



REVIEW

Recent genetic research on Japanese soybeans in response to the escalation of food use worldwide

Kyuya Harada · Akito Kaga 

Received: 18 September 2018 / Accepted: 7 March 2019
© Springer Nature B.V. 2019

Abstract Soybeans are an important ingredient in traditional foods of Japan, such as tofu, natto, miso, boiled beans, soy sauce, and edamame. Japanese soybeans have been subjected to selection for use as a food for many years and have different characteristics from those of oilseed soybeans. Useful genomic resources for studying Japanese soybeans, such as high-density linkage maps, chromosome segment substitution lines, genome sequences, high-density mutant libraries, and germplasm sets, have been developed. Because traditional foods made from Japanese soybeans are highly influenced by seed characteristics, comprehensive studies have been conducted on seed quality and composition using natural and mutant genetic resources, and several new varieties with special seed characteristics have been successfully developed. Recent advances in the genetic characterization of agriculturally important

traits in Japanese soybeans, including plant type, physiological characteristics, and resistance to biotic and abiotic stresses will contribute to marker-assisted selection of new soybean varieties.

Keywords Japanese soybean · Genetic resource · Quantitative trait locus · Marker-assisted selection · Map-based cloning · Linkage map

Introduction

In Japan, soybeans [*Glycine max* (L.) Merr.] are used to prepare traditional foods, such as tofu, natto (fermented beans), miso (fermented bean pastes), nimame (boiled beans), soy sauce, and edamame (vegetable beans), as well as for new foods, including soy-milk-derived and separated protein-based foods. The soybean is the most important legume worldwide because of the high content of high-quality protein in its seeds and its production of oil for food and industrial materials. In East Asia, rice is a staple food and soybeans are combined with rice as a nutritional supplement in food. Recently, numerous physiologically functional constituents have been identified in soybean seeds and food-grade soybeans or soy foods are now considered very important dietary items for human health (Zhang et al. 2010).

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10681-019-2396-3>) contains supplementary material, which is available to authorized users.

K. Harada
Department of Biotechnology, Graduate School of
Engineering, Osaka University, Suita, Osaka 565-0871,
Japan

A. Kaga (✉)
Institute of Crop Science, NARO, 2-1-2 Kannondai,
Tsukuba, Ibaraki 305-8602, Japan
e-mail: kaga@affrc.go.jp

The demand for soybeans for food use in Japan is approximately 1,000,000 tons per year and almost all soybeans produced in Japan are used for food, accounting for only 20–25% of their use as food. Seed characteristics for food processing are important targets in soybean breeding, and comprehensive studies have been conducted on seed quality, including seed constituents. The most serious problems in soybean production in Japan have been its unstable and low yield, particularly because soybeans are being grown in paddy fields instead of rice. Information regarding flood stress and disease resistance genes, especially under lowland conditions, together with tolerance genes to other stresses, as well as improvement in plant types and physiological characteristics to achieve higher yield, are useful for breeding both in Japan and worldwide.

In this review, we report on recent progress in the development of genomic and genetic resources for Japanese soybeans and genetic studies of agriculturally important traits, including seed quality, plant type, physiological characteristics, resistance to diseases and pests, and resistance to abiotic stresses. The information in this review will be useful for food-type soybean development and for worldwide food security.

Genetic and genomic resources

Germplasm

Wild soybeans [*Glycine soja* Sieb. and Zucc. or *Glycine max* (L.) Merr. subsp. *soja* (Sieb. & Zucc.) Ohashi] are distributed in disturbed habitats in Japan, eastern China, the Korean peninsula, and the Far East of Russia and are thought to be the direct ancestor of domesticated soybeans (Hymowitz 1970). Wild soybeans are important sources of novel alleles for broadening the genetic base of cultivated soybeans because soybean diversity has been greatly reduced by the genetic bottleneck of domestication (Lam et al. 2010). Domestication of soybeans from wild soybeans is thought to have occurred approximately in the eleventh century B.C. in the eastern half of northern China and spread to surrounding countries in the first century A.D. (Hymowitz and Kaizuma 1981). Based on recent archaeological discoveries and phylogenetic studies, domestication of soybeans occurred in

multiple locations in East Asia (Lee et al. 2011). The phylogeny and diversity of cultivated and wild soybeans have been extensively analyzed based on cytoplasmic genome variation and reviewed by Shimamoto (2001). The genetic base of the Japanese soybean gene pool is distinct from that of the world germplasm (Abe et al. 2003, Kaga et al. 2012). Using the replication method, a recent study strongly suggested that soybean seeds first appeared in the initial Jomon period, became larger in size through the later Jomon period in central Japan, and cultivated types were distinguished from wild soybeans based on seed size by the middle Jomon period in the latter half of the 4th millennium BC (Nakayama 2015). Thus, Japanese soybeans, particularly Japanese landraces, may have unique genetic diversity because of their domestication history, in addition to the geographic isolation of the Japanese Archipelago from the Asian continent.

Seeds of many landraces are consumed as tofu, miso, kinako (roasted bean flour), nimame (boiled beans), hitashimame (boiled beans with a modicum of soy sauce), and edamame. Fukui and Arai (1951) classified Japanese germplasms into 9 ecotypes based on days to flowering and maturity, which differs from the maturity grouping used in North America. Compared to world germplasms, the range of Japanese soybean seed size is approximately twofold greater, whereas the range for days to flowering and plant height is narrower (Kaga et al. 2012). Japanese soybean accessions are clustered into 8 major groups based on 197 single-nucleotide polymorphism (SNP) markers. The clusters correspond to their agro-morphological characteristics, including ecological types rather than their geographic origin. Structure analysis of 12,000 accessions of the United States Department of Agriculture's (USDA) soybean germplasm collection using a 50 K-SNP chip demonstrated the relative uniqueness of Japanese germplasms (Bandillo et al. 2015).

Most soybean varieties in Japan have been bred at public agricultural experiment stations. Recently, biotic stress or pod shattering-resistance genes or maturity genes were introduced into leading cultivars by recurrent back-crossing using marker-assisted selection (MAS) to quickly improve specific traits. Newly developed cultivars with biotic-stress resistance and pod-shattering resistance are described in the Genetics of agriculturally important traits section.

A total of 145 soybean varieties with the ‘Soybean Norin’ name was registered by the Ministry of Agriculture, Forestry and Fisheries (MAFF) in Japan during 1939–2014 (Supplemental Table S1). Authentic seeds of the old 91 varieties released from 1939 to 1989 were preserved at the National Agriculture and Food Organization (NARO) Genebank (Miyazaki et al. 1995). Recent varieties bred in public breeding programs are stored in the corresponding breeding stations where they have the breeder’s rights. In contrast, most edamame seeds in Japan were released from private companies or universities. Information, including variety names, registrant names, breeder names, and characteristics of traits related to 202 soybean and edamame varieties registered during the period from 1981 to 2017, in the plant variety protection system of 1980 in Japan, are available from the website (http://www.hinsyu.maff.go.jp/en/en_top.html confirmed 02/09/2018). The variety registration system to protect breeder’s rights and variety names is authorized by seed and seedling law and was strengthened in 1998 in harmony with UPOV (Union International Pour la Protection des Obtentions Vegetales).

Approximately 13,100 soybean accessions are conserved at the NARO Genebank (02/03/2018). Among them, information on 9,700 accessions can be accessed and ordered through an online search system (http://www.gene.affrc.go.jp/databases-plant_search_en.php) from among 7,900 domestic soybeans and 1,800 wild soybeans. The soybean germplasms include Japanese local landraces and varieties from other countries, improved varieties, and breeding lines developed by regional Japanese agricultural research institutes or those introduced from overseas agricultural research institutes. The germplasms conserved in Japan will supplement the overseas genetic resources for breeding and gene discovery.

Experimental genetic resources

To provide a platform for unexploited Japanese soybean germplasms in the NARO Genebank for breeding and diversity research, 1,603 representative accessions retaining the diversity of the whole collection (11,300 accessions, 05/29/2009) were selected as a core collection, including 832 Japanese local landraces, 341 world landraces from 16 Asian countries, 109 old and 57 recent Japanese varieties, and 264 wild Japanese soybeans (Kaga et al. 2012). Based on

the assessment of SNP markers and 11 agro-morphologic traits, accessions retaining the genetic diversity of the whole collection were selected to develop three soybean sets of different sizes using a heuristic approach. A minimum of 12 accessions represent the observed gene diversity, and two mini-core collections, each consisting of 96 accessions from Japanese (Fig. 1) and world germplasms, represent the major proportion of both geographic origin and agro-morphologic trait variation. For large-scale analysis, 1,250 accessions of the core collection have been registered as separate accessions of single-seed-derived germplasm in the NARO Genebank (Takeya et al. 2013). These selected sets of germplasms provide an effective platform for studies that enhance soybean diversity and assist in the detection of novel traits for crop improvement.

Methods for preventing the transfer of radiocesium into food or developing soybeans that accumulate little or no radiocesium are urgently needed because of the accident at the Fukushima Daiichi nuclear power station of Tokyo Electric Power Company in March 2011. Takagi et al. (2015) surveyed variation in seed Cs concentrations in the mini core collections and identified nine low Cs-accumulating varieties. *Phytophthora* stem and root rot by *Phytophthora sojae* is among the most serious of the soybean diseases in Japan. Jiang et al. (2017) identified two Japanese accessions with resistance to a broad spectrum of *P. sojae* isolates from the Japanese mini-core collection. Because waterlogging often occurs in paddy fields in Japan, soybean seedlings are damaged by hypoxia, resulting in poor root development and plant growth. Suematsu et al. (2017) evaluated hypoxia tolerance among the mini-core collections and identified three Japanese accessions with a strong ability to develop roots under hypoxia conditions.

The development of experimental resources facilitates the evaluation of useful genes. The objectives of the National BioResource Project (NBRP) in Japan are to collect, conserve, and distribute biological materials for life science research. NBRP *Lotus* and *Glycine* aim to support the development of legume research. *Lotus japonicus* is a perennial legume that grows naturally throughout Japan and is used as a model plant for soybeans and legumes. The current status of the genomic resources preserved in LegumeBase (<http://www.legumebase.brc.miyazaki-u.ac.jp/strain/glycineRiLinesList.jsp>) is presented in Table 1.



Fig. 1 Seeds of representative accessions of Japanese mini-core collection

Table 1 *Glycine max*/*G. soja* resources preserved in LegumeBase

Name of resource	No. of stocked resources	Depositor	Reference
<i>G. soja</i> accessions	715	Hokkaido Univ.	Hong et al. (2003)
(Research set)	(64)		Xu et al. (2002)
<i>G. max</i> accessions	265	Hokkaido Univ.	Abe et al. (2003)
RILs (Misuzudaizu × Moshidou Gong 503)	167	Chiba Univ.	Tajuddin et al. (2003)
			Watanabe et al. (2004)
RILs (TK780 × B01176)	96	Hokkaido Univ.	Liu et al. (2007)
Edamame (cultivars)	8	Yamagata Univ.	Akazawa and Egashira (2005)
Mutant			Takagi et al. (2000)
•Fatty acid mutants	21	Saga Univ.	Yan et al. (2014)
•Flower color mutant	3	Saga Univ.	Akao and Kouchi (1992)
•Symbiotic mutant	4	NIAS	Francisco and Akao (1993)
M2 bulked seeds	1 ^a	Saga Univ.	Hoshino et al. (2010)
Full-length cDNA	37,890	<i>Glycine</i> full-length cDNA consortium, RIKEN ^c	Umezawa et al. (2008)

^aThe M2 seed set was derived from approximately 5,000 M1 plants

^bInstitute of Agrobiological Sciences, NARO

^cInstitute of Physical and Chemical Research

Genome sequences

Accumulation of genome sequence information for a wide range of soybean cultivars that differ from ‘Williams 82’ is necessary to understand genetic diversity and develop molecular markers for breeding. Because ‘Enrei’ is a leading Japanese cultivar that produces high-quality seeds for food processing and its production area in Japan accounted for 9% of the total soybean cultivation areas in 2014, Shimomura et al. (2015) sequenced the whole genome of ‘Enrei’ using the next-generation sequencing (NGS) platform Illumina HiSeq 2000 and Roche 454 FLX Titanium as a representative cultivar to characterize the genome structure of Japanese soybeans. The sequencing average read coverage was $22.2 \times$ and approximately two million SNPs and insertions/deletions were identified between ‘Enrei’ and ‘Williams 82.’ Additionally, numerous genes related to the biosynthesis of anthocyanin and flavonoids in the Williams 82 genome were not detected in the ‘Enrei’ genome. The recent re-sequencing for diversity analysis provided a large amount of NGS read data for 14 Japanese soybean landraces and 9 Japanese wild soybean accessions (Zhou et al. 2015), and 9 Japanese landraces and 2 wild soybean accessions (Valliyodan et al. 2016). Re-sequencing information is very useful for collecting allele information unique to Japanese soybeans.

DNA libraries

Large genomic DNA insert-containing libraries are useful tools for physical mapping, positional cloning, and genome-wide sequencing. The bacterial artificial chromosome (BAC) and transformation-competent bacterial artificial chromosome (TAC) libraries of ‘Misuzudaizu’ were constructed by Xia et al. (2005) and Watanabe et al. (2009), respectively. The BAC for ‘Enrei’ was developed by Shimomura et al. (2015). A large collection of full-length cDNA is essential for correct annotation of genomic sequences and for functional studies of genes. A total of 39,936 soybean cDNA clones was obtained as a full-length-enriched cDNA library that was constructed from the cultivar ‘Norin No. 2’ grown under various conditions (Umezawa et al. 2008). Among these, 37,890 cDNA clones with sequence information are available from LegumeBase (Table 1).

Genetic linkage maps

Integration of markers used for MAS and quantitative trait loci (QTL) mapping into the common genetic linkage map allowed for the determination of the relative genetic relationships among QTLs based on marker positions. High-resolution genetic linkage maps have been constructed in the United States (Hyten et al. 2010; Lee et al. 2015; Song et al. 2016). The first genetic linkage map for a Japanese cultivar was constructed using an F_2 population derived from a cross between the Japanese cultivar ‘Misuzudaizu’ and Chinese cultivar ‘Moshidou Gong 503’ based on restriction fragment length polymorphism (RFLP) markers (Yamanaka et al. 2001). The progenies from the cross combination between ‘Misuzudaizu’ and ‘Moshidou Gong 503’ have been widely used to construct basic genetic linkage maps in Japan, and recombinant inbred lines (RILs) with genotype information can be obtained as a genetic resource from LegumeBase (Table 1). Watanabe et al. (2004) constructed a linkage map based on 360 markers consisting of 177 RFLPs, 150 simple sequence repeats (SSRs), 28 amplified fragment length polymorphisms (AFLPs), and five phenotypic markers covering 2663.6 cM for the same RILs. Harada and Xia (2004) constructed a new linkage map based on 853 markers consisting of 412 RFLPs, 117 SSRs, 318 AFLPs, one random amplified polymorphic DNA (RAPD), and five phenotypic markers using 190 F_2 individuals from the cross combination between ‘Misuzudaizu’ and ‘Moshidou Gong 503.’ Xia et al. (2007) further integrated SSR and sequence-tagged site (STS) markers into the above F_2 map reported by Harada and Xia (2004) and constructed a linkage map consisting of 1,276 markers covering 3080 cM. Hisano et al. (2007) constructed a linkage map of RILs between ‘Misuzudaizu’ and ‘Moshidou Gong 503’ based on expressed sequence-tag-derived SSR markers covering 2700.3 cM. Hwang et al. (2009) reported a high-density integrated linkage map based on 1,810 SSR markers covering 2,442.9 cM by integrating three linkage maps from RILs between ‘Misuzudaizu’ and ‘Moshidou Gong 503,’ RILs between the United States cultivar ‘Jack’ and Japanese cultivar ‘Fukuyutaka,’ and RILs between Chinese ‘Peking’ and the Japanese landrace ‘Akita’ into a single composite map. Selected SSR markers with higher polymorphism information content (PIC)

among the 24 representative genotypes are widely used in soybean breeding in Japan.

