetic diversity centers of cultivated soybean in China using variation in these 15 traits and genetic diversity indexes (Shannon index). Cultivated soybean is widely distributed throughout China. As an indication of its distribution, a line can be roughly drawn from the Daxinganling mountains in northeastern China to the Qingzang plateaus in southwestern China based on the abundance of accessions and locations of the collections. Of the 22,637 known accessions in China, the 20,570 collected over a vast area between latitudes 18° and 53°N and longitudes 80° and 136°E were used in this study. The Shannon indexes of various morphological traits were calculated. Cultivated soybean accessions were found to exhibit a higher genetic diversity in the area between 34°–41°N and 110°–115°E. On the basis of the geographical distribution of a number of accessions, and their genetic diversity, one genetic diversity center—downstream of the Yellow River Valley—is proposed. Based on these results and on Vavilov's theory on crop origins, one possible diversity center was proposed.

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Introduction

Cultivated soybean [*Glycine max* (L.) Merrill] belongs to family *Leguminosae*, subfamily *Papilionoideae*, genus *Glycine*. It has a very broad distribution in China and is cultivated at broadly diverse geographical locations and under many different growing conditions, which may have contributed to the its large genetic diversity.

Early studies on genetic diversity of cultivated and wild soybean focused on isoenzyme polymorphism and phenotypic trait analysis. Chiang (1986) studied polymorphism in 72 accessions of wild soybean (*G. soja*) from Japan and the Republic of Koreausing 43 isoenzyme loci and found that the average genetic variation among the accessions was 67.4%. Gorman (1984) examined genetic diversity in 400 cultivars of *G. max* and more than 100 accessions of *G. soja* that originated from different geographical distributions using 15 enzymes and concluded that Northeastern China had slightly higher levels of diversity for *G. max*, while Korea had significantly higher diversity levels for *G. soja*. Some studies, however, showed that the genetic diversity of domesticated soybean is low. On the basis of an analysis in which they used nine enzymes to study 383 accessions of cultivated soybeans from Japan and 28 accessions from Korea, Abe and Ohara (1992) suggested that Korea may be a center of genetic diversity for cultivated soybean. Yu and Kiang (1993) demonstrated that South Korea might be one of the major soybean gene centers in a study of 17 enzymes and one non-enzyme protein from annual wild soybeans that came from six natural populations. Kiang et al. (1992) studied four natural populations of *G. soja* by analyzing

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15 enzymes and one non-enzyme protein and showed that genetic diversity was 0.07 and 0.3 between- and within-populations, respectively, and that the coefficient of differentiation among populations was 0.2. Vaughan et al. (1995) analyzed the genetic diversity of ten annual wild soybean populations collected within a 20-km radius of Tsukuba using randomly amplified polymorphic DNA (RAPD) analysis and found a relatively high degree of local variation for *G. soja* on the Kanto plain and a mosaic of variation rather than small-scale clonal variation. Xu (1995) reported that northeastern China and the Yellow River Valley of China are the two soybean genetic diversity centers based on an analysis of the geographical distribution of seed characters of cultivated soybean in China, while Zhou (1998) concluded that soybean dissemination was from west to east, centering downstream of the Yellow River Valley.

A comprehensive collection of cultivated soybean germplasms was initiated in late 1970s in China. More than 22,637 accessions have been collected, characterized, evaluated, and documented with the support from the National Soybean Germplasm Evaluation Project of China (NGEPC). A database was established on the basis of the results of this project. In order gain an understanding of the overall genetic diversity, distribution of genetic diversity, and genetic diversity centers of cultivated soybean, we have analyzed data obtained from the NGEPC database using several parameters. Our goals were to provide a reference for other studies on the genetic diversity of cultivated soybean as well as to improve the utilization, conservation and management of this crop.

