

Korean Wild Soybeans

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Domesticated crops suffer from major genetic bottlenecks while wild relatives retain higher genomic diversity. Wild soybean (*Glycine soja* Sieb. & Zucc.) is the presumed ancestor of cultivated soybean (*Glycine max* [L.] Merr.), and is an important genetic resource for soybean improvement. Among the East Asian habitats of wild soybean (China, Japan, Korea, and Northeastern Russia), the Korean peninsula is of great importance based on archaeological records, domestication history, and higher diversity of wild soybeans in the region. The collection and conservation of these wild soybean germplasms should be put on high priority. Chung's Wild Legume Germplasm Collection maintains more than 10,000 legume accessions with an intensive and prioritized wild soybean germplasm collection (>6000 accessions) guided by the international code of conduct for plant germplasm collection and transfer. The center holds a library of unique wild soybean germplasms collected from East Asian wild habitats including the Korean mainland and nearby islands. The collection has revealed interesting and useful morphological, biochemical, and genetic diversity. This resource could be utilized efficiently in ongoing soybean improvement programs across the globe.

Keywords: *Glycine soja* ; Korean wild soybean ; in situ conservation ; germplasm conservation ; wild legumes ; genetic diversity ; crop wild relatives

1. Introduction

Soybean (*Glycine max* [L.] Merr.) is an economically important legume worldwide with diverse applications in food, feed, and biofuel industries ^{[1][2]}. Increasing per capita food consumption and limited land and water resources, coupled with a growing population and changing dietary habits, are projected to escalate the pressure on global food supplies ^{[3][4]}. It is estimated that food consumption is growing faster than production, particularly in Asia, which will lead to grain and soybean deficits. This deficit in food supply must be addressed through a global effort. Additionally, global climate change, together with the above-mentioned factors, has outpaced the forecasted crop yields, while at the same time having a negative effect on the state of diversity in the farmer's field ^[5]. To alleviate negative effects due to climate change on crops and ecosystems and to increase crop yields, the resilience and sustainability of current agricultural systems have become pressing issues ^[6]. The development of new soybean varieties and cropping systems with the ability to adapt to a changing environment and new socio-economic conditions is crucial for yield enhancement. While the genetic improvement of crops plays an important role, the genetic base of major crops is narrow, due to genetic bottlenecks and human selection ^[7]. Therefore, it is essential to investigate novel sources of genetic diversity and to expand gene pools by exploiting crop wild relatives (CWRs) ^{[8][9][10]}. The search for novel genetic diversity will result in an increased demand for novel breeding material from the world's gene banks.

The wild (*Glycine soja* Sieb. & Zucc.) and cultivated (*G. max*) soybeans are both annual plants belonging to one of the two subgenera of the genus *Glycine* and are distinguished from other wild perennial *Glycine* species. It has been shown that wild soybean can be used in the genetic improvement of cultivated soybean ^[11].

The taxonomic and phylogenetic knowledge based on the concept of gene pools provides important information for wild x cultivated soybean hybridization. The primary gene pool (GP-1) includes *G. max* and its wild progenitor, *G. soja*, resulting in the production of vigorous hybrids, normal meiotic chromosome pairing, and fertile offspring. As far as secondary (GP-2) and tertiary (GP-3) gene pools of *G. max* are concerned, all the 26 perennial species are included in GP-3, while no *Glycine* species has been found in GP-2 ^[11]. Some researchers have previously attempted to hybridize *G. max* with five GP-3 member species, but their success was limited ^[12]. Among GP-3 members, only three perennial species (*Glycine argyrea*, *Glycine canescens*, and *Glycine tomentella*) have been successfully hybridized with cultivated soybean. The F1 hybrids were either sterile or could not develop beyond the amphidiploid stage ^[13]. Further information could be found in the paper by Singh (^[14] and references therein).