A high-density linkage map can provide information for assembling genome sequences and identifying regions in the sequence assembly where information must be resolved based on the relationships between physical and genetic distances. A high-density genetic linkage map consisting of 1,667 SSR and 510 SNP markers was constructed using the F₂ progeny of a cross between the Japanese soybean variety ‘Enrei’ and Chinese soybean landrace ‘Peking’ (Watanabe et al. 2018). Although the marker order on the linkage map and Wm82.a2.v1 assembly were similar, their differences provide information for resolving the order and/or orientation of the contigs and assigning unaligned scaffolds on the chromosomes.

Mutant libraries

Reverse genetic approaches based on Targeting Local Lesions IN Genome (TILLING) or NGS technology to screen mutant libraries are expected to efficiently provide new material to gain insights into the functions of uncharacterized genes in soybeans. A screening platform used for TILLING has been developed for more than 40,000 mutant lines (Anai 2012). Among them, 7,200 ethyl methanesulfonate (EMS) mutant lines and 1,800 X-ray mutant lines were constructed for the Japanese soybean cultivar ‘Fukuyutaka.’ M2 bulked seeds from the 5,000 EMS mutant lines are available from LegumeBase (Table 1). In the United States, TILLING has been applied to three EMS-treated populations and one *N*-nitroso-*N*-methylurea (NMU)-treated population (Cooper et al. 2008).

According to Anai (2012), the mutation rate can be increased by repeated EMS treatment. Another soybean mutant library consisting of 1,536 plants was constructed for the Japanese soybean ‘Enrei’ by repeated EMS treatment (Tsuda et al. 2015). The mutation frequency, at 1 mutation per 74 kbp, was nearly saturated and sufficiently high to obtain a plant with a nonsense mutation in each gene from the mutant library. The proposed method for mutant screening by NGS is useful for identifying mutants for functional studies of soybean genes and may yield new alleles for soybean breeding.

Chromosomal segment substitution lines

Chromosomal segment substitution lines (CSSLs) were developed using the progeny of a cross between the Japanese soybean variety ‘Enrei’ and Chinese soybean landrace ‘Peking’ (Watanabe et al. 2018). ‘Peking’ is famous for its resistance to the soybean cyst nematode *Heterodera glycines* and has many useful uncharacterized biotic- and abiotic-resistance genes. A series of 103 CSSLs covering all chromosomes, each with different chromosomal segments originating from ‘Peking’ in the genetic background of ‘Enrei,’ was used to detect minor QTLs as single genetic factors in a uniform genetic background. Approximately 50 reproducible QTLs related to basic agronomic traits were detected in the CSSLs. CSSLs may be a good starting material for breeding, as well as isolation of uncharacterized useful ‘Peking’ genes conferring biotic and abiotic resistance. Other CSSLs were developed using a Japanese wild soybean accession ‘JWS 156-1’ as the donor parent and the soybean variety ‘Jackson’ as their genetic background and was used to identify the QTLs for 100-seed weight (Liu et al. 2018). In China, two CSSLs using wild soybeans as the donor parents have been reported (Wang et al. 2013; Xin et al. 2016).

Genetics of agriculturally important traits

The major traits genetically analyzed are summarized in Table 2 with information, including gene or locus and a brief synopsis of the contents of each study described below.

Resistance to biotic stress

Resistance to biotic stress is essential for stable and high yield of soybeans. There are more than 20 diseases and pests in Japanese soybeans, possibly because of the natural habitat of wild soybeans and high humidity of the fields.

Major damage conferred by diseases and pests in Japanese soybeans are caused by soybean mosaic virus (SMV), soybean dwarf virus (SbDV), *Phytophthora sojae*, *Calonectria crotalaria*, cyst nematode, and common cutworm. Recently, the southern bean mosaic virus (SBMV) and peanut stunt virus (PSV)

Table 2 Major traits genetically analyzed

Traits	Locus/Gene	Comments	Reference
SMV resistance	<i>Rsv3</i>	Confirmed the resistance to SMV C and D	Kato et al. (2016)
PSV resistance	<i>Rpsv1</i>	Mapping and confirmation of the resistance	Saruta et al. (2012)
SbDV resistance	<i>Rsdv1</i>	The region was restricted to 44-kb including 6 genes	Yamashita et al. (2013)
Foxglove aphid resistance	<i>Rasv1</i>	Sufficient to confer aphid resistance but insufficient for SbDV tolerance	Ohnishi et al. (2012)
PSR resistance	<i>Rps1k</i> , <i>Rps1d</i>	The most effective resistance genes to Japanese isolates	Moriwaki (2010)
SCN resistance	<i>Rsp</i> gene of Waseshiroge <i>rhg1s</i> , <i>rhg1g</i> <i>rhg2g</i> , <i>rhg2s</i>	Allelic to <i>Rsp1</i> or tightly linked to <i>Rsp1</i> Either <i>rhg1s</i> or <i>rhg1g</i> was necessary for race 3 resistance <i>Rhg4</i> , <i>rhg1s</i> , and <i>rhg2g</i> or <i>rhg2s</i> were necessary for race 1 resistance	Sugimoto et al. (2011a) Suzuki et al. (2012) Suzuki et al. (2012)
Antibiosis resistance to CCW	<i>CCW-1</i> , <i>CCW-2</i>	Two QTLs were introgressed into Fukuyutaka and a new variety Fukuminori was developed	Komatsu et al. (2005)
Antixenosis resistance to CCW	<i>qRslx1</i> , <i>qRslx2</i>	The position of <i>qRslx1</i> was similar to that of <i>CCW-1</i> and pubescence characteristics might contribute to the resistance	Oki et al. (2012)
Chilling tolerance	<i>qRslx3</i> , <i>qRslx4</i>	Two QTLs were identified from wild soybean (<i>Glycine soja</i>)	Oki et al. (2017)
Hypoxia tolerant	<i>qCTTSW1</i> <i>QTLs</i> for root development	The QTL was associated with <i>T</i> locus Root length development and root surface development showed no development decrease after hypoxia treatment in the tolerant allele	Funatsuki et al. (2005) Nguyen et al. (2017)
Salt tolerance	<i>Ncl</i>	Encodes cation-chloride cotransporter	Tuyen et al. (2016)
Low seed cadmium concentration	<i>cd1</i>	Several dominant SSR markers were developed for selection of genotypes with low seed cadmium concentration	Benitez et al. (2010)
Cold-induced seed coat discoloration tolerance	<i>GmIRCHS</i>	<i>GmIRCHS</i> itself or a closely located region is responsible for cold induced coat discoloration	Ohnishi et al. (2011)
Hard seediness	<i>qHS1</i>	Encodes endo-1,4- β -glucanase	Jang et al. (2015)
Boiled seed hardness	<i>qHbs3-1</i>	Encodes pectin methylesterase	Toda et al. (2015)
Seed size	<i>GmPPD1</i> , <i>GmPPD2</i>	Knock down of both genes produced <i>mog</i> phenotype	Naito et al. (2017)
Beta-conglycinin deficiency	<i>Scg-1</i>	Inverted repeat of the α subunit genes	Tsubokura et al. (2012)
Popcorn-like aroma	<i>GmAMADH2</i>	Dysfunction of <i>GmAMADH2</i> induce the biosynthesis of 2AP	Arikiti et al. (2011a, b)
Nuclear inherited green-cotyledon	<i>GmSR1</i> , <i>GmSR2</i>	Encode Mg-dechelutase	Nakano et al. (2014)
Cytoplasmically inherited greencotyledon	<i>CytG</i>	A frame-shift in <i>psbM</i> encoding a small subunit of photosystem II	Kohzuma et al. (2017)

Table 2 continued

Traits	Locus/Gene	Comments	Reference
Structural diversity of glycosylation in group A saponin	<i>Sg-1</i>	UDP-sugar-dependent- glycosyltransferase gene	Sayama et al. (2012)
Soyasapogenol A biosynthesis	<i>Sg-5</i>	Encodes the cytochrome P450 enzyme, CYP72A69	Yano et al. (2017)
Gamma-tocopherol concentration	γ - <i>TMT3</i>	γ -tocopherol methyltransferase	Dwiyanti et al. (2011)
Growth habit	<i>Dt1</i>	<i>GmTFL1b</i> , a ortholog of <i>TERMINAL FLOWER1</i>	Liu et al. (2010)
Fasciation	<i>f</i>	Deletion of one or both genes, encoding a leucine-rich repeat receptor-like kinase and a WD-repeat protein will be responsible for fasciation	Onda et al. (2011)
Pod dehiscence	<i>Pdh1</i>	Encodes a dirigent protein	Funatsuki et al. (2014)
Flowering time	<i>E1</i>	Encodes a novel transcription protein	Xia et al. (2012)
Flowering time	<i>E2</i>	<i>GmGla</i> , an ortholog <i>GIGANTEA</i> gene	Watanabe et al. (2011)
Flowering time	<i>E3</i>	<i>GmPhyA3</i> encodes phytochrome A	Watanabe et al. (2009)
Flowering time	<i>E4</i>	<i>GmPhyA2</i> encodes phytochrome A	Liu et al. (2008)
Flowering time	<i>E9</i>	<i>FT2a</i> , an ortholog of <i>FLOWERING LOCUS T</i> is responsible for the locus	Zhao et al. (2016)
Flowering time	<i>qDTF-J</i>	<i>FT5a</i> , an ortholog of <i>FLOWERING LOCUS T</i> is responsible for the QTL	Takeshima et al. (2016)
Terminal raceme length	<i>qTRL18-1</i>	Located in proximal region of the <i>Dt2</i> locus	Yamada et al. (2014)
Lodging tolerance	<i>qLS19-1</i>	<i>E3</i> or <i>Dt1</i> may not be responsible for the QTL	Yamaguchi et al. (2014b)
Duration of reproductive period	<i>qDfml</i>	Control duration from flowering to maturation with negligible impact on duration from sawing to flowering	Komatsu et al. (2012)
Non-nodulation	<i>GmNFR1</i>	Dysfunctions of <i>GmNFR1α</i> and <i>GmNFR1β</i> induce non-nodulation	Hayashi et al. (2012)
Hypernodulation	<i>nts1</i>	Dysfunction of <i>NTS1</i> gene encoding leucine-rich repeat Ser/Thr receptor-like kinase	Nishimura et al. (2002)
Restriction of nodulation for specific bacterial strains	<i>Rj4</i>	Encodes a thaumatin-like protein	Hayashi et al. (2014)

have also been considered serious pathogens affecting seed quality.

SMV infection causes mosaic discoloration and deformation of leaves and seed mottling, resulting in reduced seed yield and seed quality. The virus is classified into six strains, A, A2, B, C, D, and E, based on its pathogenicity to a set of Japanese differential varieties. Many Japanese varieties are resistant to the A and B strains. Resistance to the C and D strains was introduced from ‘Harosoy’ and resistant varieties, such as ‘Fukuibuki,’ were developed. ‘Harosoy’ harbors *Rsv3*, which confers resistance to the SMV strain groups G5–G7 in the United States. To confirm that *Rsv3* confers resistance to strains C and D, resistance was introduced from ‘Fukuibuki’ into the leading variety ‘Ohsuzu’ by recurrent backcrossing using MAS. All lines selected with markers near *Rsv3* showed resistance to the strains, suggesting that the *Rsv3* locus is responsible for the resistance (Kato et al. 2016).

Soybean plants infected with PSV show yield loss because of decreased seed number size, and quality following molting of the seeds. Using two PSV isolates (PSV-K and PSV-T), the PSV resistance of 132 soybean cultivars was investigated. Of these, 73 cultivars exhibited resistance to both PSV isolates. PSV resistance in these cultivars is controlled by a single dominant gene, *Rpsv1*. *Rpsv1* was mapped near Satt435 on soybean chromosome 7 using RILs of ‘Hyuga’ × ‘Enrei’ (Saruta et al. 2012).

SbDV causes serious dwarfing, yellowing, and sterility and leads to significant yield losses in soybean production in northern Japan. The Indonesian soybean cultivar ‘Wilis’ shows a high level of SbDV resistance. Using RILs derived from a cross between ‘Wilis’ and the susceptible cultivar ‘Toyokomachi,’ the SbDV resistance in ‘Wilis’ was found to be mainly controlled by a single QTL located on chromosome 5 (Uchibori et al. 2009). The QTL was named *Rsdv1* and finely mapped within the 44 kb region between Sat_11 and Sct_13 (Yamashita et al. 2013). In northern Japan, the foxglove aphid transmits SbDV from SbDV-infected red or white clovers to soybeans during spring and summer. The soybean cultivar ‘Adams’ is tolerant to SbDV infection in the field and exhibits antibiosis to the foxglove aphid. A major QTL, *Rasol*, was reported for foxglove aphid resistance and mapped to a 63 kb interval on chromosome 3 (Ohnishi et al. 2012). *Rasol* was introduced into ‘Toyomusume’ by

backcrossing and the degree of aphid antibiosis to the foxglove aphid and degree of tolerance to SbDV in the field were investigated. The results demonstrated that *Rasol* alone was sufficient to confer aphid resistance but insufficient to confer SbDV tolerance. Accordingly, *Rsdv1* may be useful for developing an SbDV-resistant variety.

Phytophthora stem and root rot (PSR) caused by the soil-borne Oomycete *Phytophthora sojae* is one of the most serious and widespread diseases of soybeans in Japan. When soybean plants are infected by *P. sojae*, the plant stem appears to be water-soaked and turns red-brown, resulting in wilting and plant death. Moriwaki (2010) examined the effectiveness of 14 *Rps* genes using 109 *P. sojae* isolates from 14 regions in Japan and found that *Rps1d* and *Rps1k* were the most effective resistance genes. Kasuga et al. (1997) constructed a high-density linkage map of *Rps1k*, and the locus was mapped to a 0.13 cM interval between two amplified fragment length polymorphism (AFLP) markers. Sugimoto et al. (2008) mapped *Rps1d* to chromosome 3 using the progeny from a cross between the black soybean cultivar ‘Tanbakuro’ and ‘PI 103091’ (*Rps1d*). Sugimoto et al. (2011a) identified a novel *Rps* in the cultivar ‘Waseshiroge.’ A method for evaluating the field resistance of soybeans to *P. sojae* was developed (Yamashita et al. 2012). One Japanese variety with high partial resistance was discovered in field experiments (Sugimoto et al. 2011b). Although race-specific resistance by certain *Rps* genes has been effective for many years, partial resistance is also important because it should be more durable and broader than resistance dependent on a single major gene.

The soybean cyst nematode (SCN) (*Heterodera glycines* Ichinohe) is one of the most damaging pests of soybeans. In Japan, races 1, 3, and 5 have been reported. Most race 3 resistance is derived from ‘Gedenshirazu,’ a landrace from the Akita Prefecture. ‘PI84751’ has been used as a genetic source of resistance to races 1 and 3. The genotype of ‘Gedenshirazu’ is *rhg4/rhg1 g/rhg2 g*, whereas that of ‘PI84751’ is *Rhg4/rhg1 s/rhg2 s*. Genetic analysis using DNA markers revealed that *rhg1 g* and *rhg1 s* are allelic, whereas *rhg2 g* and *rhg2 s* are not allelic and are closely located on the same chromosome. *Rhg4*, *rhg1 s*, and *rhg2 g* or *rhg2 s* are necessary for race 1 resistance, and either *rhg1 s* or *rhg1 g* is necessary for race 3 resistance (Suzuki et al. 2012).