Materials and methods

The data used in this study came from the NGEPC database, which was established by characterizing and evaluating 22,637 accessions of cultivated soybean collected from 25 provinces of China. Of these, only those landraces that best represent the genetic diversity pattern were used—i.e., varieties and breeding lines developed by modern breeding programs during the last 50 years were eliminated. Thus, 2,067 accessions were excluded from this study. The remaining 20,570 accessions of landraces that varied with respect to ecological regions were selected, characterized, and evaluated in experimental plots (three 2-m-long rows) in the original ecological regions of the accession. Ecological regions refer to the original ecological area where that particular accession of cultivated soybean grows normally, as defined for wild soybean (Dong et al. 2001). Protein and oil contents were analyzed at the Jilin Academy of Agricultural Sciences, Gongzhuling, Jilin, Nanjing Agricultural University, Najing, Jiangsu, and the Oil Crops Institute of Chinese Academy of Agricultural Sciences, Wuhan, Hubei, using standardized methods. Several groups in China carried out the investigation for more than 20 years.

Fifteen traits, including ten qualitative traits—sowing type, stem type, leaf shape, pubescent color, flower color, growth habit, seed shape, seed-coat color, cotyledon color, hilum color—and five quantitative traits—growth period, plant height, 100-seed weight, seed protein content and seed oil content—were used to calculate the genetic diversity index. The quantitative traits were classified into various intervals: 10 days was one class for growth period; 2 g was one class for 100-seed weight; 10 cm was one class for plant height; 1% was one class for seed protein content and seed oil content. The distribution areas of cultivated soybean in China were divided into 119 sections based on latitude and longitude. Each section covered two degrees of latitude and three degrees of longitude. Those sections with fewer that 30 accessions were excluded from this study. Sowing type was defined by the time of sowing. The stem type was defined as erect, half-erect, or twining. The growth habit was defined as indeterminate, half-determinate, or determinate. The growth period was defined as the length of time from sowing to seed maturity.

The genetic diversity index of each of these 15 traits was calculated with DPS software (Data Processing System; Tang 1997) for all 119 sections using the following two formulas.

The Shannon genetic diversity index H′ (Tang 1997) was calculated as:

$$H' = -\sum_{i=1}^{s} P_i \ln(P_i)$$

where S is the number of types in a section, i is the ith type in a section and P_i is the proportion of ith type in a section.

The average genetic diversity index of 15 traits was calculated for every section in Table 4 using the following formulas:

The Shannon genetic diversity index H was calculated as:

$$H = \frac{1}{M}\sum_{j=1}^{m} H'$$

where $H'$is the Shannon genetic diversity index of one trait in one section, m is the amount of Shannon genetic diversity index in one section, and j is the jth Shannon genetic diversity index in a section.

Results

Geographical distribution of cultivated soybean in China

Soybean has been cultivated as an important oil and food crop in China since ancient times. Its wide distribution is affected by landscape, soil, and climate conditions. Based on the number of accessions and place of origin of the accessions, we were able to roughly draw a line from the Daxinganling mountains in northeastern China to the Qingzang plateaus in southwestern China (Fig. 1). While most of the accessions were collected from the southeastern part of the line, some originated from between the Bayankela mountains and the Qilian Mountain, and others were found south of the Aertai mountains and north of the Tianshan mountains, in northwestern China. In southeastern China, cultivated soybean accessions were found in the area north of the Ximalaya mountains and south of the Sandis mountains. Thus, the 20,570 accessions studied were collected over a wide range of latitude (18°–53°N) and longitude (80°–136°E).

More than 44.9% of the accessions were distributed in two areas—the Yellow River valley and the Changjiang River valley (Fig. 1). Those distributed in the middle part of the Yellow River valley and downstream of it were concentrated in eight sections that encompassed latitude 34°–41°N and longitude 107°–121°E. There were 4,466 accessions that accounted for 21.7% of the total number of accessions in this area. The second area with a large number of collections was located downstream of the Changjiang River valley. This region encompassed latitude 26°–31°N and longitude 104°–121°E, and 4,782