Wild soybean accessions, the wild relatives of cultivated soybean, are mainly found in East Asia ^[15]. They harbor abundant and unique gene/allele resources, due to their widespread distributions in complex geographic topographies

with diverse microclimates ^[16]. Cultivated soybeans have lower adaptive potential to climatic changes and reduced genetic diversity when compared to wild soybeans ^{[3][17]}. More than half of the genetic variations in soybean were lost due to habitat fragmentation and genetic bottlenecks ^[18]. Therefore, wild soybeans are important genetic resources for gaining a deeper understanding of the genetic diversity, genomic variations, and environmental adaptations of soybean ^{[10][19]}.

Preliminary assessments of germplasm conservation in many parts of the world have revealed substantial gaps, which should be filled by expanding the collection of wild soybean germplasm resources from the main distribution areas ^{[20][21]}. Such efforts are being adopted by many countries and germplasm centers around the globe, including Korea, which is one of the main distribution areas of wild soybeans.

2. Distribution and Conservation of Wild Soybean in Korea

2.1. Geographical Distribution of Wild Soybean in Korea

Wild soybean grows in moist habitats from 0 to 2650 MASL (meters above sea level), spanning subtropical and subarctic zones (between 24° N and 53° N latitude) ^[16], and is restricted to East Asia. Occasionally, it can also be found in dry and salt-affected areas. In the Korean peninsula, wild soybeans are distributed throughout the mainland as well as on nearby islands. They can be found growing almost everywhere in Korea, including farmlands, roadsides, and river banks, and from mountain tops to deep valley bottoms. There are over 3000 islands off the coast of the Korean peninsula and nearly 400 are inhabited. A few of these inhabited islands have already been surveyed for wild soybean distribution ^[22].

2.2. Archaeological Records and Background

Despite the importance of soybean to the world economy, the history of soybean has been mostly restricted to phylogenetics and historical documents mentioning the domestication of soybean in East Asia. *G. soja* is the only wild member of the subgenus *Soja* native to the East Asian countries mentioned above ^{[15][23]}. Many reports suggest that soybean was first domesticated in China around 5000 years ago, but this statement is still controversial ^[24]. However, it is generally agreed that the ancient geographical region comprising China, Japan, and Korea (the CJK region) harbored one of the three pioneering societies to domesticate and cultivate this important legume ^[25]. In an attempt to rectify the domestication history of soybean, Lee et al. ^[26] pointed out that the differences between domesticated plants and their wild relatives/progenitors are not always clear, and therefore it is sometimes impossible to discern between wild and domesticated soybean in archaeological specimens which are not always well preserved. Despite their different appearances and growing conditions, cultivated soybean plants can cross-breed with wild soybean plants and produce fertile F₁ hybrids, making it quite challenging to understand and interpret the archaeological seed records ^[11]. There is still an ongoing debate over the archaeological records in southeastern Korea and China (^[26] and references therein).

Figure 1 shows the archaeological sites in Korea. The Nam River valley contains multiple sites, e.g., Oun 1, Okbang 1, 2, 4, 6, 9, Sangchon B, and Pyeonggeodong, dating back to the Chulmun (8000~3500 CAL. B.P.), Mumun (~3500-2000 CAL. B.P.), and Three Kingdom Periods (2000~1200 CAL. B.P.). Other sites include Daundong in Ulsan and Dongsamdong shell midden in Busan. A detailed examination and comparison of archaeological seed records showed that the morphology of the seeds in the Korean soybean archaeological records resembles that of smaller domesticated varieties in more modern times ^{[26][27]} because there is a range of seed morphologies among soybean cultivars with ovate seeds. However, the report is based on archaeobotanical seed size measurements. A genomic approach could be more rewarding in terms of species identification. Another report ^[27] did not mention wild soybean in Korean flotation samples at all. Due to a higher number of landraces, as well as the presence of wild soybean in the area, the authors were not able to link any archaeological findings to a particular species (most probably *G. max*) or a soybean landrace. However, these studies confirm that the Korean peninsula is a region of great importance for early soybean domestication.



Figure 1. Map showing the archaeological sites of soybeans in Korea. Bullets under each city show the names of the archaeological sites while the dates in brackets show the carbon dating information on charred soybean seeds. If there is no carbon dating of the soybean samples, then the reported chronological year is given [26][28].