Resistance to races 1 and 3 was introduced into ‘Yukihomare,’ a leading variety in Hokkaido with race 3 resistance, from a line with race 1 and 3 resistance using DNA markers for *rhg1 s* and *Rhg4*. The developed variety ‘Yukihomare R’ showed higher yield than ‘Yukihomare’ in a field contaminated with cyst nematodes and agricultural performance was equivalent between the two varieties (Suzuki et al. 2017). ‘Suzumaru R’ was developed by recurrent back-crossing of the non-recurrent parent ‘Chukou 1901’ with resistance to races 1 and 3 and the recurrent parent ‘Suzumaru,’ which is a suitable variety for natto, but susceptible to SCN. Resistance was selected using DNA markers linked to *Rhg4*, *rhg1 s*, and *rhg2 g*. Agricultural characteristics and food suitability for natto of ‘Suzumaru R’ were similar to those of ‘Suzumaru,’ except for the resistance to races 1 and 3 (Kurosaki et al. 2017). In the United States, alleles at *Rhg1* have been shown to vary by copy number and type (F, P, and W). Among repeat types, an increase in repeat number was associated with greater resistance. Although plants with P-type *Rhg1* required *Rhg4* to achieve full resistance, *Rhg4* did not increase resistance in the background of an F + W-type *Rhg1* repeat (Yu et al. 2016).

To introduce multiple disease and pest resistance, an SSR marker set located near each resistance locus was selected and simultaneously analyzed using a high-resolution PCR fragment analysis system (Kato et al. 2017). The researchers introduced SCN and SMV resistance genes, as well as SMV and SbDV resistance genes into the respective target varieties (Kato et al. 2017).

Asian soybean rust (ASR), caused by the biotrophic basidiomycete *Phakopsora pachyrhizi* Std. & P. Syd., occurs in major soybean-growing regions of all tropical and sub-tropical areas. Seven dominant genes (*Rpp1*–*Rpp6* and *Rpp1b*) controlling race-specific resistance to ASR have been identified and mapped to different loci. Seven pyramided lines carrying multiple *Rpp* genes have been developed and evaluated for their resistance to one ASR isolate from Japan and two from Brazil. Significantly greater resistance was observed in the three pyramided lines than in the original sources, which were ‘PI 230970’ (*Rpp2*), ‘Hyuga’ (*Rpp3*), ‘PI 459025’ (*Rpp4*), and ‘Kinoshita’ (*Rpp5*) that carried a single *Rpp*. These pyramided lines are useful in soybean breeding for conferring broad-spectrum high resistance to ASR

isolates, which are virulent to varieties carrying single-resistance genes (Yamanaka et al. 2015).

In southwestern Japan, damage to soybean plants caused by the common cutworm (CCW, *Spodoptera litura* Fabricius) is a serious problem. Evaluating the soybean germplasm for resistance to CCW facilitated the identification of a cultivar, ‘Himeshirazu,’ with a high level of resistance (Komatsu et al. 2004). Using a population derived from a cross between ‘Fukuyutaka’ and ‘Himeshirazu,’ two QTLs for antibiosis resistance to CCW, *CCW-1*, and *CCW-2*, were detected on chromosome 7 (Komatsu et al. 2005). Two QTLs were successfully introgressed into ‘Fukuyutaka’ by recurrent back-crossing, and a new variety ‘Fukuminori’ was developed (Takahashi et al. 2017). The resistance to CCW by ‘Fukuminori’ was moderate and nearly all of its characteristics were the same as those of ‘Fukuyutaka,’ except for slightly smaller seed size. Furthermore, QTL analysis of antixenosis resistance to CCW was performed using RILs derived from a cross between ‘Fukuyutaka’ and ‘Himeshirazu.’ Two QTLs for antixenosis resistance, *qRslx1* and *qRslx2*, were identified on chromosomes 7 and 12, respectively (Oki et al. 2012). The position of *qRslx1* was similar to that of *CCW-1*. They also analyzed the pubescence characteristics. Two QTLs for pubescence length on chromosomes 7 and 12 and two QTLs for pubescence density on chromosomes 1 and 12 were identified. The pubescence QTLs on chromosomes 7 and 12 were close to *qRslx1* and *qRslx2*, respectively. These results suggested that pubescence characteristics may contribute to soybean antixenosis resistance to CCW (Oki et al. 2012). Using RILs derived from a cross between ‘Fukuyutaka’ and a wild soybean (*G. soja*), two new QTLs for antixenosis resistance, *qRslx3* and *qRslx4*, were identified on chromosomes 7 and 2, respectively (Oki et al. 2017). Both new QTLs from *G. soja* have the potential to enhance the CCW resistance of soybean cultivars. A cultivar ‘Suzukaren’ with moderate resistance to CCW was developed from the progeny derived from the cross of ‘Suzuotome’ and ‘IAC 100’ (Takahashi et al. 2013). ‘Suzuotome’ is suitable for natto, whereas ‘IAC 100’ is resistant to bacterial pustules and the CCW. ‘Suzukaren’ is highly resistant to bacterial pustules, as well as suitable for natto processing. The DNA markers and candidate genes for bacterial pustule resistance (*rxp*) were reported by Kim et al. (2010).

Further research is necessary for resistance genes against purple stain, root necrosis, downy mildew, stem rot, and bacterial blight. Resistance to stinkbugs is also very important but has not been found in Japanese soybeans.

Resistance to abiotic stress

Global climate change is a major factor regarding abiotic stress for crops and drought tolerance has become a worldwide problem. Cold tolerance in the northern regions of Japan, drought and high-temperature tolerance in the southwestern region of Japan, and waterlogging tolerance throughout Japan are important for Japanese soybeans.

Chilling tolerance is an important trait in Hokkaido, the northernmost island of Japan. It has been reported that tawny-pubescence soybeans are more chilling tolerant than gray-pubescence soybeans (Kurosaki et al. 2004; Takahashi et al. 2005). The *T* locus controls pubescence color and encodes flavonoid 3'-hydroxylase. The dominant *T* allele produces tawny pubescence and the recessive *t* allele with the single-base deletion produces gray pubescence (Toda et al. 2002). Using RILs between chilling tolerant 'Hayahikari' and chilling-sensitive 'Toyomusume,' three QTLs for chilling tolerance and seed-yielding ability, *qCTTSW1*, *qCTTSW2*, and *qCTTSW3*, were identified on chromosomes 6, 19, and 12, respectively. Among them, *qCTTSW1* was basically independent of the QTL for the flowering time but directly associated with the *T* locus (Funatsuki et al. 2005).

To develop early-maturing lines without decreasing seed yield, 'Yukihomare,' the standard cultivar in Hokkaido, was crossed with the Polish cultivars 'Polan' and 'Progres' and two chilling-tolerant breeding lines, 'Tokei 1067' (T1067) and 'Toiku 251' (T251), were developed (Yamaguchi et al. 2015). To screen chilling-tolerant soybeans developed in high-latitude countries, including Canada, Switzerland, Poland, and the Czech Republic, 28-day chilling temperatures after flowering were applied in a phytotron and six chilling-tolerant cultivars were identified. Five breeding lines derived from a cross between the chilling-tolerant cultivar 'Mazowia' and 'Toyoharuka,' a relatively high chilling-tolerant cultivar in Hokkaido were developed. All five breeding lines matured earlier than 'Toyoharuka' and showed similar

yields to that of 'Toyoharuka' in the field under normal conditions (Yamaguchi et al. 2018).

Waterlogging stress can occur during any growing stage; however, waterlogging in the early stage substantially reduces grain yield. Seed-flooding tolerance at the germinating stage is important because soybean production in paddy fields is higher than that in upland areas in Japan. QTL analysis for seed-flooding tolerance based on the germination rate and normal seeding rate was conducted. To analyze the mechanism of seed-flooding tolerance, three flood-tolerant mutant lines were generated by gamma-ray irradiation of 'Enrei' seeds (Komatsu et al. 2013). Sayama et al. (2009) found that QTLs on chromosomes 12 and 8 had the greatest effect on germination rate and normal seedling rate, respectively, based on the damage to seedlings on agar medium after soaking treatment at 25 °C for 24 h. Soil hypoxia is a major problem associated with waterlogging because of the slow diffusion of oxygen in water. The QTL analysis of root development under hypoxic conditions was performed using RILs developed from a cross between a hypoxia-sensitive cultivar, 'Tachinagaha,' and a tolerant landrace, 'Iyodaizu.' Seedlings were exposed to hypoxia conditions and development was evaluated as the difference in the change in root traits before and after treatments. QTLs for root length development and surface area development on chromosome 12 were stable for over 2 years (Nguyen et al. 2017). QTL analyses of flooding tolerance at the vegetative growth stage were performed overseas (VanToai et al. 1994; Cornelious et al. 2005; Nguyen et al. 2012).

There are few salt-affected soils in Japan, but soil salt and related problems generally occur in arid or semi-arid climates. *Ncl*, the dominant salt tolerance gene on chromosome 3, was isolated from a Brazilian soybean cultivar 'FT-Abyara' using a map-based strategy (Tuyen et al. 2016). *Ncl* (*Glyma03g32900*) encodes a protein related to the cation-chloride cotransporter. Transfer of *Ncl* by *Agrobacterium*-mediated transformation into the soybean cultivar 'Kariyutaka' significantly enhanced its salt tolerance. Introgression of the tolerance allele into the soybean cultivar 'Jackson,' using DNA MAS produced an improved salt-tolerant line (Tuyen et al. 2016). A major alkaline salt-tolerance QTL from wild soybeans was identified on chromosome 17. Using progenies of RILs derived from a cross between the alkaline salt-sensitive cultivar 'Jackson' and the tolerant wild

soybean accession JWS156-1, the QTL was narrowed to a region of 771 kb on chromosome 17 (Tuyen et al. 2010).

Cadmium is a heavy metal pollutant that is naturally present in soils and highly toxic to biological organisms even at low concentrations. Significant differences were observed among soybean cultivars in the uptake of cadmium and its posterior translocation to the shoots and seeds. One major QTL for seed cadmium concentration, *cdl* on chromosome 9, was identified using progenies derived from a cross between ‘Harosoy’ with high seed-cadmium concentrations and ‘Fukuyutaka’ with low uptake of cadmium (Benitez et al. 2010). The same locus for seed-cadmium accumulation was described overseas in two papers (Jegadeesan et al. 2010; Vollmann et al. 2015).

Seed quality

For food-grade soybeans, appearance, characteristics, and composition of soybean seeds for food processing or human health are important traits.

Patterns of seed coat pigmentation are determined by four alleles, *I*, *i^l*, *i^k*, and *i* at the *I* locus on chromosome 8, which controls the spatial distribution of anthocyanin and proanthocyanidins in the seed coat. Most commercial soybean cultivars produce yellow seeds with yellow cotyledons and non-pigmented seed coats, which are important traits of high-quality seeds. Plants carrying the *I* allele show complete inhibition of pigmentation in the seed coat. The mRNA reduction of the chalcone synthase (CHS) gene in the yellow soybean seed coat results from post-transcriptional gene silencing (PTGS) of *CHS* (Senda et al. 2004). Similar results were obtained in the United States (Tuteja et al. 2004). A candidate for the *I* allele was identified in the yellow soybean genome and designated *GmIRCHS* (*G. max* inverted repeat of *CHS* pseudogene) (Kasai et al. 2007). CHS is a key enzyme in the flavonoid pathway and leads to the biosynthesis of anthocyanin and proanthocyanidins.

In yellow soybeans, low temperature ($\leq 15\text{ }^{\circ}\text{C}$) at the early stages of seed development causes the expression of pigmentation around the hilum region. This phenomenon referred to as ‘cold-induced seed coat discoloration’ (CD), is a severe problem in Hokkaido (Kasai et al. 2009). CD reduces the commercial value of yellow soybeans. Moreover, cracks that easily occur after low-temperature treatment are

related to enhanced pigmentation in some seed coat cells (Kasai et al. 2009). The QTL analysis of CD tolerance using two sets of RILs between ‘Toyoharuka’ and CD-susceptible cultivars showed that *GmIRCHS* or nearby genes are responsible for CD tolerance (Ohnishi et al. 2011). At low temperatures, ‘Toyohomare’ and ‘Toiku-238’ were more tolerant in terms of seed cracking than were ‘Yukihomare’ and ‘Toyomusume’ (Yamaguchi et al. 2014a).

Hard seededness of soybeans is an important attribute for soy foods and food processing because it affects water permeability, cookability, and overall texture. It is also an important characteristic of the adaptation of plants, particularly germination rate and viability, to unstable and unpredictable environments. The QTL *qHS1* for hard seededness located on chromosome 2 is common across different cross combinations and has the greatest effect on water impermeability (Jang et al. 2015). Fine-mapping and subsequent expression and sequencing analyses revealed that *qHS1* encodes an endo-1,4- β -glucanase. Transformation of the genomic region of the hard-seeded near-isogenic line (NIL) into the soft-seeded cultivar ‘Kariyutaka’ resulted in the accumulation of β -1,4 glucan in the outer layer of palisade cells and the production of hard seeds (Jang et al. 2015). Overseas researchers showed that seed-coat impermeability in wild soybeans is controlled by a single gene, *GmHs1-1*, which encodes a calcineurin-like metallophospho-esterase transmembrane protein (Sun et al. 2015).

Boiled seed hardness is an important factor in the processing of soybean food products. Boiled seed hardness in ‘Natto-shoryu’ is approximately twofold greater than that in ‘Hyookei-kuro3.’ Using RILs developed from a cross between ‘Natto-shoryu’ and ‘Hyookei-kuro 3,’ two significant stable QTLs, *qHbs3-1* and *qHbs6-1*, were identified on chromosomes 3 and 6, respectively. For both QTLs, ‘Hyookei-kuro 3’ alleles decreased boiled seed hardness (Hirata et al. 2014). Using the progeny from the RIL, one candidate gene, *Glyma03g3360*, was identified in the *qHbs3-1* region (Toda et al. 2015). *Glyma03g3360* encodes pectin methylesterase (PME). PME deesterifies pectins in the cell wall, converting methoxyl groups into carboxyl groups on the polygalacturonic acid chain and releases both methanol and protons. The carboxyls can be cross-linked by calcium, which structurally rigidifies the cell wall. The protein truncation of PME

results in softer cotyledons of cooked soybeans (Toda et al. 2015).

Controlling seed size is important for the food use of soybeans. Larger seeds are preferable for boiled beans, whereas smaller seeds are preferable for natto. Seed size is a typical quantitative trait controlled by multiple loci with small effects. However, in blackgram (*Vigna mungo* (L.) Hepper) a doubled seed size mutant was obtained by gamma-ray irradiation (Chinchest and Nakeeraks 1990). The mutant plant also had larger leaves and stems, and thus was designated a *multiple organ gigantism* (*mog*) mutant. The *mog* phenotype was observed because of the increase in cell number but not in cell size. The *mog* mutant also showed a *rippled leaf* (*rl*) phenotype. Naito et al. (2017) identified an 8 bp deletion in the coding sequence of *VmPPD* in the *mog* region. *VmPPD* is an ortholog of *Arabidopsis PEAPOD* (*PPD*), which regulates the arrest of cell division in meristematic cells. Knockdown of *PPD* orthologs, *GmPPD1* (*Glyma.10g244400*) and *GmPPD2* (*Glyma.20g150000*), in soybeans by RNAi produced both the *mog* and *rl* phenotypes (Naito et al. 2017).