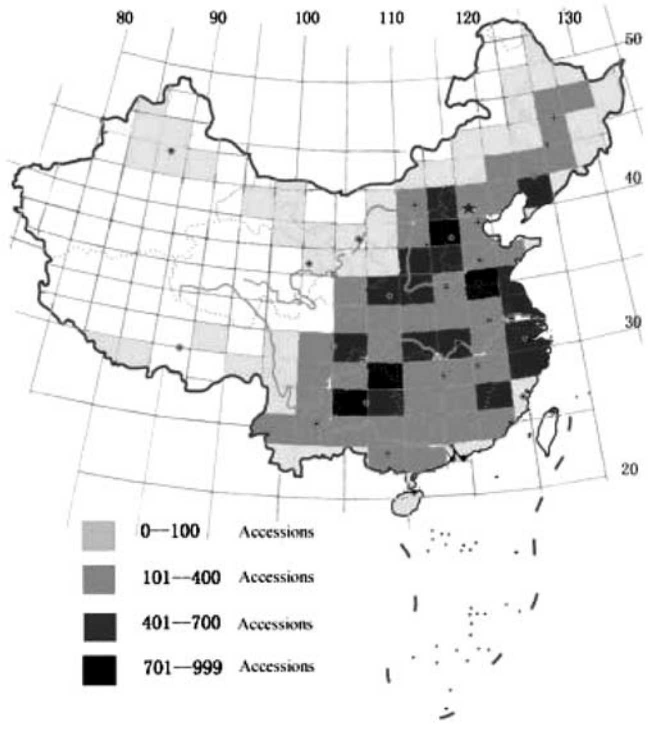

Fig. 1 Geographical distribution of cultivated soybean collected in China

accessions (accounting for 23.2% of the total number) were concentrated in eight sections.

The genetic diversity of cultivated soybeans

The genetic diversity of cultivated soybean was detected by analyzing variation in 15 traits (ten qualitative and five quantitative). The results are shown in Table 1. Seed-coat color showed the highest variation among the ten qualitative traits followed by the hilum color, seed shape, growth habit, leaf shape, sowing type, stem type, flower color, pubescent color, and cotyledon color (in decreasing order). The five quantitative traits revealed a greater genetic diversity. The Shannon indexes of growth period, plant height, 100-seed weight, seed protein content, and seed oil content were 2.91, 3.56, 3.39, 3.47, and 2.61, respectively. Plant height showed the highest genetic diversity followed by the seed protein content, 100-seed weight, growth period, and seed oil content.

Table 1 The genetic diversity index of cultivated soybean grown in China

Traits	Number of accessions	Shannon (H) index
Sowing type	20,570	1.18
Stem type	20,491	1.18
Leaf shape	19,890	1.34
Pubescent color	20,472	1.03
Flower color	20,543	1.07
Growth habit	20,544	1.45
Seed shape	20,541	1.76
Seed coat color	20,480	2.58
Hilum color	14,112	1.98
Cotyledon color	20,546	0.20
Growth period	20,552	2.91
Plant height	19,775	3.56
100-Seed weight	20,516	3.39
Protein content	19,099	3.47
Oil content	18,840	2.61

The genetic diversity of the ten qualitative traits is summarized in Table 2. The most frequent sowing types were spring and summer, which accounted for 45% and 52%, respectively. The typical phenotype of the stem was erect (65%), followed by semi-erect (28%), and only a few twining. The percentage of accessions with leaf shapes of ellipse-round, ovate-round, and lanceolate-round was 52%, 42%, 3% and 3%, respectively. The pubescent color was brown (55%) or gray (45%) for most accessions. The percentage of accessions having white, purple and light-purple flowers was 45%, 54% and 1%, respectively. The main growth habit was determinate (53%), while 29% were indeterminate and18% were semi-determinate. The percentage of accessions with flat-ellipse, flat-round, long-ellipse, nephroid-round, and ellipse seed shape were 14%, 7%, 10%, 4%, 14% and 62%, respectively. Most accessions had a yellow seed coat (47%); others were black (13%), green (10%), light-yellow (7%), light-green (6%), brown (5%) or another color (12%). The main hilum colors were brown (45%) and black (25%), while a small number of accessions were brown-black (14%), light-brown (13%) or other colors (3%). The diversity for cotyledon color was low, with 97% of the accessions having yellow cotyledons and the remainder, other colors.