3. Collection of Wild Soybean Germplasm in Korea

The second report on the state of the world's plant genetic resources for food and agriculture stated that public awareness of the importance of crop diversity and the use of CWRs is growing in both developing and developed countries. A 20% increase in the number of global accessions conserved *ex-situ* has been observed since 1996. Major *ex-situ* soybean collections are reported to be present in China, Russia, Ukraine, and the United States of America, with a total of 229,944 accessions. However, 23% of the total collection is held by only two organizations, i.e., the Institute of Crop Germplasm Resources at The Chinese Academy of Agricultural Sciences (ICGR-CAAS) and SOY (USA) [5]. Among these soybean germplasm collections, the majority of the wild accessions are held by organizations in China, the USA, Korea, Japan, and Russia (Table 1). According to the second report on plant genetic resources, there has been a significant increase in nationally designated protected areas since 1928. However, the report did not include priority genetic reserve locations for wild soybean relatives. The most likely reason for the omission is that this report based its information on another report by Maxted and Kell which focused only on 12 major food crops, excluding soybean [29]. A recent report on global conservation priorities classified soybean wild relatives as medium priority [21]. This classification is based on the consideration given to the situations of all food crops. Therefore, a classification system based solely on the rankings within legumes or oilseeds could help advocate for a higher priority for conserving wild soybean.

Table 1. Global soybean germplasm collections by the institute.

Instcode	Institute	No. of Accessions	%	WS	LR	BL	AC	OT
CHN001	ICGR-CAAS	32,021	14	21				79
USA033	SOY	21,075	9	10	80	5	4	1
KOR011	RDAGB-GRD	17,644	8	<1	45	5	1	50
TWN001	AVRDC	15,314	7		<1		<1	100
BRA014	CNPSO	11,800	5					100
JPN003	NIAS	11,473	5	5	33	21		40
RUS001	VIR	6439	3		9	40	41	11
IND016	AICRP-Soybean	4022	2	<1				100
CIV005	IDESSA	3727	2					100
TWN006	TARI	2745	1					100

[illegible]

Wild soybean, being able to hybridize with cultivated soybean, becomes an extended source of diversity to broaden the gene pool [11]. The utilization of wild soybean is expected to increase as a result of ongoing improvements in the information on the species' genome and genetic diversity, and advances in breeding tools [21]. This expectation is based on the assumption that the wild accessions will be readily available for research and soybean breeding, which requires their conservation as germplasms in gene banks. Urbanization, road construction, deforestation, intensive agriculture, climate change, and soil erosion are all threatening wild soybean in its natural habitats. Since wild soybean is mainly distributed in the CJK region, greater conservation efforts should be made by the local authorities in charge of biological conservation in these countries. In East Asia, major wild soybean germplasm centers in these three countries include the Chinese Crop Germplasm Information System, in China, the National Institute of Agrobiological Sciences Genebank and the Legume Base, in Japan, and the National Agrobiodiversity Center and the Chung's Wild Legume Germplasm Collection (CWLGC) (described in this work), in Korea. In Korea, there are >6000 accessions in CWLGC and 3229 accessions at the National Agrobiodiversity Center.

Soybean breeding in Korea started in the early 1900s and, since then, more than 178 varieties/cultivars have been registered. Major soybean breeding work has been completed in the past three decades, particularly after the establishment of the National Agrobiodiversity Center in 1987 [30]. Cultivated soybean has received greater attention regarding germplasm collection when compared to wild soybean. This is quite logical because most of the germplasm centers were busy collecting, breeding, and documenting major crops during their early establishment. However, the recent trend of utilizing CWRs in breeding and preliminary assessments of the comprehensiveness of the conservation of CWRs in gene banks have reported substantial gaps [21]. A report by FAO on the state of diversity indicated that the number of accessions of CWRs has substantially increased since 1996. However, they are still under-represented [5]. Considering this scenario, as well as the limited number of wild soybean accessions collected from Korea, large-scale individual as well as collective efforts are needed to enhance wild soybean collections. Although the information is available about the conservation status of this species in Korea, the lack of information and access to wild soybean in North Korea is a big limitation. [Table 2](#) details the conservation efforts by the CWLGC in Korea, placing its major focus on wild soybean collection.