Approximately 70% of total protein in soybean seeds consists of two major storage proteins, glycinin (11S globulin) and β -conglycinin (7S globulin). Glycinin is composed of five subunits, $A_{1a}B_{1b}$, $A_{1b}B_2$, A_2B_{1a} (group I), A_3B_4 , and $A_4A_5B_3$ (group II). Beta-conglycinin is composed of three subunits, α , α' , and β , in varying proportions. Glycinin contains more sulfur-containing amino acids than β -conglycinin. Recently, new protein fractions, lipophilic proteins (LP), were found, which accounted for approximately 30% of soy protein isolates (Samoto et al. 2007). The major component of LP is a complex of oleosin-phospholipids (Matsumura et al. 2017). Kitamura and Kaizuma (1981) identified two mutants, 'Keburi' and 'Moshidou Gong 503,' with reduced β -conglycinin levels. 'Keburi' lacked the α' subunit, whereas 'Moshidou Gong 503' showed lower levels of the α , β subunits. A line obtained by crossing 'Keburi' and 'Moshidou Gong 503' was crossed with 'Tohoku 80' to produce 'Karikei 434,' a line with α' subunit deletion and lower levels of the α , β subunits. A mutant line completely lacking both the α and α' subunits was identified from the progeny of 'Karikei 434' seeds by gamma-ray irradiation (Takahashi et al. 1994). A 4 bp insertion in the first exon of the wild *CG-2* encoding the α subunit, which was derived from

'Moshidou Gong 503,' introduced a premature stop codon, leading to α deficiency (Ishikawa et al. 2006). This line was named 'Yumeminori' and released in 2001 (Takahashi et al. 2004). This cultivar is rich in glycinin and lacks two major allergens, the α subunit and Gly m Bd 28 K. A β -conglycinin-deficient mutant QT2 was identified in the wild soybean (Hajika et al. 1996), and the phenotype was found to be controlled by the single dominant gene *Scg-1* (*suppressor of β -conglycinin-1*) (Hajika et al. 1998). *Scg-1* is located on chromosome 11 (Tsubokura et al. 2006b) and was introduced into the soybean cultivar 'Fukuyutaka' from QT2; this NIL was designated as QY7-25. The QY7-25 line lacked all three subunits of β -conglycinin and a much lower number of β -conglycinin transcripts was amplified from QY7-25 than from 'Fukuyutaka' (Tsubokura et al. 2006a). Beta-conglycinin deficiency in QT2 is controlled by post-transcriptional gene silencing through the inverted repeat of the α subunit genes (Tsubokura et al. 2012).

The absence of the $A_4A_5B_3$ subunit is controlled by a single recessive allele, and approximately 25% of Japanese landraces lack the $A_4A_5B_3$ subunit. A mutant line lacking all group I ($A_{1a}B_{1b}$, $A_{1b}B_2$, A_2B_{1a}) subunits was induced by γ -ray irradiated seeds of 'Wasesuzunari' (Odanaka and Kaizuma 1989). Kitamura et al. (1993) found one accession of wild soybeans lacking the A_3B_4 subunit. F_2 seeds from a cross between a mutant line lacking group I and $A_5A_4B_3$ subunits and a wild accession lacking the A_3B_4 subunit produced eight phenotypes, including a wild-type with all glycinin subunits, three phenotypes with single deficiencies, three phenotypes with double deficiencies, and a triple deficiency lacking all subunits (Yagasaki et al. 1996). A soybean cultivar named 'Nanahomare' lacking all glycinin subunits was developed in the progeny from a cross between the NILs of 'Tamahomare' (Yagasaki et al. 2010). 'Nanahomare' displayed similar growth characteristics, yield, and seed quality, including protein content and a 1.8-fold increase in β -conglycinin content over that in 'Tamahomare.' 'Nanahomare' is an effective source for isolating β -conglycinin.

QF2 lacks all the major subunits of glycinin and β -conglycinin (Takahashi et al. 2003). QF2 was developed from a cross between QY2 and EnB1. QY2 is a β -conglycinin-deficient mutant described previously and EnB1 is a NIL of 'Enrei' lacking all glycinin subunits. Despite the absence of storage protein subunits, QF2

grew normally and the nitrogen content of its seeds was similar to that of the wild-type variety. QF2 maintains its seed nitrogen content by accumulating free amino acids and increasing the abundance of certain seed proteins (Takahashi et al. 2003). QF2 may accumulate foreign proteins by transformation for biotechnological needs.

Soybeans are one of the most important oil crops, providing approximately 30% of the world's food oil production. Soybean oil with a high content of polyunsaturated fatty acids (linoleic acid and linolenic acid) produces undesirable flavor and odor when maintained for long periods at high-room temperature. Oils with a high content of mono-unsaturated fatty acids (oleic acid) are more stable during high-temperature heating in cooking than oil with a normal oleate content. Two high-oleic-acid soybean mutants, M23 and KK21, were induced by X-ray irradiation to 'Bay' (Anai et al. 2008). Different nucleotide modifications were identified in *GmFAD2-1a* between M23 and KK21. Novel mutant alleles of *GmFAD2-1b* were isolated from the EMS mutant population using TILLING. The two mutant lines, B12 and E11, contained near-null and null alleles for enzyme activity, respectively, as evaluated by a yeast heterologous expression system. By combining the *GmFAD2-1a* and *GmFAD2-1b* mutant alleles, soybean lines with > 80% oleic acid content were developed (Hoshino et al. 2010).

Microsomal omega 3-fatty acid desaturase (FAD3) is responsible for the synthesis of α -linolenic acid. By combining three non-functional alleles, *GmFAD3-1a*, *GmFAD3-1b*, and *GmFAD3-2a*, soybean lines containing < 2% α -linolenic acid in their seeds were developed (Hoshino et al. 2014). Recently, omega 3 fatty acids were found to be important for human health. Alpha linolenic acid is an essential omega 3 fatty acid and a metabolic precursor of eicosapentaenoic acid (EPA) and docosahexaenoic acids (DHA). Therefore, another target of breeding is to develop varieties with high contents of α -linolenic acid. Wild soybeans typically have higher α -linolenic acid content than domesticated soybeans, and accessions containing more than 20% of α -linoleic acid were detected (Shibata et al. 2008).

The black soybean landrace 'Tanbaguro,' consumed as edamame, is characterized by its high maltose production after heat processing, which contributes to its enhanced sweetness (Hirota et al.

2018). The low gelatinization temperature of starch predominantly appears to be contributed to the increased maltose production and associated with the increased proportion of short-chain amylopectin. Although β -amylase activity does not correlate with maltose productivity, amylase content may promote maltose production by the progression of starch gelatinization together with its effectiveness as a substrate of β -amylase (Hirota et al. 2018).

Soybean seed flavor is an important trait affecting soybean quality and food processing. Normal soybean seeds contain three types of lipoxygenases: L-1, L-2, and L-3. These enzymes are responsible for generating grassy beany flavors by oxidizing polyunsaturated fatty acids, limiting the wide utilization of soybean seeds and soybean protein in certain food products. Natural mutants lacking each of L-1, L-2, and L-3 were identified in the early 1980 s. The absence of L-1, L-2, or L-3 in the seeds is controlled by single recessive alleles, *lx1* (Hildebrand and Hymowitz 1981), *lx2* (Kitamura et al. 1985; Davies and Nielsen 1986), and *lx3* (Kitamura et al. 1983), respectively. A tight linkage between *lx1* and *lx2* was observed. Lenis et al. (2010) and Wang et al. (1994, 1995) conducted the molecular characterization of these null mutants. Two types of double mutants lacking both L-1 and L-3, as well as L-2 and L-3 have been obtained (Kitamura et al. 1985). Hajika et al. (1991) induced a soybean line lacking all lipoxygenases by gamma-ray irradiation of the seeds obtained from crosses between soybean lines lacking L-1 and L-3, and L-2 and L-3. The first lipoxygenase-less cultivar, named as 'Ichihime,' was developed using the progeny of this mutant (Hajika et al. 2002). Several lipoxygenase-less Japanese cultivars including 'L-star' and 'Suzusayaka' have been developed. 'L-star' is derived from the cross 'Fukuyutaka' $\times$ 'Ichihime' and backcrossing to 'Fukuyutaka.' 'Suzusayaka' is derived from the cross 'Suzuyutaka' $\times$ 'Kyuko355F2(γ)-M4' (the lipoxygenase-less mutant).

2-acetyl-1-pyrroline (2AP) confers the popcorn-like aroma in a wide variety of cereals and food products. The pleasant aroma of a special group of edamame in Japan is attributable to the presence of 2AP (Fushimi and Masuda 2001). These aromatic soybeans lack amino aldehyde dehydrogenase (AMADH) enzyme activity. Two genes, *GmAMADH1* and *GmAMADH2*, which encode AMADH, were characterized. The transcription level of *GmAMADH2*

was lower in aromatic varieties than in nonaromatic varieties, whereas the expression of *GmAMADH1* did not differ. A double nucleotide (TT) deletion causes a frame-shift and premature stop codon in exon 10 of *GmAMADH2* in all aromatic varieties (Arikiti et al. 2011a) and has been used as a codominant PCR-based marker for the aroma trait (Arikiti et al. 2011b). Among the soybean germplasms in Japan, ‘Nishiyamahitashi 98-5’ and ‘Shinanokurakake’ have an intense seaweed-like flavor after cooking. Large amounts of dimethyl sulfide (DMS) were observed after heat treatment of these seeds. DMS is formed from S-methylmethionine (SMM), which was detected in all soybean varieties examined; however, its concentration in the two seeds was > 100-fold higher than in other varieties (Morisaki et al. 2014).

Green-cotyledon soybean seeds are consumed after boiling and used for tofu. Hot water extracts of green-cotyledon soybeans were found to have great potential as an orally active immune modulator to treat various allergic diseases (Imai 2014). Green-cotyledon soybeans are stay-green mutants exhibiting two types of inheritance for the stay-green trait: nuclear and cytoplasmic inheritance. The nuclear inherited green-cotyledon/stay-green phenotype of ‘Tenshindaishitou’ was found to be caused by defects in *GmSGR1* and *GmSGR2*, which are orthologs of *Arabidopsis* *SGR* encoding Mg-dechelatase that catalyzes the first step of chlorophyll degradation (Nakano et al. 2014). The cytoplasmic inherited green-cotyledon/green-stay trait of ‘Kiyomidori’ was attributed to a defect in a chloroplast gene, which encodes PsbM, a small subunit of photosystem II (Kohzuma et al. 2017).

Many secondary metabolites, including glycosides, isoflavones, and saponins, are present in soybean seeds. Isoflavones in soybeans are categorized into three groups: daidzein derivatives, genestein derivatives, and glycitein derivatives. The large variation in the total content of isoflavones observed in the RILs derived from a cross between ‘Peking’ and ‘Tamahomare’ may have resulted from the combined effects of alleles at the four QTLs derived from distantly related varieties (Yoshikawa et al. 2010). There are many QTL analyses of individual and total isoflavone content worldwide. Primomo et al. (2005) and Han et al. (2015) reported common QTLs with those of Yoshikawa et al. (2010) on chromosomes 5 and 2, respectively. Cultivars such as ‘Fukuibuki’ (Sakai

et al. 2002) and ‘Yukipirika’ with high contents of isoflavones were developed.

The soybean saponins are divided into two groups, group A saponins and 2,3-dihydro-2,5-dihydroxy-6-methyl-4H-pyran-4-one (DDMP) saponins, according to their aglycone components. Group A saponins are detected only in seed hypocotyls and are bisdesmosidic saponins with a soyasapogenol A aglycone bearing two sugar chains on the C-3 and C-22 hydroxyl groups. In contrast, DDMP saponins are found in both the seed hypocotyls and cotyledons. They are monodesmosidic saponins with one carbohydrate at the C-3 of soyasapogenol B and the DDMP moiety at C-22. DDMP saponins and their derivatives have health-promoting functions, such as the prevention of dietary hypercholesterolemia, suppression of colon cancer cell proliferation, antiperoxidation of lipids, and liver-protecting activities. Group A saponins Aa and Ab have different sugar chain sequences at the C-22 position, each with an acetylated sugar at the terminal position. The phenotypes of saponins Aa and Ab are controlled by codominant alleles, *Sg-1a* and *Sg-1b*, respectively, at the single locus *Sg-1* (Shiraiwa et al. 1990; Tsukamoto et al. 1993). A mutant line A-b(F) was found to accumulate saponin A0- α g, which lacks an acetylated sugar at C-22 (Kikuchi et al. 1999). Another mutant that accumulates the novel saponin diacetyl-Af and lacks an acetylated sugar at C-22 was found in wild soybeans (Tsukamoto et al. 1992, 1993). The absence of the group A acetyl saponin was found to be controlled by a recessive allele *sg-1⁰* at *Sg-1* (Kikuchi et al. 1999). The *Sg-1* locus was mapped near Satt336 on soybean chromosome 7 (Takada et al. 2010). The structural diversity of glycosylation was determined by multiple alleles at a single locus, *Sg-1*, and led to the identification of a UDP-sugar-dependent glycosyltransferase gene (*Glyma07g38460*) (Sayama et al. 2012). The soybean cultivar ‘Kinusayaka,’ lacking three lipoxygenase enzymes and group A acetyl saponin, was developed. ‘Kinusayaka’ is highly suitable for processing soy milk and tofu with a less beany and astringent flavor (Kato et al. 2007). The absence of soyasapogenol A is controlled by a single recessive allele, *sg-5*, mapped to chromosome 15 (Takada et al. 2013). The endogenous levels of DDMP saponins are also elevated by the *sg-5* mutant allele. The natural *sg-5* mutant contains a premature stop codon in *Glyma15g39090* (Yano et al. 2017).

Glyma15g39090 was identified as *Sg-5* and encodes a soyasapogenol B C-21 hydroxylase essential for soyasapogenol A biosynthesis. The results demonstrated that metabolic switching from undesirable group A saponins to beneficial DDMP saponins can be achieved with *sg-5* mutations (Yano et al. 2017).

The vitamin E family comprises tocopherols and tocotrienols; α -tocopherol possesses the highest vitamin E activity in mammals. Three soybean varieties with high α -tocopherol concentrations of 20–30% have been identified (Ujiiie et al. 2005). Two SSR markers on chromosome 9 were strongly correlated with α -tocopherol concentration (Dwiyantri et al. 2007). QTL analysis and fine mapping revealed that γ -TMT3 encoding γ -tocopherol methyltransferase may be responsible for the high α -tocopherol concentration because of its high promoter activity (Dwiyantri et al. 2011). The γ -tocopherol methyltransferase gene isolated from *Perilla frutescens* was over-expressed in soybeans using a seed-specific promoter (Tavva et al. 2007). In the progeny of one transgenic plant, a 10.4-fold increase in the α -tocopherol content was observed, suggesting that the activity of γ -tocopherol methyltransferase is significant for the α -tocopherol content. Several wild soybeans with a high content of lutein were identified (Kanamaru et al. 2006). It is possible to select progenies with high contents of α -tocopherol and lutein by crossing a high α -tocopherol soybean variety and a high lutein wild soybean accession without decreasing seed weight (Wang et al. 2007).

Besides the traits described above, the molecular mechanism to control relative content of proteins, lipids, and carbohydrates is a vital problem to be elucidated, which will promote the development of soybeans for various uses.

Plant type and growth characteristics

Traits related to plant type and growth characteristics, including growth habit, raceme phenotype, fasciation, lodging, green stem disorder, branching, leaf shape, number of pods per plant, number of seeds per pod, and pod shattering have great influence on the seed yield of soybeans.