Genetic diversity for the five quantitative traits is summarized in Table 3. Most of the cultivated soybean accessions studied here matured within 91–150 days (90.8%). Only a few accessions matured in fewer than 90 days or more than 150 days. Accessions with a plant height ranging between 30.1 cm and 100.0 cm accounted for 80% of the total. The majority of accessions (84.3%) had a 100-seed weight in the range of 8.1–22.0 g, whereas 5.9% ranged in 100-seed weight from 0 to 8.0 g and 9.8% were heavier than 22.0 g. With respect to percentage of protein content, 93.8% of the accessions had a protein content of 39.1–48.0%. The lowest protein content was 31.0%. Those accessions with protein contents lower than 39.0% or higher than 49.1% accounted for 3.2% and 3.0% of the total number, respectively. Most of the accessions (92.4%) had an oil content of between 15.1% and 20.0%; 7.6% had an oil content of less than 15.1% or more than 20.0%.

Geographical distribution of genetic diversity

The genetic diversity index based on ten quality characters and five quantitative ones of the cultivated soybean accessions collected from each of the 119 sections described above was calculated on the Shannon index. The Shannon index varied greatly from one section to another (Table 4). One region where the cultivated soybean accessions exhibited higher genetic diversity was located between 34–41°N and 110–115°E. Shannon index values of 1.95–2.04 appeared in six sections of this region. The genetic diversity of southern and southeastern accessions was much lower.

Discussion

Cultivated soybean is a self-pollinated species which is very widely dispersed throughout China. Most accessions grow in eastern China where the climate is warm and moist. A northeast-to-southwest dispersal line, which extends from the Daxinganling mountains to the Qingzang plateaus, can be drawn (Fig. 1). Almost all of the cultivated soybean accessions are to be found at the eastern end of this line. Most aggregate at two centers of diversity; only a few are located in west of the line. Distribution was also affected by landscape, soil, and other factors. This distribution pattern is very similar to that of annual wild soybean (Dong et al. 2001).

The data used in this investigation were obtained from the National Database of soybeans, which includes all of the 20,570 accessions collected in China. The genetic diversity of the different traits analyzed and the geographical distribution of genetic diversity varied. Fifteen traits—ten qualitative and five quantitative—were used to calculate the genetic diversity index, which ranged from large to small in the order: plant height, protein content, 100-seed weight, growth period, oil content, seed-coat color, hilum color, seed shape, growth habit, leaf shape, sowing type, stem type, flower color, pubescent color, and cotyledon color. In this respect, the genetic diversity index is different from that for annual wild soybean. For the latter, the genetic diversity index from large to small is in the order: 100-seed weight, growth period, oil content, leaf shape, protein content, seed color, hilum color, stem type, bloom color, pubescent color, flower color and cotyledon. The geographical distribution of the accessions and genetic diversity indexes calculated using the Shannon formula showed that a genetic diversity center with the highest genetic diversity of cultivated soybean was in the area of 34–39°N and 110–115°E, which is very similar to that of the annual wild soybean.

Several hypotheses have been proposed with respect to the origin of the cultivated soybean: the Northeast (Fukuda 1933), the North (Hymowitz 1970), the Yangtze River valley and the area to the south (Wang 1973),the middle of the Yellow River valley and downstream of it (Wang 1985; Xu 1986, 1993), and the multi-center theory (Lu 1978; Dong 1998). The evidence used by these authors included cultivation history, literature records, archaeological data, geographical distribution of accessions, and genetic diversity for wild soybean and cultivated soybean (Zhou 1998).