Table 2. List of wild legume germplasm accessions at Chung's Wild Legume Germplasm Collection.

Species	No. of Accessions
<i>Glycine max</i> (L.) Merr	600
<i>Glycine soja</i>	6232
<i>Amphicarpaea edgeworthii</i>	1300
<i>Vigna vexillata</i>	810
<i>Rhynchosia volubilis</i>	225
<i>Phaseolus nipponensis</i>	700
Other wild legumes	
<i>Dunbaria villosa</i> (Thunb.) Makino	
<i>Vigna umbellata</i> (Thumb.) Ohwi & Ohashi	700
<i>Vigna angularis</i> var. <i>nipponensis</i> (ohwi) ohwi & ohashi	
<i>Vigna angularis</i> (Willd.) Ohwi & Ohashi	
Total	10,567

3.1. Chung's Wild Legume Germplasm Collection

Founded by Professor Gyuhwa Chung in 1983 and located in the Yeosu campus of the Chonnam National University, the CWLGC now possesses the most comprehensive collection of wild soybean in Korea. Guided by the international code of conduct for plant germplasm collecting and transfer (<http://www.fao.org/3/x5586e/x5586e0k.htm>), the main focus of this center is on the direct collection, acquisition, conservation, evaluation, characterization, documentation, and distribution of wild legume germplasms. CWLGC followed the guidelines of the National Agrobiodiversity Center, Genebank of Rural Development Administration, Korea, and became a local sub-bank in 2007. The list of species and the respective number of accessions available at CWLGC is shown in [Table 2](#). The wild legume accessions were directly collected by the CWLGC team from Korea, Japan, China, and Russia, or acquired from Australia, India, Taiwan, and Zambia. The wild soybean collections include 5050 accessions originating from Korea.

3.2. In situ Conservation of *G. soja* at CWLGC

In the last 30 years, a major effort at CWLGC has been dedicated to wild soybean germplasm collection, acquisition, development, and characterization. *In situ* wild soybean germplasm propagation and characterization at CWLGC is done throughout the year and is ongoing. About 500-1000 accessions/year are propagated and characterized at two outdoor planting and propagation sites: Yeosu (Chonnam Province) and Jinju (Gyeongsangnam Province) (Figure 2).



Figure 2. Wild soybean germplasm. (a) Wild soybean germplasm distribution and collection. (b) Different stages of *in situ* propagation and characterization at CWLGC.

One important feature of CWLGC is that it holds wild soybean accessions collected from ~130 islands along the coast of the Korean peninsula. These accessions could be used to address questions related to the adaptations to microclimatic conditions in geographically isolated areas. With increasing land exploitations by humans and decreasing wild soybean habitats in Korea, CWLGC is focusing on extensive surveys and germplasm collections. The germplasm characterization performed at CWLGC has revealed interesting and useful morphological and biochemical variations. Examples of the morphological diversity in leaf shape and root architecture are shown in Figure 3.