The determinate habit of soybeans is controlled by a recessive allele at the determinate stem (*Dt1*) locus. *TERMINAL FLOWER1* (*TFL1*) in *Arabidopsis* maintains indeterminate growth of the shoot apical

meristem (SAM) by delaying the up-regulation of floral meristem identity genes. The two orthologs of *TFL1*, *GmTFL1a* and *GmTFL1b*, are located on soybean chromosomes 3 and 19, respectively. Liu et al. (2010) and Tian et al. (2010) found that *Dt1* encodes *GmTFL1b* and stem growth is determined by the variation in this gene. The indeterminate parent-derived *GmTFL1b* allele exhibits partial dominance over the determinate parent-derived *GmTFL1b* allele. *GmTFL1b* was expressed only in the root and stem tip, whereas *GmTFL1a* was expressed at high levels in immature seeds and slightly expressed in the cotyledon and stem tip. Transformation of the determinate cultivar ‘Kariyutaka’ with a 4,216 bp genomic region covering the functional *GmTFL1b* allele from the indeterminate ‘Moshidou Gong 503’ complemented the determinate habit. To evaluate the benefits of indeterminate growth habit in breeding to improve the yield potential of Japanese soybean varieties, two populations of RILs derived from crosses between determinate Japanese cultivars and indeterminate United States cultivars were grown in Akita and Kyoto (Kato et al. 2015). The indeterminate growth habit was an advantageous characteristic for breeding high-yield early-maturing soybean varieties in the Tohoku region.

Soybean fasciation is controlled by the recessive allele *f*, which affects the shape of aerial parts of the plant and is characterized by a flattened stem, infrequent branches, and clustering of flowers and pods on shoot apices; it has been traditionally used in flower arrangements in Japan. The corresponding loci of the three Japanese fasciation landraces, ‘Shakujodaizu,’ ‘Taikadaizu,’ and ‘Shakujomame,’ were found to be same and located on chromosome 2 (Onda et al. 2011). Deletion of the region, including the two predicted genes, *Glyma02g36940* and *Glyma02g36960*, each encoding a leucine-rich repeat receptor-like kinase (LRR-RLK) and a WD-repeat protein, respectively, resulted in co-segregation with the fasciation phenotype in the fine mapping population. The candidate gene responsible for branch development has been recently identified using the Korean soybean core collection (Shim et al. 2019). Narrow leaflets of soybeans are controlled by the recessive allele *ln* and have been suggested to increase the number of seeds per pod. Jeong et al. (2012) found that *Gm-JAG1* (*Glyma20g25000*) encodes a gene controlling *Ln* by using *Arabidopsis*. Sayama et al. (2017) found that

soybean *Ln* pleiotropically controls leaflet shape and number of seeds per pod by using *Gm-jag1* mutants from a high-density mutant library.

Pod dehiscence (shattering) is a major cause of yield loss during the mechanical harvesting of soybeans. A major QTL for pod dehiscence, designated as *qPDH1*, was confined to a 134 kb region on chromosome 16 using RILs derived from a cross between the shattering-susceptible cultivar ‘Toyomusume’ and shattering-resistant cultivar ‘Hayahikari’ (Suzuki et al. 2010). Funatsuki et al. (2014) further narrowed the candidate region down to a 20 kb region and identified a nonsense variant at the 31st amino acid residue of the Pod dehiscence 1 (*Pdh1*) gene in the shattering-resistant cultivars. Transformants of the shattering-resistant cultivar ‘Jack’ with a 3.4 kb genomic region containing the gene from the shattering cultivar exhibited a significantly higher degree of pod dehiscence than that of the control. The protein encoded by *Pdh1* is a member of the dirigent (DIR) superfamily and may promote pod dehiscence by influencing the physical properties of the inner sclerenchyma. Introduction of *pdh1* into Japanese leading varieties by MAS for recurrent backcrossing progenies is underway, and new pod dehiscence-resistant soybean cultivars, ‘Sachiyutaka A1 gou’ (Hajika et al. 2016) and ‘Fukuyutaka A1 gou’ (Yamada et al. 2017), were recently released. The distribution of the *pdh1* allele was surveyed using the NARO mini-core collection (Kaga et al. 2012). They found only two accessions containing *pdh1* among the Japanese landraces, whereas more than half of the Chinese landraces possessed *pdh1* (Funatsuki et al. 2014).

Identification of responsible genes for plant type and growth characteristics is limited, as described above. Physiological works, including photosynthesis, are also necessary to promote the development high-yield soybeans.

Flowering time

Flowering, maturity, and photoperiod sensitivity are very important traits involved in adaptation and productivity of soybeans.

Soybeans are grown over a wide range of latitudes, from the equator to at least 50°N and 35°S. However, the cultivation area of each cultivar is restricted to a very narrow range of latitudes. The wide adaptability of soybeans has been selected from natural variation in

the genes controlling flowering time. Ten major genes, *E1–E9* and *J*, have been reported to control time to flowering and maturity (Watanabe et al. 2012), whereas the *E5* locus may not exist (Dissanayaka et al. 2016). Recently, a new maturity locus *E10* was found in Canada and the *Arabidopsis* homolog soybean *FT4* was identified as a candidate underlying the locus (Samanfar et al. 2017). An update on recent studies on the molecular mechanism of flowering under long days was presented by Cao et al. (2017).

The populations derived from a cross between ‘Harosoy’ (*e1/e2/E3*) and ‘Harosoy-E1’ (*E1/e2/E3*) were used for fine-mapping of the *E1* locus. In the progenies of this population, the *E1* locus was limited to a 17.4 kb region containing an intron-free gene by using more than 13,000 plants (Xia et al. 2012). *E1* encodes a protein containing a putative bipartite nuclear localization signal and region distantly related to the B3 domain, suggesting that this protein is a transcriptional factor. *E1* is thought to suppress the expression of *GmFT2a* and *GmFT5a*, which are both orthologs of *Arabidopsis* *FLOWERING LOCUS T* (*FT*) (Kong et al. 2010), under the regulation of the *E3* and *E4* loci (Xia et al. 2012).

GmGla (*Glyma 10g36600*), an ortholog of *Arabidopsis* *GIGANTAE* (*GI*), was found to be responsible for the *E2* locus using RILs and RHLs derived from a cross between ‘Misuzudaizu’ and ‘Moshidou Gong 503’ (Watanabe et al. 2011; Harada et al. 2011). *GmGla* suppressed *GmFT2a* expression, and recessive alleles at the *E2* locus showed early flowering possibly because of the dysfunction of suppression (Watanabe et al. 2011). Using the same RILs as described above and progenies of an RHL, a responsible gene for the *E3* locus was identified as a phytochrome A gene, *GmPhyA3* (Watanabe et al. 2009; Harada et al. 2011). The gene responsible for the *E4* locus was identified as another phytochrome A gene, *GmPhyA2*, using a candidate gene approach (Liu et al. 2008).

Recently, *FT2a* was found to be responsible for the *E9* locus (Zhao et al. 2016). Comparison of the expression levels of different alleles among NILs and photoperiod-insensitive cultivars indicated that *SORE-1*, a Ty1/copia-like retrotransposon, insertion in *E9* (the allele *e9*) attenuated *FT2a* expression via its allele-specific transcription repression (Zhao et al. 2016). Fine-mapping delimited a QTL for flowering time on chromosome 16 (*qDTF-J*) to a genomic region of 107 kb harboring *FT5a* (Takeshima et al. 2016).

The transcript abundance of *FT5a* was higher in NILs for the early-flowering (*ef*) than those in late-flowering (*lf*), suggesting that different transcriptional activities or mRNA stability caused differences in flowering time (Takeshima et al. 2016).

The soybean genome contains two *E1* homologs, *E1La* (*Glyma04g24640*) and *E1Lb* (*Glyma18g22670*). Under long-day conditions, all three genes in ‘Harosoy’ showed two peaks of expression, before dusk and after dawn the next day. Experiments using the transition between light and dark phases and night-break experiments revealed that the *E1* family genes were expressed only during light periods and their induction after dawn in long days required a period of light before dusk the previous day (Xu et al. 2015). In the cultivar ‘Toyomusume,’ which lacks *E1*, virus-induced silencing of *E1La* and *E1Lb* up-regulated the expression of *FT2a* and *FT5a* and led to early flowering. Therefore, *E1La* and *E1Lb* have a similar function as *E1* in flowering (Xu et al. 2015). Light regulation of *E1* and *E1L* expression is controlled by

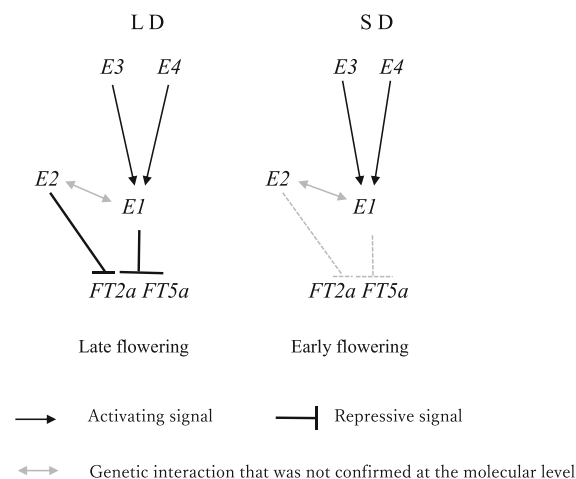


Fig. 2 Proposed molecular network regulating flowering time. The *E1* and *E1* homologs, *E1La* and *E1Lb*, suppress the expression of *GmFT2a* and *GmFT5a*, orthologs of *Arabidopsis* *FLOWERING LOCUS T*, under regulation of *E3* and *E4* encoding phytochrome A. *E2* is an ortholog of *Arabidopsis* *GIGANTAE* (*GI*), which suppresses *GmFT2* expression. Recessive alleles of *E1* are *e1-as*, *e1-fs*, *e1-nl* (Xia et al. 2012), *e1-re*, and *e1-p* (Tsubokura et al. 2014). The *e1-as* allele is hypomorphic (Xia et al. 2012). A nonsense mutation allele of *E2*, *e2-ns*, was found by Watanabe et al. (2011). Recessive alleles in *E3* are *e3-Mo*, *e3-tr* (Watanabe et al. 2009), *e3-ns*, and *e3-fs* (Xu et al. 2013). Recessive alleles of *E4* are *e4-SORE-1* (Liu et al. 2008), *e4-oto*, *e4-tsu*, *e4-kam*, and *e4-kes* (Tsubokura et al. 2013)

E3 and *E4*, which encode phytochrome A proteins, and the regulation of *FT2a* and *FT5a* expression is controlled by *E1* and *E1L* (PHYA-E1 module). The PHYA-E1 module may be a major controller of photoperiodic flowering of soybeans and is not similar to that in *Arabidopsis* and rice (Fig. 2).

Natural variation in genes at the *E1*, *E2*, *E3*, and *E4* loci was determined for 62 soybean accessions and one wild soybean (Tsubokura et al. 2014). Fifty-three photoperiod-insensitive accessions were classified into 15 multi-locus genotypes at the *E1*, *E2*, *E3*, and *E4* loci. All 53 accessions contained a recessive allele at either the *E3* or *E4* locus. When one of these loci had a dominant allele, the *E1* locus always had a loss-of-function of *e1-fs* or *e1-nl* or the hypomorphic *e1-as* allele (Xu et al. 2013). However, these accessions markedly differed in their post-flowering vegetative and reproductive growth characteristics, such as reproductive period and stem growth after flowering. Accessions carrying *E3* or *E4* were sensitive to the photoperiod for post-flowering characteristics. The phytochrome A-regulated expression of the determinate growth habit gene *Dt1* was involved in the persistence of vegetative activity at the SAM of flower-induced plants under long-day conditions (Xu et al. 2013). Association of maturity of soybean varieties and adaptation to different latitudes with allelic variation of *E1* to *E4* was also observed to some extent in China (Jiang et al. 2014; Zhai et al. 2014), the United States (Wolfgang and An 2017), and Europe (Kurasch et al. 2017).

Watanabe et al. (2017) used a combination restriction site-associated DNA sequencing (RAD-seq) and bulked segregant analysis to identify QTLs for flowering time in a segregating population derived from a cross between Japanese soybean cultivars. Despite the homogeneous genetic background of the parents, over 7000 SNPs were identified and are useful for detecting QTLs. By comparing the genotype frequency between early and late flowering bulks from the F3 generation, a QTL on chromosome 10, which corresponds to the *E2* locus, and a QTL on chromosome 4 close to the *E8* locus were identified (Watanabe et al. 2017). This approach may improve the efficiency of genetic mapping.

‘Enrei’ (*E1/e2/e3/E4*) is one of the leading cultivars in Japan. To expand the adaptability of ‘Enrei,’ NILs for *E2* and *E3* were developed and their flowering, maturity, seed productivity, and seed quality traits

were evaluated in five different locations (Yamada et al. 2012). The dominant alleles *E2* and *E3* were introduced from ‘Sachiyutaka’ (*E1/E2/e3/E4*) and ‘Fukuyutaka’ (*E1/E2/E3/E4*), respectively, by recurrent backcrosses based on functional DNA markers. Modification of the genotypes at maturity loci provides new varieties adapted to environments at different latitudes while retaining nearly the same seed quality as that of the original cultivar. Modification of maturity loci is currently being assessed for several other cultivars.

QTL analyses for the branching phenotypes (Sayama et al. 2010), a raceme phenotype (Yamaguchi et al. 2014b), duration of the reproductive period (Komatsu et al. 2012), green stem disorder insensitivity (Yamada et al. 2014), and lodging tolerance (Yamaguchi et al. 2014c) were performed. Because these traits are affected by *E* genes to various degrees, attempts to remove the effects were made in these studies.

To facilitate molecular dissection of flowering control and other agricultural important traits affected by flowering in soybeans, further analyses of QTLs for flowering are necessary by the combined approach, including fine mapping and use of candidate gene information from model plant species.

Symbiosis

Among the major legume crops, soybeans are most highly dependent on atmospheric nitrogen fixed in the nodules, which contributes to soil fertility through rhizobial symbiosis. Symbiotic nitrogen fixation is critical in soybean seed productivity. Symbiotic interactions of legume plants and Rhizobium bacteria exhibit strict species–species specificity. This specificity is determined by the structures of lipochitin oligosaccharide signal molecules, known as Nod factors (NFs), which are secreted from rhizobia (Cullimore et al. 2001). Putative NF receptors in legumes belong to a family of LysM-RLK (lysine-motif receptor-like kinase), which have a common structure of a single transmembrane domain with an extracellular lysine motif (LysM) receptor domain and intracellular Ser/Thr kinase domain. In *Lotus japonicus*, two genes encoding LysM-RLK, *NFR1* and *NFR5*, were identified. The soybean genome contains two *LjNFR1* orthologs, *GmNFR1α* and *GmNFR1β*, and two *LjNFR5* orthologs, *GmNFR5α* and *GmNFR5β*.

Nitrogen-fixing nodules consume large amounts of photosynthates from the host plants, and thus excessive nodulation retards plant growth. To avoid inappropriately excessive nodulation and maintain the balance of symbiosis, legume plants use a negative feedback regulatory system known as autoregulation, in which developed nodules or nodule primordia suppress the emergence of further nodules. Hypernodulation mutants can form a considerable excess of nodule numbers even under high concentrations of soil nitrates, which inhibits nodulation in wild-type plants (Akao and Kouchi 1992). This trait is controlled by a single recessive gene, *rj7* (*nts*). Through reciprocal and self-grafting studies using *L. japonicus* hypernodulation *har1* mutants, the shoot genotype is responsible for negatively regulating nodule development (Nishimura et al. 2002). *HAR1*, which encodes a protein containing 21 leucine-rich repeats, a single transmembrane domain, and serine/threonine kinase domains, is an ortholog of the soybean *NTS1/GmNARK*. The hypernodulation mutant line En6500 originated from ‘Enrei,’ which is allelic to the *nts1* mutant and contains a stop codon near the transmembrane domain (Nishimura et al. 2002).