Table 2 The genetic diversity of soybean quality traits

Sowing type	Number of accessions	Seed coat color	Number of accessions	Cotyledon color	Number of accessions	Hilum color	Number of accessions	Seed shape	Number of accessions	Stem habit	Number of accessions	Growth habit	Number of accessions	Pubescence color	Number of accessions	Flower color	Number of accessions	Leaf shape	Number of accessions
Spring	9,314	More color	176	Light green	2	Light brown	1,765	Flat, ellipse	2,776	Half erect	5,663	Without limit	5,860	Gray	9,147	White	9,224	Long, ellipse	9
Summer	1,0538	Dark yellow	577	Yellow	19,898	Brown	6,459	Flat, round	833	Vine	1,408	Half-limit	3,791	Gray-brown	43	Light purple	222	Ovat, round	8,257
Autumn	718	Dark green	107	Green	646	Brown-black	1,973	Long, ellipse	1,500	Erect	1,3420	Limit	10,893	No hilum	41	Purple	11,097	Lanceolate	675
		Light yellow	1,376			Black	3,480	Ovate, round	4					Brown	11,241			Ellipse, round	10,332
		Black-brown	141			Yellow	274	Nephroid shape	582									Round	617
		Light brown	140			Blue	49	Round	2,027										
		Light green	1,187			No color	112	Ellipse	12,819										
		Brown	988																
		Black	2,863																
		Tiger-spotted color	364																
		Yellow	9,893																
		Green	2,145																
		Dark brown	171																
		Dark black	201																
		Purple-red	151																

Table 3 The genetic diversity of soybean quantity traits

Growth period (days)	Number of accessions	100-Seed weight (g)	Number of accessions	Plant height (cm)	Number of accessions	Protein content (%)	Number of accessions	Oil content (%)	Number of accessions
70–80	34	0–2.0	1	0–10.0	3	30.1–31.0	1	10.0–11.0	1
81–90	542	2.1–4.0	19	10.1–20.0	47	31.1–32.0	1	11.1–12.0	4
91–100	2,157	4.1–6.0	256	20.1–30.0	468	32.1–33.0	2	12.1–13.0	24
101–110	3,265	6.1–8.0	935	30.1–40.0	1,472	33.1–34.0	5	13.1–14.0	112
111-120	4,124	8.1–10.0	2,225	40.1–50.0	2,728	34.1–35.0	10	14.1–15.0	502
121–130	4,158	10.1–12.0	3,192	50.1–60.0	3,168	35.1–36.0	46	15.1–16.0	2,080
131–140	3132	12.1–14.0	3,443	60.1–70.0	2,842	36.1–37.0	104	16.1–17.0	4,338
141–150	1842	14.1–16.0	2,950	70.1–80.0	2,245	37.1–38.0	219	17.1–18.0	5,131
151–160	892	16.1–18.0	2,413	80.1–90.0	1,890	38.1–39.0	216	18.1–19.0	3,839
161–170	281	18.1–20.0	1,843	90.1–100.0	1,450	39.1–40.0	596	19.1–20.0	2,020
171–180	72	20.1–22.0	1,226	100.1–110.0	957	40.1–41.0	976	20.1–21.0	472
181–190	35	22.1–24.0	763	110.1–120.0	757	41.1–42.0	1,476	21.1–22.0	221
191–200	3	24.1–26.0	434	120.1–130.0	528	42.1–43.0	1,950	22.1–23.0	79
201–210	12	26.1–28.0	292	130.1–140.0	387	43.1–44.0	2,504	23.1–24.0	16
211–220	3	28.1–30.0	168	140.1–150.0	250	44.1–45.0	2,967	24.1–25.0	1
		30.1–32.0	118	150.1–160.0	204	45.1–46.0	2,843		
		32.1–34.0	99	160.1–170.0	126	46.1–47.0	2,202		
		34.1–36.0	45	170.1–180.0	87	47.1–48.0	1,564		
		36.1–38.0	36	180.1–190.0	54	48.1–49.0	840		
		38.1–40.0	27	190.1–200.0	41	49.1–50.0	405		
		40.1–42.0	17	200.1–210.0	24	50.1–51.0	138		
		42.1–44.0	11	210.1–220.0	13	51.1–52.0	26		
		44.1–46.0	3	220.1–230.0	10	52.1–53.0	8		
				230.1–240.0	3				
				240.1–250.0	7				
				250.1–260.0	6				
				260.1–270.0	2				
				270.1–280.0	2				
				280.1–290.0	4				

Table 4 Geographical distribution of the cultivated soybean genetic diversity index (Shannon index)