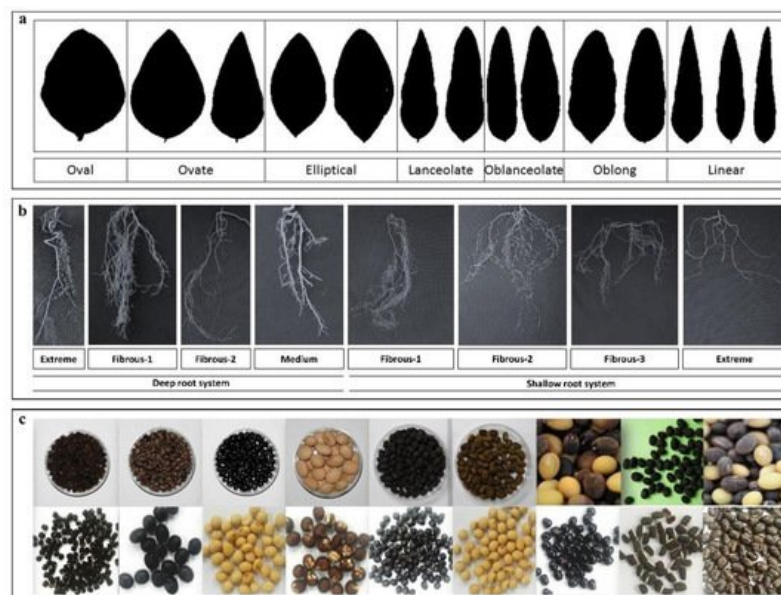


Figure 3. Morphological diversity of soybeans in the CWLGC collection. (a) Leaf shape variations in *G. soja* accessions. (b) Root structure variations in *G. soja* accessions. (c) Samples of the legume seed collection at CWLGC.

The germplasm collection at CWLGC exhibits high genetic and morphological variations [22][26]. For instance, microsatellite marker-based genetic diversity has been investigated in the wild soybean at CWLGC that originated from the southern islands of Korea. Five hundred and thirty wild soybean accessions originating from China, Japan, and Korea

included in the CWLGC have also been utilized for the successful identification of *GmSALT3* haplotypes and the development of molecular markers related to salt tolerance [31].

Moreover, the CWLGC germplasms were studied for their natural variations in saponin contents and were used to help identify different group-A acetylsaponin-deficient mutants [32][33][34][35]. The wild soybean soyasaponin mutants from CWLGC have been used to identify and characterize the genes involved in the saponin biosynthesis pathway, e.g., *Sg-1* locus (CWS2133), *sg-5* locus (CWS5095), and *Sg-6* locus [36][34][37][38][39]. In addition to saponins, wild soybean accessions at the CWLGC have also been screened for the presence of Kunitz trypsin inhibitor polymorphism, alpha-linolenic acid concentration, and soyisoflavone profile diversity [40][41][42][43]. Furthermore, the germplasms have been used to functionally characterize two seed-specific flavonoid glycosyltransferases and a β -amyrin synthase gene [39][44].

Another interesting discovery using the CWLGC collection is the identification of the *W1* locus and the analysis of four new alleles at this locus associated with flower color in soybean [45]. A complete range of flower color has been observed in the CWLGC wild soybean collection and different flower color variants have been studied to help understand the genetic and molecular basis of flower color e.g., the pinkish-white flowers of accession CW13133 [46] (Figure 4).