It has been well-documented that some soybean genotypes differentially restrict nodulation with specific serogroups of *Bradyrhizobium* or *Ensifer/Sinorhizobium*. Identification of genes that exclude or substantially reduce nodulation with the ineffective indigenous strains may provide insight into improving the efficiency of symbiotic nitrogen fixation in soybeans by application of inoculants. *Rj4* of ‘Peking’ restricts nodulation with specific strains, such as *B. elkanii* USDA61 and *B. japonicum* Is-34, and the responsible gene has been identified on chromosome 1 by fine mapping using progenies derived a cross between ‘Enrei’ (*rj4/rj4*) and ‘Peking’ (*Rj4/Rj4*) (Hayashi et al. 2014). *Rj4* encodes a thaumatin-like protein, with approximately 200 amino acid residues sharing sequence similarity with thaumatin. Research from the United States claimed that the encoding protein of *Rj4* is another thaumatin-like protein (Tang et al. 2016). Mutants of the type III secretion system of the incompatible *Bradyrhizobium* strains enable normal nodulation in *Rj4* and *Rfg1* genotypes, suggesting that the type III secretion system is involved in determining host specificity through a gene-for-gene interaction mechanism (Okazaki et al. 2009). Introducing the Tn5 transposon into *B. elkanii* USDA61

resulted in the formation of nitrogen-fixation nodules on the roots of 'BARC2' carrying *Rj4*. Among the Tn5-flanking gene regions, a cysteine protease mutant shared high similarity with the type 3 effector protein XopD of *Xanthomonas campestris* (Faruque et al. 2015). Further studies are necessary to understand the interaction between the thaumatin-like protein and effector(s) of rhizobia.

In addition, because symbiotic nitrogen fixation critically contributes to soybean seed productivity, as well as biological nitrogen supply, identification of soybean genes involved in nitrogen fixation ability is important for sustainable cropping system worldwide.

Prospects

Soybeans are one of the most important crops for ensuring food security worldwide. Because soybean seeds have a high content of high-quality protein and numerous physiologically functional constituents, fibers, minerals, and so on, whole beans or its derived-foods are ideal for human health. In addition to boiling or steaming the seeds for use in a variety of recipes, soy flour for cakes and bread, and soy paste for meat-alternatives, soups, stews, and soufflés can be prepared from whole beans. As described above, the genetic background of the Japanese germplasms is clearly different from that of world germplasms. Seeds of various Japanese landraces have been consumed as nimame (boiled beans), mushimame (steamed beans), hitashimame (boiled beans with a modicum of soy sauce), and edamame (vegetable soybean). They are unique to Japan and tasty having a very slight beany flavor and sometimes various other pleasant flavors.

For worldwide food use of such soybeans, identification of the genes responsible for physiologically functional constituents and good sensory quality of taste and flavor are important for the development of new varieties for worldwide food uses. New plant breeding techniques, particularly genome editing techniques, may accelerate the development of soybean varieties. Because these traits are controlled by many genetic factors, genome-wide association analysis, and genomic selection are expected to be useful for assessing the Japanese soybean germplasms and developing new varieties with more suitable cultivation, growth characteristics, and high yield.

Because soybean yield in Japan remains low and unstable, increasing productivity is an urgent problem. It is crucial to effectively use gene information obtained in recent studies of biotic and abiotic stress tolerances in MAS breeding. Additionally, it is essential to develop high-throughput phenotyping methods for analyzing lodging resistance and spatial and temporal plant architecture-related traits that are difficult to evaluate but highly related to productivity. Platforms for ground vehicles and unmanned aerial vehicles with multiple sensors may become valuable tools for assessing traits, such as spatial and temporal growth rate, population density, canopy biomass, and branching, which were previously estimated using destructive methods with a large population. Plant architecture for light capture and physiological characteristics, including photosynthesis and translocation of the photosynthate will also be important for improving productivity. Identification of genes that improve biotic and abiotic stress resistance will be accelerated by using Japanese soybean genomic resources, such as whole genome sequences and SNP information, core collection, chromosome segment substitution lines, and mutant libraries.

Acknowledgements We thank Dr. Masatsugu Hashiguchi, Dr. Satoshi Watanabe, and Dr. Fukuhiro Yamasaki for their kind assistance in preparing the statistics for the genetic resources in the National BioResource Project, the figure for the flowering network, the statistics of the NARO Genebank, and the picture for the soybean mini-core collection, respectively.

References

- Abe J, Xu DH, Suzuki Y, Kanazawa A, Shimamoto Y (2003) Soybean germplasm pools in Asia revealed by SSR. *Theor Appl Genet* 106:445–453
- Akao S, Kouchi H (1992) A supernodulating mutant isolated from soybean cultivar Enrei. *Soil Sci Plant Nutr* 38:183–187
- Akazawa T, Egashira H (2005) Dadachamame (in Japanese). *J Jpn Soc Edamame Sci* 3:2–10
- Anai T (2012) Potential of a mutant-based reverse genetic approach for functional genomics and molecular breeding in soybean. *Breed Sci* 61:462–467
- Anai T, Yamada T, Hideshima R, Kinoshita T, Rahman SM, Takagi Y (2008) Two high-oleic-acid soybean mutants, M23 and KK21, have disrupted microsomal omega-6 fatty acid desaturase, encoded by *GmFAD2-1a*. *Breed Sci* 58:447–452
- Arikat S, Yoshihashi T, Wapchana S, Uyen TT, Huong NTT, Wongpornchai S, Vanavichit A (2011a) Deficiency in the amino aldehyde dehydrogenase encoded by *GmAMADH2*,

- the homologue of rice *Os2AP*, enhances 2-acetyl-1-pyrroline biosynthesis in soybeans (*Glycine max* L.). Plant Biotechnol J 9:75–87
- Arikrit S, Yoshihashi T, Wanchana S, Tanya P, Juwattanasomran R, Srinives P, Vanavichit A (2011b) A PCR-based marker for a locus conferring aroma in vegetable soybean (*Glycine max* L.). Theor Appl Genet 122:311–316
- Bandillo N, Jarquin D, Song Q, Nelson R, Cregan P, Specht J et al (2015) A population structure and genome-wide association analysis on the USDA soybean germplasm collection. The Plant Genome 8. <https://doi.org/10.3835/plantgenome2015.04.0024>
- Benitez ER, Hajika M, Yamada T, Takahashi K, Oki N, Yamada N et al (2010) A major QTL controlling seed cadmium accumulation in soybean. Crop Sci 50:1728–1734
- Cao D, Takeshima R, Zhao C, Liu B, Abe J, Kong F (2017) Molecular mechanisms of flowering under long days and stem growth habit in soybean. J Exp Bot 68:1873–1884
- Chinchest A, Nakeeraks P (1990) Mutation breeding of blackgram (*Vigna mungo*). Mungbean Meet 90:43–46
- Cooper JK, Till BJ, Laport RG, Darlow MG, Kleffner JM, Jamai A et al (2008) TILLING to detect induced mutations in soybean. BMC Plant Biol. <https://doi.org/10.1186/1471-2229-8-9>
- Cornelius B, Chen P, Chen Y, de Leon N, Shannon JG, Wang D (2005) Identification water-logging tolerance in soybean. Mol Breed 16:103–112
- Cullimore JV, Ranjeva R, Bono JJ (2001) Perception of lipochitooligosaccharidic Nod factors in legumes. Trends Plant Sci 6:24–30
- Davies CS, Nielsen NC (1986) Genetic analysis of a null-allele for lipoxygenase-2 in soybean. Crop Sci 26:460–462
- Dissanayaka A, Rodriguez TO, Di S, Yan F, Githiri SM, Rodas FR et al (2016) Quantitative trait locus mapping of soybean maturity gene *E5*. Breed Sci 66:407–415
- Dwiyanti MS, Ujiie A, Thuy LTB, Yamada T, Kitamura K (2007) Genetic analysis of high α -tocopherol content in soybean seeds. Breed Sci 57:23–28
- Dwiyanti MS, Yamada T, Sato M, Abe J, Kitamura K (2011) Genetic variation of γ -tocopherol methyltransferase gene contributes to elevated α -tocopherol content in soybean seeds. BMC Plant Biol 11:152
- Faruque OM, Miwa H, Yasuda M, Fuji Y, Kaneko T, Sato S, Okazaki S (2015) Identification of *Bradyrhizobium elkanii* genes involved in incompatibility with soybean plants carrying the *Rj4* allele. Appl Environ Microbiol 81:6710–6717
- Francisco PB, Akao S (1993) Autoregulation and nitrate inhibition of nodule formation in soybean cv. Enrei and its nodulation mutants. J Exp Bot 44:547–553
- Fukui J, Arai M (1951) Ecological studies on Japanese soy-bean varieties. I. Classification of soy-bean varieties on the basis of the days from germination to blooming and from blooming to ripening with special reference to their geographic differentiation. Jpn J Breed 1:27–39
- Funatsuki H, Kawaguchi K, Matsuba S, Sato Y, Ishimoto M (2005) Mapping of QTL associated with chilling tolerance during reproductive growth in soybean. Theor Appl Genet 111:851–861
- Funatsuki H, Suzuki M, Hirose A, Inaba H, Yamada T, Hajika M et al (2014) Molecular basis of a shattering resistance boosting global dissemination of soybean. Proc Natl Acad Sci USA 111:17797–17802
- Fushimi T, Masuda R (2001) 2-Acetyl-1-pyrroline concentration of the aromatic vegetable soybean “Dadacha-Mame”. In: Proceeding of second international vegetable soybean conference, Washington State University, Tacoma, Washington, 39
- Hajika M, Igita K, Kitamura K (1991) A line lacking all the seed lipoxygenase isozymes in soybean [*Glycine max* (L.) Merrill] induced by gamma-ray irradiation. Jpn J Breed 41:507–509
- Hajika M, Takahashi M, Igita M (1996) A new genotype of 7S globulin (β -conglycinin) detected in wild soybean (*Glycine soja* Sieb. et Zucc). Breed Sci 46:385–386
- Hajika M, Takahashi M, Sakai S, Matsunaga R (1998) Dominant inheritance of a trait lacking β -conglycinin detected in a wild soybean line. Breed Sci 48:383–386
- Hajika M, Takahashi M, Igita K, Sakai S, Nakazawa Y (2002) A new soybean variety “Ichihime”. Bull Natl Agric Res Cent Kyushu Okinawa Reg 40:79–94
- Hajika M, Funatsuki H, Yamada T, Takahashi K, Hishinuma A, Hirata K et al (2016) Development of a new pod dehiscence-resistant soybean cultivar ‘Sachiyutaka A1 gou’. Bull NARO Inst Crop Sci 16:1–34
- Han VP, Teng WL, Wang Y, Zhao X, Wu L, Li DM (2015) Unconditional and conditional QTL underlying the genetic interrelationships between soybean seed isoflavone, and protein or oil contents. Plant Breed 134:300–309
- Harada K, Xia Z (2004) Soybean genomics: efforts to reveal the complex genome. Breed Sci 54:215–224
- Harada K, Watanabe S, Xia Z, Tsubokura Y, Yamanaka N, Anai T (2011) Positional cloning of the responsible genes for maturity loci *E1*, *E2*, and *E3* in soybean. In: D. Krezhova (ed.) “Soybean-genetics and novel techniques for yield enhancement”. IntechOpen, Croatia, pp 51–76
- Hayashi M, Saeki Y, Haga M, Harada K, Kouchi H, Umehara Y (2012) *Rj* (*rj*) genes involved in nitrogen-fixing root nodule formation in soybean. Breed Sci 61:544–553
- Hayashi M, Shiro S, Kanamori H, Mori-Hosokawa S, Sasaki-Yamagata H, Sayama T et al (2014) A thaumatin-like protein, Rj4, controls nodule symbiotic specificity in soybean. Plant Cell Physiol 55:1679–1689
- Hildebrand DF, Hymowitz T (1981) Two soybean genotypes lacking lipoxygenase-1. J Am Oil Chem Soc 58:583–586
- Hirata K, Masuda R, Tsubokura Y, Yasui T, Yamada T, Takahashi K et al (2014) Identification of quantitative trait loci associated with boiled seed hardness in soybean. Breed Sci 64:362–370
- Hirota T, Yoshida S, Sawada T, Nakamura Y (2018) Starch properties affecting maltose production ability in vegetative black soybean seeds (edamame) with different maturation period. Hort J 87:236–249
- Hisano H, Sato S, Isobe S, Sasamoto S, Wada T, Matsuno A et al (2007) Characterization of the soybean genome using EST-derived microsatellite markers. DNA Res 14:271–281
- Hong JS, Masuda C, Nakano M, Abe J, Ueda I (2003) Adaptation of cucumber mosaic virus soybean strains (SSVs) to cultivated and wild soybeans. Theor Appl Genet 107:49–53
- Hoshino T, Takagi Y, Anai T (2010) Novel *GmFAD2-1b* mutant alleles created by reverse genetics induce marked elevation