Latitude (°N)	Longitude (°E)																		
	80–82	83–85	86–88	89–91	92–94	95–97	98–100	101–103	104–106	107–109	110–112	113–115	116–118	119–121	122–124	125–127	128–130	131–133	134–136
53–52																			
51–50																			
49–48																1.39			
47–46															1.66	1.61	1.59	1.54	
45–44														1.76	1.65	1.75	1.56	1.43	
43–42													1.84	1.96	1.74	1.84	1.82		
41–40											1.63	1.95**	1.95	1.86	1.68				
39–38									1.44	1.64	1.98**	2.04**	1.89	1.84	1.40				
37–36									1.68	1.84	1.95**	2.01**	1.71	1.77	1.79				
35–34									1.85	1.90	2.02**	1.89	1.82	1.78					
33–32									1.66	1.68	1.63	1.86	1.94	1.82	1.66				
31–30								1.58	1.69	1.71	1.60	1.74	1.67	1.86	1.80				
29–28								1.75	1.67	1.68	1.52	1.76	1.58	1.82					
27–26							1.56	1.75	1.75	1.75	1.55	1.59		1.55					
25–24							1.62	1.68	1.81	1.58	1.61	1.63	1.81	1.50					
23–22								1.57	1.51	1.52	1.38	1.37	1.17						
21–20											1.32								
19–18																			

**Significance at $P \leq 0.05$

The geographical distribution of the accessions and the genetic diversity data provide the most valuable information for determining the origin of cultivated soybean. That only one genetic diversity center for cultivated soybean exists in China can be proposed on the basis of our results. There were 4,466 accessions in the area downstream of the Yellow River valley. This represents 21.7% of the total number of accessions in the area, with the highest genetic diversity index being 2.04. This value is significantly higher than any found elsewhere. These data provide compelling evidence that the downstream area of the Yellow River valley is the genetic diversity center of cultivated soybean in China. This conclusion is in agreement with the hypothesis proposed by Wang (1985). The second area with a high percentage of collections was downstream of the Changjiang River valley, between latitudes 26°-31°N and longitudes 104°-121°E. Eight sections contained 4,782 accessions (23.2% of the total). Nevertheless, in contrast to the downstream region of the Yellow River valley, where the highest genetic diversity index was 2.04, the highest genetic diversity index of the downstream region of the Changjiang River valley was only 1.81. This implies that the latter is probably not a center of genetic diversity. Our results also indicate that there is no correlation between number of accessions and genetic diversity.

Our proposal on the possible formation of genetic diversity centers for soybean is in accordance with that of Dong et al. (2001) and Vavilov's (1973) theory, in which each plant species has a special genetic diversity center that was the original center of distribution. The species subsequently dispersed from this center to other larger areas, and the geographical distribution was successive. The mode of formation is as follows. The wild soybean genetic diversity center in northeastern China was the primary original center from which wild soybean spread out in other directions. To the east, southeast and north, this primary center of wild soybean contributed to distribution in Korea, Japan, and the most eastern parts of Russia. To the west and south, it supported the formation of the secondary centers and the tertiary wild soybean centers in China. In one of these secondary wild soybean centers, the Yellow River valley, wild soybean was utilized and domesticated by humans. The cultivated soybean primary original center was thus formed in the Yellow River valley, and other cultivated soybean accessions found throughout the world derived from this center.

The database used in this study was established on the basis of characterized and evaluated phenotypic traits of cultivated soybean, and the analyzed data include morphological and biochemical characters. Although phenotypic traits represent the combined action of genetic and environmental factors, large numbers of accessions can normalize the influence of environment. Thus, although molecular analysis could supplement and reinforce our analysis on genetic diversity and elucidation of plant species origin, it can not substitute for morphological analysis. Therefore, for genetic diversity studies on large numbers of accessions, phenotypic traits are usually analyzed (Dong 1998; Dong et al. 2001; Perry and McIntosh 1991; Xu 1993) and, thereafter, a subset of the materials can be used for molecular analysis (Doldi et al. 1997; Keim et al. 1989; Skorupska et al. 1993; Zhou 1998). In this respect, the results of the present study provide a solid framework for our future efforts to conduct an integrated study, involving molecular analysis, on a subset of accessions of cultivated soybean in China.

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