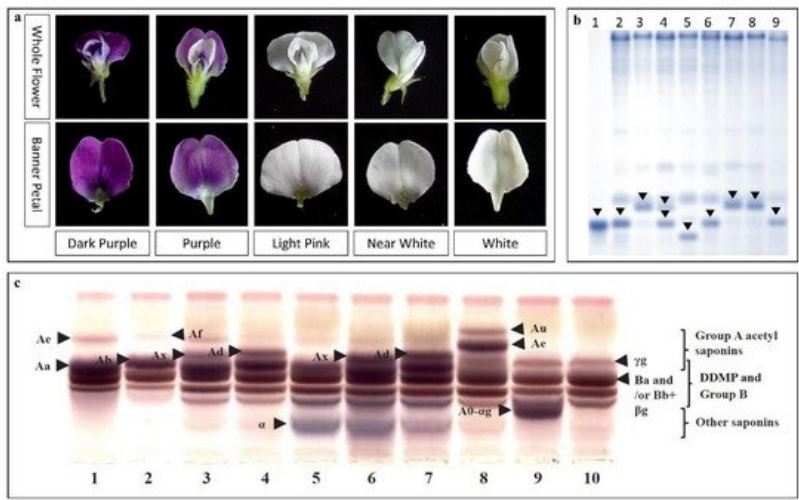


Figure 4. Demonstrations of the diversity in the CWLGC. (a) Flower color variations [45]. (b) Using Kunitz trypsin inhibitor, different KTI forms were detected in Korean *G. soja* accessions by non-denaturing PAGE. Lanes 1–9 are: Tia protein standard (Sigma), Tia, Tib, Tia/Tib, Tibi7-1, Tia, Tibi5, Tib, and Tia, respectively [40]. (c) Comparison of saponin composition phenotypes in seed hypocotyls in the Korean *G. soja* collection by thin-layer chromatography (TLC). Lanes 1–7 are the common phenotypes: Aa, Ab, AaBc, AbBc, Aa+a, AaBc+a, and AbBc+a types, respectively. Lanes 8, 9, and 10 are mutant phenotypes: AuAeBc (CWS0115), A0Bc+ag (CWS2133), and A0Bc-S (CWS5095) types, respectively [32].

Being a major source of plant oils and proteins, the demand for soybean is escalating. Soybean yield has been significantly increased since the 1960s and is forecasted to reach 3.0 metric tonnes per hectare in 2028. It was observed that soybean yields in East Asian countries have been stagnant for some time. To meet the projected demands, it is important to consider breeding soybean cultivars with higher yield potentials and better tolerance to biotic and abiotic stresses. Wild soybean has been shown to provide an important resource for soybean breeding in terms of nutrition, biotic and abiotic stress tolerance, and yield-related traits (Table 3).

Table 3. List of genes and QTLs found to be associated with specific traits using either wild soybean or a cross between wild and cultivated soybeans.

Trait	Gene/QTL	Chromosome/Locus Group	Source (accession)	Reference
Yield Related Traits				
Flower color	Dihydroflavonol-4-reductase 4 (<i>w4-s1</i> allele) (DFR)	B2 (Ch 14)	WS (CW13133)	[46]
	Flavonoid 3'5'-hydroxylase (F3'5'H) and DFR	B2 (Ch 14)	WS (CW12700 and CW13381)	[45]
	DFR2 (<i>w4-s1</i>)	B2 (Ch 14)	WS (CW13133) × CS (IT182932)	[47]

Trait	Gene/QTL	Chromosome/Locus Group	Source (accession)	Reference
Oil and local breeding related traits	QTLs	3, 8, 13, 17,	WS × CS	[17]
Shoot fresh weight	QTLs	6, 15, 19	WS (PI 483463) × CS (Hutcheson)	[48]
Biological nitrogen fixation related traits	QTLs	7,8,12,17,18	WS (W05) × CS (C08)	[49]
Small seed, Yellow seed color, Soy sprout			WS (PI135624)	[50]
High yield		B2 (U26)	WS (PI 407305)	[51]
Yield, height and maturity	QTLs	C2, E, K and M	WS × CS	[52]
Seed yield, 100-seed weight, seed filling period, maturity, height, lodging	QTLs	A1, J, N, H, F, L	WS × CS	[53]
	QTLs	Multiple	CS (NN86-4) × WS (PI342618B)	[54]
	QTLs	1, 2, 6, 8, 13, 14, 17, 20	CS (Williams 82) × WS (PI 366121)	[55]
Biotic Stress Tolerance				
	<i>Rhg1, Rhg4</i> locus and QTLs	G, A2, B1	CS (Magellan) × WS (PI 404198A)	[56]
Soybean cyst nematode resistance	Glyma18g196200, Glyma18g077900, Glyma18g078000, Glyma18g106800, Glyma18g107000, Glyma18g107100 <i>Glyma18g106800, Glyma18g064100</i>	Ch18	WS	[57]
	QTLs (cqSCN-006, cqSCN-007)	I, J, K, O	WS (PI 468916, 464925B)	[58][59]
	Markers (A245_1 and Satt598)	15, 18	WS (PI 468916)	[60]
Resistance to southern root knot nematode			WS	[61]
Foxglove aphid resistance (<i>Aulacorthum solani</i>)	<i>Raso2</i>	7	CS (Williams 82) × CS (PI 366121)	[62]
	<i>Rag3c</i> and <i>Rag6</i>	8, 16	WS (85-32)	[63]
Aphid resistance (<i>Aphis glycines</i>)	QTLs	8, 16,	WS WS (PI 518282)	[64] [65]
Sclerotinia stem rot	QTLs	3, 8, 20	WS × CS	[66][67][68]
Resistance to Mung bean yellow mosaic India virus		Ch 8 and 14	WS (PI 393551)	[69]
Resistance to <i>Phthophthora soja</i>	QTLs	J, I, G (Ch 16, 18, 20)	WS (PI 407162) × CS (V71-370)	[70]
Abiotic Stress Tolerance				
			WS (N23232 BB52)	[71]
	Allele (<i>Ncl</i> locus)		WS (PI 483463)	[72]
Salt tolerance	QTLs	D2 (Ch 17)	WS (JWS156-1)	[73]
	QTLs	3	WS	[74]
	RLKs CaMs, JA/SA Signaling genes, MAPKs, WRKYs			[67][68]