- of oleic acid content in soybean seeds in combination with *GmFAD2-1a* mutant alleles. *Breed Sci* 60:419–425
- Hoshino T, Watanabe S, Takagi Y, Anai T (2014) A novel *GmFAD3-2a* mutant allele developed through TILLING reduces α -linolenic acid content in soybean seed oil. *Breed Sci* 64:371–377
- Hwang T-Y, Sayama T, Takahashi M, Takada Y, Nakamoto Y, Funatsuki H et al (2009) High-density integrated linkage map based on SSR markers in soybean. *DNA Res* 16:213–225
- Hymowitz T (1970) On the domestication of the soybean. *Econ Bot* 24:408–421
- Hymowitz T, Kaizuma K (1981) Soybean seed protein electrophoresis profiles from 15 Asian countries or regions: hypotheses on paths of dissemination of soybeans from China. *Econ Bot* 35:10–23
- Hyten D, Choi I-Y, Song Q, Specht JE, Carter TE, Shoemaker RC et al (2010) A high density integrated genetic linkage map of soybean and the development of a 1536 universal soy linkage panel for quantitative trait locus mapping. *Crop Sci* 50:960–968
- Imai S (2014) Effect of green soybean extracts on allergy and inflammation. *Nippon Shokuhin Kagaku Kogaku Kaishi* 61:625–631
- Ishikawa G, Takada Y, Nakamura T (2006) A PCR-based method to test for the presence or absence of β -conglycinin α' - and α -subunits in soybean seeds. *Mol Breed* 17:365–374
- Jang SJ, Sato M, Sato K, Jitsuyama Y, Fujino K, Mori H et al (2015) A single-nucleotide polymorphism in an endo-1,4- β -glucanase gene controls seed coat permeability in soybean. *PLoS ONE* 10:e0128527
- Jegadeesan S, Yu K, Poysa V, Gawalko E, Morrison MJ, Shi C et al (2010) Mapping and validation of simple sequence repeat markers linked to a major gene controlling seed cadmium accumulation in soybean [*Glycine max* (L.) Merr]. *Theor Appl Genet* 121:283–294
- Jeong N, Suh SJ, Kim MH, Lee S, Moon JK, Kim HS et al (2012) *Ln* is a key regulator of leaflet shape and number of seeds per pod in soybean. *Plant Cell* 24:4807–4818
- Jiang B, Nan H, Gao Y, Tang L, Yue Y, Lu S et al (2014) Allelic combinations of soybean maturity loci *E1*, *E2*, *E3* and *E4* result in diversity of maturity and adaptation to different latitudes. *PLoS ONE* 9:e106042
- Jiang CJ, Sugano S, Kaga A, Lee SS, Sugimoto T, Takahashi M et al (2017) Evaluation of resistance to *Phytophthora sojae* in soybean mini core collections using an improved assay system. *Phytopathology* 107:216–223
- Kaga A, Shimizu T, Watanabe S, Tsubokura Y, Katayose Y, Harada K et al (2012) Evaluation of soybean germplasm conserved in NIAS Genebank and development of mini core collections. *Breed Sci* 61:566–592
- Kanamaru K, Wang S, Abe J, Yamada T, Kitamura K (2006) Identification and characterization of wild soybean (*Glycine soja* Sieb. et Zucc.) strains with high lutein content. *Breed Sci* 56:231–234
- Kasai A, Kasai K, Yumoto S, Senda M (2007) Structural features of *GmIRCHS*, candidate of the *I* gene inhibiting seed coat pigmentation in soybean: implication for inducing endogenous RNA silencing of chalcone synthase genes. *Plant Mol Biol* 64:467–479
- Kasai A, Ohnishi S, Yamazaki H, Funatsuki H, Kurauchi T, Matsumoto T et al (2009) Molecular mechanism of seed coat discoloration induced by low temperature in yellow soybean. *Plant Cell Physiol* 50:1090–1098
- Kasuga T, Salimath SS, Shi J, Gijzen M, Buzzell RI, Bhat-tacharyya MK (1997) High resolution genetic and physical mapping of molecular markers inked to the *Phytophthora* resistance gene *RpsI-k* in soybean. *Mol Plant Microbe Interact* 10:1035–1044
- Kato S, Yumoto S, Takada Y, Kono Y, Shimada S, Sakai T et al (2007) A new soybean cultivar “Kinusayaka” lacking lipoxygenase isozymes and group A acetyl saponin. *Bull Natl Agric Res Cent Tohoku Reg* 107:29–42
- Kato S, Fujii K, Yumoto S, Ishimoto M, Shiraiwa T, Sayama T et al (2015) Seed yield and its components of indeterminate and determinate lines in recombinant inbred lines of soybean. *Breed Sci* 65:154–160
- Kato S, Takada Y, Shimamura S, Hirata K, Sayama T, Taguchi-Shiobara F et al (2016) Transfer of the *Rsv3* locus from ‘Harosoy’ for resistance to soybean mosaic virus strains C and D in Japan. *Breed Sci* 66:319–327
- Kato S, Sayama T, Takada Y, Yumoto S, Ishimoto M, Shimamura S et al (2017) Breeding of soybean lines conferred multiple disease and pest resistance by marker-assisted selection with a high-resolution PCR fragment analysis system. (2017) Bulletin NARO. Agric Res Cent Tohoku Reg 119:89–106
- Kikuchi A, Tsukamoto C, Tabuchi K, Adachi T, Okubo K (1999) Inheritance and characterization of a null allele for group A acetyl saponins found in a mutant soybean (*Glycine max* (L.) Merrill). *Breed Sci* 49:167–171
- Kim DH, Kim KH, Van K, KIM MY, Lee SH (2010) Fine mapping of a resistance gene to bacterial leaf pustule in soybean. *Theor Appl Genet* 120:1443–1450
- Kitamura K, Kaizuma N (1981) Mutant strains with low levels of subunits of 7S globulin in soybean (*Glycine max* Merr.) seed. *Jpn J Breed* 31:353–359
- Kitamura K, Davies CS, Kaizuma N, Nielsen NC (1983) Genetic analysis of a null-allele for lipoxygenase-3 in soybean seeds. *Crop Sci* 23:924–927
- Kitamura K, Kumagai T, Kikuchi A (1985) Inheritance of lipoxygenase-2 and genetic relationship among genes for lipoxygenase-1, -2 and -3 isozymes in soybean seeds. *Jpn J Breed* 35:413–420
- Kitamura K, Ishimoto M, Kaizuma N (1993) Genetic relationships among genes for the subunits of soybean 11S globulin. *Japan J Breed* 43(Suppl. 2):159
- Kohzuma K, Sato Y, Ito H, Okuzaki A, Watanabe M, Kobayashi H et al (2017) The non-mendelian green gene in soybean encodes a small subunit of photosystem II. *Plant Physiol* 173:2138–2147
- Komatsu K, Okuda S, Takahashi M, Matsunaga R (2004) Antibiotic effect of insect-resistance soybean on common cutworm (*Spodoptera litura*) and its inheritance. *Breed Sci* 54:27–32
- Komatsu K, Okuda S, Takahashi M, Matsunaga R, Nakazawa Y (2005) QTL mapping of antibiosis resistance to common cutworm (*Spodoptera litura* Fabricius) in soybean. *Crop Sci* 45:2044–2048
- Komatsu K, Hwang TY, Takahashi M, Sayama T, Funatsuki H, Oki N, Ishimoto M (2012) Identification of QTL

- controlling post-flowering period in soybean. *Breed Sci* 61:646–652
- Komatsu S, Nanjo Y, Nishimura M (2013) Proteomic analysis of the flooding tolerance mechanism in mutant soybean. *J Proteomics* 79:231–250
- Kong F, Liu B, Xia Z, Sato S, Kim BM, Watanabe S et al (2010) Two coordinately regulated homologs of *FLOWERING LOCUS T* are involved in the control of photoperiodic flowering in soybean. *Plant Physiol* 154:1220–1231
- Kurasch A, Hahn V, Leiser W, Vollman J, Schori A, Betrix C-A et al (2017) Identification of mega-environments in Europe and effect of allelic variation at maturity *E* loci on adaptation of European soybean. *Plant Cell Environ*. <https://doi.org/10.1111/pce.12896>
- Kurosaki H, Yumoto S, Matsukawa I (2004) Correlation of cold-weather tolerance with pubescence color and flowering time in yellow hilum soybeans in Hokkaido. *Breed Sci* 54:303–311
- Kurosaki H, Fujita S, Ohnishi S, Kosaka F, Tanaka Y, Takeuchi T et al (2017) A new soybean variety “Suzumaru R”. *Bull Hokkaido Res Org Agric Exp Stn* 101:1–13
- Lam HM, Xu X, Liu X, Chen W, Yang G, Wong FL et al (2010) Resequencing of 31 wild and cultivated soybean genomes identifies patterns of genetic diversity and selection. *Nat Genet* 42:1053–1059
- Lee GH, Crawford GW, Liu L, Sasaki Y, Chen X (2011) Archaeological soybean (*Glycine max*) in East Asia: does size matter? *PLoS ONE* 6:e26720
- Lee S, Freewalt KR, McHale LK, Song Q, Jun TH, Michel Michel AP et al (2015) A high-resolution linkage map of soybean based on 357 recombinant inbred lines genotyped with BARCSoySNP6 K. *Mol Breed*. <https://doi.org/10.1007/s11032-015-0209-5>
- Lenis JM, Gillman JD, Lee JD, Shannon JG, Bilyeu KD (2010) Soybean seed lipooxygenase genes: molecular characterization and development of molecular marker assays. *Theor Appl Genet* 120:1139–1149
- Liu B, Fujita T, Yan Z, Sakamoto S, Xu D, Abe J (2007) QTL mapping of domestication-related traits in soybean (*Glycine max*). *Ann Bot* 100:1027–1038
- Liu B, Kanazawa A, Matsumura H, Takahashi R, Harada K, Abe J (2008) Genetic redundancy in soybean photoreponses associated with duplication of the phytochrome A gene. *Genetics* 180:995–1007
- Liu B, Watanabe S, Uchiyama T, Kong F, Kanazawa A, Xia Z et al (2010) The soybean stem growth habit gene *Dt1* is an ortholog of Arabidopsis *TERMINAL FLOWER1*. *Plant Physiol* 153:198–210
- Liu D, Yan Y, Fujita Y, Xu D (2018) Identification and validation of QTLs for 100-seed weight using chromosome segment substitution lines in soybean. *Breed Sci* 68:442–448
- Matsumura Y, Sirison J, Ishi T, Matsumiya K (2017) Soybean lipophilic proteins-Origin and functional properties as affected by interaction with storage proteins. *Curr Opin Colloid Interface Sci* 28:120–128
- Miyazaki S, Carter TE, Shiina T, Chibana T, Miyashita S, Kunihiro Y (1995) Identification of representative accessions of old cultivars that contribute to the pedigree of modern Japanese soybean varieties, based on passport data analysis. *Misc Publ Natl Ins Agrobiol Resour* 8:18–37
- Morisaki A, Yamada N, Yamanaka S, Matsui K (2014) Dime-thyl sulfide as a source of the seaweed-like aroma in cooked soybeans and correlation with its precursor, S-Methylmethionine (vitamin U). *J Agric Food Chem* 62:8289–8294
- Moriwaki J (2010) Aiming of the construction of the race distinction system of *Phytophthora sojae*. *Plant Prot* 64:508–510
- Naito K, Takahashi Y, Chaitieng B, Hirano K, Kaga A, Takagi K et al (2017) Multiple organ gigantism caused by mutation in *VmPPD* gene in blackgram (*Vigna mungo*). *Breed Sci* 67:151–158
- Nakano M, Yamada T, Masuda Y, Sato Y, Kobayashi H, Ueda H et al (2014) A green-cotyledon/stay-green mutant exemplifies the ancient whole-genome duplications in soybean. *Plant Cell Physiol* 55:1763–1771
- Nakayama S (2015) Domestication of the soybean (*Glycine max*) and morphological differentiation of seeds in the Jomon period. *Jpn J Histor Bot* 23:33–42
- Nguyen VT, Vuong TD, VanToai T, Lee JD, Wu X, Rouf Mian MA et al (2012) Mapping of quantitative trait loci associated with resistance to *Phytophthora sojae* and flooding tolerance in soybean. *Crop Sci* 52:2481–2493
- Nguyen LV, Takahashi R, Githiri SM, Rodriguez TO, Tsutsumi N, Kajihara S et al (2017) Mapping quantitative trait loci for root development under hypoxia conditions in soybean (*Glycine max* L. Merr.). *Theor Appl Genet* 130:743–755
- Nishimura R, Hayashi M, Wu GJ, Kouchi H, Imaizumi-Anraku H, Murakami Y et al (2002) *HAR1* mediates systemic regulation of symbiotic organ development. *Nature* 420:426–429
- Odanaka H, Kaizuma N (1989) Mutants on soybean storage proteins induced with γ -ray irradiation. *Jpn J Breed* 39(Suppl. 1):430–431
- Ohnishi S, Funatsuki H, Kasai A, Kurauchi T, Yamaguchi N, Takeuchi T et al (2011) Variation of *GmIRCHS* (*Glycine max* inverted-repeat CHS pseudogene) is related to tolerance of low temperature-induced seed coat discoloration in yellow soybean. *Theor Appl Genet* 122:633–642
- Ohnishi S, Miyake N, Takeuchi T, Kousaka F, Hiura S, Kanehira O et al (2012) Fine mapping of foxglove aphid (*Aulacorthum solani*) resistance gene *Rasol* in soybean and its effect on tolerance to *Soybean dwarf virus* transmitted by foxglove aphid. *Breed Sci* 61:618–624
- Okazaki S, Zehner S, Hempel J, Lang K, Gottfert M (2009) Genetic organization and functional analysis of the type III secretion system of *Bradyrhizobium elkanii*. *FEMS Microbiol Lett* 295:88–95
- Oki N, Komatsu K, Sayama T, Ishimoto M, Takahashi M, Takahashi M (2012) Genetic analysis of antixenosis resistance to the common cutworm (*Spodoptera litura* Fabricius) and its relationship with pubescence characteristics in soybean (*Glycine max* (L.) Merr.). *Breed Sci* 61:608–617
- Oki N, Kaga A, Shimizu T, Takahashi M, Kono Y, Takahashi M (2017) QTL mapping of antixenosis resistance to common cutworm (*Spodoptera litura* Fabricius) in wild soybean (*Glycine soja*). *PLoS ONE* 12:e0189440
- Onda R, Watanabe S, Sayama T, Komatsu K, Okano K, Ishimoto M, Harada K (2011) Genetic and molecular analysis of fasciation mutation in Japanese soybeans. *Breed Sci* 61:26–34

- Primomo VS, Poysa V, Ablett GR, Jackson C-J, Gijzen M, Rajcan I (2005) Mapping QTL for individual and total isoflavone content in soybean seeds. *Crop Sci* 45:2454–2464
- Sakai T, Takada Y, Kono Y, Shimada S (2002) Characteristics of a new soybean variety “Fukuibuki”. *Tohoku Agric Res* 55:65–66
- Samanfar B, Molnar SJ, Charette M, Schoenrock A, Dehne F, Golshani A et al (2017) Mapping and identification of a potential candidate for a novel maturity locus, *E10*, in soybean. *Theor Appl Genet* 130:377–390
- Samoto M, Maebuchi M, Miyazaki C, Kugitani H, Kohno M, Hirotsuka M, Kito M (2007) Abundant proteins associated with lecithin in soy protein isolate. *Food Chem* 102:317–322
- Saruta M, Takada Y, Kikuchi A, Yamada T, Komatsu K, Sayama T et al (2012) Screening and genetic analysis of resistance to peanut stunt virus in soybean: identification of the putative *Rpsv1* resistance gene. *Breed Sci* 61:625–650
- Sayama T, Nakazaki T, Ishikawa G, Yagasaki K, Yamada N, Hirota N et al (2009) QTL analysis of seed-flooding tolerance in soybean (*Glycine max* [L.] Merr.). *Plant Sci* 176:514–521
- Sayama T, Hwang TY, Yamazaki H, Yamaguchi N, Komatsu K, Takahashi M et al (2010) Mapping and comparison of quantitative trait loci for soybean branching phenotype in two locations. *Breed Sci* 60:380–389
- Sayama T, Ono E, Takagi K, Takada Y, Horikawa M, Nakamoto Y et al (2012) The *Sg-1* glycosyltransferase locus regulates structural diversity of triterpenoid saponins of soybean. *Plant Cell* 24:2123–2138
- Sayama T, Tanabata T, Saruta M, Yamada T, Anai T, Kaga A et al (2017) Confirmation of the pleiotropic control of leaflet shape and number of seeds per pod by the *Ln* gene in induced soybean mutants. *Breed Sci* 67:363–369
- Senda M, Masuta C, Ohnishi S, Goto K, Kasai A, Sano T et al (2004) Patterning of virus infected *Glycine max* seed coat is associated with suppression of endogenous silencing of chalcone synthase genes. *Plant Cell* 16:807–818
- Shibata M, Takayama K, Ujiie A, Yamada T, Abe J, Kitamura K (2008) Genetic relationship between lipid content and linolenic acid concentration in soybean seeds. *Breed Sci* 58:361–366
- Shim S, Ha J, Kim MY, Choi MS, Kang S-T, Jeong S-C et al (2019) *GmBRC1* is a candidate gene for branching in soybean (*Glycine max* (L.) Merrill). *Int J Mol Sci*. <https://doi.org/10.3390/ijms20010135>
- Shimamoto Y (2001) Polymorphism and phylogeny of soybean based on chloroplast and mitochondrial DNA analysis. *JARQ* 35:79–84
- Shimomura M, Kanamori H, Komatsu S, Namiki N, Mukai Y, Kurita K et al (2015) The *Glycine max* cv. Enrei genome for improvement of Japanese soybean cultivars. *Int J Genom* 2015:358127
- Shiraiwa M, Yamauchi Harada K, Okubo K (1990) Inheritance of “Group A saponin” in soybean seed. *Agric Biol Chem* 54:1347–1352
- Song Q, Jenkins J, Jia G, Hyten D, Pantalone V, Jackson SA et al (2016) Construction of high resolution genetic linkage maps to improve the soybean genome sequence assembly Glyma1.01. *BMC Genomics*. <https://doi.org/10.1186/s12864-015-2344-0>
- Suematsu K, Abiko T, Nguyen VL, Mochizuki T (2017) Phenotypic variation in root development of 162 soybean accessions under hypoxia condition at the seedling stage. *Plant Prod Sci* 20:323–335
- Sugimoto T, Yoshida S, Watanabe K, Aino M, Kanto T, Mae-kawa K, Irie K (2008) Identification of SSR markers linked to the *Phytophthora* resistance gene *Rps1-d* in soybean. *Plant Breed* 127:154–159
- Sugimoto T, Yoshida S, Kaga A, Hajika M, Watanabe K, Aino M et al (2011a) Genetic analysis and identification of DNA markers linked to a novel *Phytophthora sojae* resistance gene in the Japanese soybean cultivar Waseshiroge. *Euphytica* 182:133–145
- Sugimoto T, Yoshida S, Aino M, Yamamoto R, Kuroda T, Maeda M, Irie K (2011b) Evaluation of several soybeans for field resistance to *Phytophthora sojae* and selection of parental soybeans for breeding new resistant cultivars. *Jpn J Phytopathol* 71:157
- Sun L, Miao Z, Cai C, Zhang D, Zhao M, Wu Y et al (2015) *GmHs1-1*, encoding a calcineurin-like protein, controls hard-seededness in soybean. *Nat Genet* 47:939–943
- Suzuki M, Fujino K, Nakamoto Y, Ishimoto M, Funatsuki H (2010) Fine mapping and development of DNA markers for the *qPDH1* locus associated with pod dehiscence in soybean. *Mol Breed* 25:407–418
- Suzuki C, Tanaka Y, Takeuchi T, Yumoto S, Shirai S (2012) Genetic relationships of soybean cyst nematode resistance originated in Gedenshirazu and PI84751 on *Rhg1* and *Rhg4* loci. *Breed Sci* 61:602–607
- Suzuki C, Miyoshi T, Shirai S, Yumoto S, Tanaka Y, Hagiwara S et al (2017) A new variety “Yukihomare R” introduced resistance for soybean cyst nematode race1 into “Yukihomare” by marker assisted selection. *Bull Hokkaido Res Org Agric Exp Stns* 101:33–47
- Tajuddin T, Watanabe S, Yamanaka N, Harada K (2003) Analysis of quantitative trait loci for protein and lipid contents in soybean seeds using recombinant inbred lines. *Breed Sci* 53:133–140
- Takada Y, Sayama T, Kikuchi A, Kato S, Tatsuzaki N, Nakamoto Y et al (2010) Genetic analysis of variation in sugar chain composition at the C-22 position of group A saponin in soybean, *Glycine max* (L.) Merrill. *Breed Sci* 60:3–8
- Takada Y, Sasama H, Sayama T, Kikuchi A, Kato S, Ishimoto M, Tsukamoto C (2013) Genetic and chemical analysis of a key biosynthetic step for soyasapogenol A, an aglycone of group A saponins that influence soymilk flavor. *Theor Appl Genet* 126:721–731
- Takagi Y, Rahman SM, Anai T (2000) Construction of novel fatty acid composition in soybean oil by induced mutation. *Gamma F Symp* 37:17–28
- Takagi K, Kaga A, Ishimoto M, Hajika M, Matsunaga T (2015) Diversity of seed cesium accumulation in soybean mini-core collections. *Breed Sci* 65:372–380
- Takahashi K, Banba H, Kikuchi A, Ito M, Nakamura S (1994) An induced mutant line lacking the α -subunit of β -conglycinin in soybean [*Glycine max* (L.) Merrill]. *Breed Sci* 44:65–66
- Takahashi K, Uematsu Y, Kashiwaba K, Yagasaki K, Hajika M, Matsunaga R et al (2003) Accumulation of high levels of