Trait	Gene/QTL	Chromosome/Locus Group	Source (accession)	Reference
Tolerance to herbicide metribuzin			WS (PI 245331, PI 163453)	[75]
Root traits	QTLs	8, 12	WS (PI 326582A) × CS (PI 552538)	[76]
Root architecture	<i>Glyma15g42220, Glyma06g46210, Glyma06g45910, Glyma06g45920, Glyma07g32480</i>	6, 7, 15	WS (PI 407162) × CS (V71-370)	[77]
Alkalinity tolerance	ALMT, LEA, ABC transporter, GLR, NRT/POT and SLAH genes	Multiple	WS (N24852)	[78]
Drought tolerance	<i>GsWRKY20</i>			[79]
Nutrition				
Seed protein content	Marker pA-245	C	CS (A81-356022) × WS (PI 468916)	[80]
Seed saturated fatty acid contents	SNPs			
	<i>Glyma14g121400, Glyma16g068500</i>	14, 16	GS	[81]
Seed unsaturated fatty acids	<i>Glyma16g014000, Glyma07g112100</i>	7, 16		
Linolenic acid	QTLs	Multiple	WS × CS	[82]
Pearl Japanese fermented product (Natto)			WS	[61]
Protein, oil, palmitic acid, stearic acid, oleic acid, linoleic acid, lenolenic acid	QTLs	2, 7, 14, 16	WS	[81]
	<i>Sg-1</i>	Ch 7	WS	[65][83]
Saponin A	<i>Sg-5 (Glyma15g39090)</i>	Ch 15	WS × CS	[84][69]
	<i>Glyma15g39090</i>	Ch 15	WS	[36]
Seed antioxidant, phenolics, and flavonoids	<i>GmMATE1,2,4</i>	Ch 18,19	WS (W05) × CS (C08)	[85]

So far, only a few characteristics of wild soybean contained in the CWLGC have been explored. Phenotypic screening towards biotic and abiotic resistance under diverse climate conditions would reveal more relevant results to meet current needs. In this regard, the CWLGC *G. soja* collection has been initially explored for the diversity in root system architecture (Figure 3b). Regarding biotic stress tolerance, no screening has yet been done, leaving the opportunity open for researchers interested in disease and insect pest resistance. Soybean cyst nematode, soybean mosaic virus, bacterial blight and wilt, and a whole list of fungal diseases could be the initial screening targets. Furthermore, early emergence and vigor traits in wild soybean have not yet been examined. Wild soybean seeds can survive in extreme climatic conditions in their native habitats, making them a good target for studying dormancy as well as longevity traits. These traits are important in terms of soybean improvement as well as *ex-situ* germplasm conservation. By analyzing the morphological variations in leaf shape in the CWLGC *G. soja* accessions, we can potentially unveil the process of domestication of this trait and enhance our understanding of the regulation of photosynthesis. A comparative and in-depth genome resequencing of *G. soja* chloroplast genomes could enhance our understanding of the domestication process of *G. max*, as well as of the traits regulated by the plastid genome. Up until now, only limited knowledge of these aspects is available [86][87].

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