- free amino acids in soybean seeds through integration of mutations conferring seed protein deficiency. *Planta* 217:577–586
- Takahashi K, Shimada S, Shimada H, Takada Y, Sakai T, Kono Y et al (2004) A new soybean cultivar “Yumeminori” with low allergenicity and high content of 11S globulin. *Bull Natl Agric Res Cent Tohoku Reg* 102:23–39
- Takahashi R, Benitez ER, Funatsuki H, Ohnishi S (2005) Soybean maturity and pubescence color genes improve chilling tolerance at high latitude regions. *Crop Sci* 45:1387–1393
- Takahashi M, Takahashi M, Oki N, Komatsu K, Nakazawa Y, Matsunaga R et al (2013) New soybean cultivar “Suzukaren”. *Bull NARO Kyushu Okinawa Agric Res Cent* 59:1–22
- Takahashi M, Oki N, Takahashi M, Komatsu K, Nakazawa Y, Matsunaga R (2017) Breeding of new cultivar “Fukumitori” with resistance to common cutworm (*Spodoptera litura* Fabricius). *Bull NARO Kyushu Okinawa Agric Res Cent* 66:21–45
- Takeshima R, Hayashi T, Zhu J, Zhao C, Xu M, Yamaguchi N (2016) A soybean quantitative trait locus that promotes flowering under long days is identified as *FT5a*, a *FLOWERING LOCUS T* ortholog. *J Exp Bot* 67:5247–5258
- Takeya M, Yamasaki F, Hattori S, Kaga A, Tomooka N (2013) Systems for making NIAS core collections, single-seed-derived germplasm, and plant photo images available to the research community. *Genet Resour Crop Evol* 60:1945–1951
- Tang F, Yang S, Liu J, Zhu H (2016) *Rj4*, a gene controlling nodulation specificity in soybeans, encodes a thaumatin-like protein but not the one previously reported. *Plant Physiol* 170:26–32
- Tavva VS, Kim Y-H, Kagan IA, Dinkins RD, Kim K-H, Collins GB (2007) Increased α -tocopherol content in soybean seed overexpressing the *Perilla frutescens* γ -tocopherol methyltransferase gene. *Plant Cell Rep* 26:61–70
- Tian ZX, Wang XB, Lee R, Li YH, Specht JE, Nelson RL (2010) Artificial selection for determinate growth habit in soybean. *Proc Natl Acad Sci USA* 107:8563–8568
- Toda K, Yang D, Yamanaka N, Watanabe S, Harada K, Takahashi R (2002) A single-base deletion in soybean flavonoid 3'-hydroxylase gene is associated with gray pubescence color. *Plant Mol Biol* 50:187–196
- Toda K, Hirata K, Masuda R, Yasui T, Yamada T, Takahashi K et al (2015) Relationship between mutations of the pectin methylesterase gene in soybean and the hardness of cooked beans. *J Agric Food Chem* 63:8870–8878
- Tsubokura Y, Hajika M, Harada K (2006a) Molecular characterization of a β -conglycinin deficient soybean. *Euphytica* 150:249–255
- Tsubokura Y, Hajika M, Harada K (2006b) Molecular markers associated with β -conglycinin deficiency in soybean. *Breed Sci* 56:113–117
- Tsubokura Y, Hajika M, Kanamori H, Xia Z, Watanabe S, Kaga A et al (2012) The β -conglycinin deficiency in wild soybean is associated with the tail-to-tail inverted repeat of the α -subunit genes. *Plant Mol Biol* 78:301–309
- Tsubokura Y, Matsumura H, Xu M, Liu B, Nakashima H, Anai T et al (2013) Genetic variation in soybean at the maturity locus *E4* is involved in adaptation to long days at high latitudes. *Agronomy* 3:117–134
- Tsubokura Y, Watanabe S, Xia Z, Kanamori H, Yamagata H, Kaga A et al (2014) Natural variation in the genes responsible for maturity loci *E1*, *E2*, *E3* and *E4* in soybean. *Ann Bot* 113:429–441
- Tsuda M, Kaga A, Anai T, Shimizu T, Sayama T, Takagi K et al (2015) Construction of a high-density mutant library in soybean and development of a mutant retrieval method using amplicon sequencing. *BMC Genom* 16:1014
- Tsukamoto C, Kikuchi A, Kudou S, Harada K, Kitamura K, Okubo K (1992) Group A acetyl saponin-deficient mutant from the wild soybean. *Phytochemistry* 31:4139–4142
- Tsukamoto C, Kikuchi A, Harada K, Kitamura K, Okubo K (1993) Genetic and chemical polymorphism of saponins in soybean seed. *Phytochemistry* 34:1351–1356
- Tuteja JH, Clough SJ, Chan WC, Vodkin LO (2004) Tissue-specific gene silencing mediated by a naturally occurring chalcone synthase gene cluster in *Glycine max*. *Plant Cell* 16:819–835
- Tuyen DD, Lal SK, Xu DH (2010) Identification of a major QTL allele from wild soybean (*Glycine soja* Sieb. & Zucc.) for increasing alkaline salt tolerance in soybean. *Theor Appl Genet* 121:229–236
- Tuyen DD, Chen H, Vu HTT, Hamwieh A, Yamada T, Sato T et al (2016) *Ncl* synchronously regulates Na^+ , K^+ , and Cl^- in soybean and greatly increases the grain yield in saline field conditions. *Sci Rep* 6:19147
- Uchibori A, Sasaki J, Takeuchi T, Kamiya M, Tazawa A, Inukai T, Masuta C (2009) QTL analysis for resistance to *Soybean dwarf virus* in Indonesian soybean cultivar Wilis. *Mol Breed* 23:323–328
- Ujiie A, Yamada T, Fujimoto K, Endo Y, Kitamura K (2005) Identification of soybean varieties with high α -tocopherol content. *Breed Sci* 55:123–125
- Umezawa T, Sakurai T, Totoki Y, Toyoda A, Seki M, Ishikawa A et al (2008) Sequencing and analysis of approximately 40,000 soybean cDNA clones from a full-length cDNA library. *DNA Res* 15:333–346
- Valliyodan B, Qiu D, Patil G, Zeng P, Huang J, Dai L et al (2016) Landscape of genomic diversity and trait discovery in soybean. *Sci Rep* 6:23598
- VanToai TT, Beuerlein AF, Schmitthenner SK, St Martin SK (1994) Genetic variability for flooding tolerance in soybean. *Crop Sci* 34:1112–1115
- Vollmann J, Losak T, Pachner M, Watanabe D, Musilova L, Hlusek J (2015) Soybean cadmium concentration: validation of a QTL affecting seed cadmium accumulation for improved food safety. *Euphytica* 203:177–184
- Wang WH, Takano T, Shibata D, Kitamura K, Takeda G (1994) Molecular basis of a null mutation in soybean lipoxygenase 2: substitution of glutamine for an iron-ligand histidine. *Proc Natl Acad Sci USA* 91:5828–5832
- Wang WH, Kato T, Takano T, Shibata D, Kitamura K, Takeda G (1995) Two single-base substitutions involved in altering in a paired box of AAATAC in the promoter region of soybean lipoxygenase L-3 gene impair the promoter function in tobacco cells. *Plant Sci* 109:67–73
- Wang S, Kanamaru K, Li W, Abe J, Yamada T, Kitamura K (2007) Simultaneous accumulation of high content of α -

- tocopherol and lutein is possible in seeds of soybean (*Glycine max* (L.) Merr.). *Breed Sci* 57:297–304
- Wang W, He Q, Yang H, Xiang S, Zhao T, Gai J (2013) Development of a chromosome segment substitution line population with wild soybean (*Glycine soja* Sieb. & Zucc.) as donor parent. *Euphytica* 189:293–307
- Watanabe S, Tajuddin T, Yamanaka N, Hayashi M, Harada K (2004) Analysis of QTLs for reproductive development and seed quality traits in soybean using recombinant inbred lines. *Breed Sci* 54:399–407
- Watanabe S, Hideshima R, Xia Z, Tsubokura Y, Sato S, Nakamoto Y et al (2009) Map-based cloning of the gene associated with the soybean maturity locus *E3*. *Genetics* 182:1251–1262
- Watanabe S, Xia Z, Hideshima R, Tsubokura Y, Sato S, Yamanaka N et al (2011) A map-based cloning strategy employing a residual heterozygous line reveals that the *GIGANTEA* gene is involved in soybean maturity and flowering. *Genetics* 188:395–407
- Watanabe S, Harada K, Abe J (2012) Genetic and molecular bases of photoperiodic responses of flowering in soybean. *Breed Sci* 61:531–543
- Watanabe S, Tsukamoto C, Oshita T, Yamada T, Anai T, Kaga A (2017) Identification of quantitative trait loci for flowering time by a combination of restriction site-associated DNA sequencing and bulked segregant analysis in soybean. *Breed Sci* 67:277–285
- Watanabe S, Shimizu T, Machita K, Tsubokura Y, Xia X, Yamada T et al (2018) Development of a high-density linkage map and chromosome segment substitution lines for Japanese soybean cultivar Enrei. *DNA Res* 25:123–136
- Wolfgang G, An Y (2017) Genetic separation of southern and northern soybean breeding programs in North America and their associated allelic variation at four maturity loci. *Mol Breed*. <https://doi.org/10.1007/s11032-016-0611-7>
- Xia Z, Sato H, Watanabe S, Kawasaki S, Harada K (2005) Construction and characterization of a BAC library of soybean. *Euphytica* 141:129–137
- Xia Z, Tsubokura Y, Hoshi M, Hanawa M, Yano C, Okamura K et al (2007) An integrated high-density linkage map of soybean with RFLP, SSR, STS, and AFLP markers using a single F2 population. *DNA Res* 14:257–269
- Xia Z, Watanabe S, Yamada T, Tsubokura Y, Nakashima H, Zhai H et al (2012) Positional cloning and characterization reveal the molecular basis for soybean maturity locus *E1* that regulates photoperiodic flowering. *Proc Natl Acad Sci USA* 109:E2155–E2164
- Xin DW, Qi ZM, Jian HW, Hu ZB, Zhu RS, Hu JH et al (2016) QTL location and epistatic effect analysis of 100-seed weight using wild soybean (*Glycine soja* Sieb. & Zucc.) chromosome segment substitution lines. *PLoS ONE* 11:e0149380
- Xu DH, Abe J, Gai AJ, Shimamoto Y (2002) Diversity of chloroplast DNA SSRs in wild and cultivated soybeans: evidence for multiple origins of cultivated soybean. *Theor Appl Genet* 105:645–653
- Xu M, Xu Z, Liu B, Kong F, Tsubokura Y, Watanabe S et al (2013) Genetic variation in four maturity genes affects photoperiod insensitivity and PHYA-regulated post-flowering responses of soybean. *BMC Plant Biol* 13:91
- Xu M, Yamaguchi N, Zhao C, Takeshima R, Kasai M, Watanabe S et al (2015) The soybean-specific maturity gene *E1* family of floral repressor controls night-break responses through down-regulation of *FLOWERING LOCUS T* orthologs. *Plant Physiol* 168:1735–1746
- Yagasaki K, Kaizuma N, Kitamura K (1996) Inheritance of glycinin subunits and characterization of glycinin molecules lacking the subunits in soybean (*Glycine max* (L.) Merr.). *Breed Sci* 46:11–15
- Yagasaki K, Sakamoto H, Seki K, Yamada N, Takamatsu M, Taniguchi T, Takahashi K (2010) Breeding of a new soybean cultivar “Nanahomare” (in Japanese). *Hokuriku Crop Sci* 45:61–64
- Yamada T, Hajika M, Yamada N, Hirata K, Okabe A, Oki N et al (2012) Effects on flowering and seed yield of dominant alleles at maturity loci *E2* and *E3* in a Japanese cultivar, Enrei. *Breed Sci* 61:653–660
- Yamada T, Shimada S, Hajika M, Hirata K, Takahashi K, Nagaya T et al (2014) Major QTLs associated with green stem disorder insensitivity of soybean (*Glycine max* (L.) Merr.). *Breed Sci* 64:331–338
- Yamada T, Hajika M, Funatsuki H, Takahashi K, Hirata K, Hishinuma A, Tanaka J (2017) Causal analysis of yield-increase by introgression of shattering resistance gene *pdh1* in soybean. *Jpn J Crop Sci* 86:251–257
- Yamaguchi N, Sayama T, Sasama H, Yamazaki H, Miyoshi T, Tanaka Y, Ishimoto M (2014a) Mapping of quantitative trait loci associated with terminal raceme length in soybean. *Crop Sci* 54:2461–2468
- Yamaguchi N, Sayama T, Yamazaki H, Miyoshi T, Ishimoto M, Funatsuki H (2014b) Quantitative trait loci associated with lodging tolerance in soybean cultivar ‘Toyoharuka’. *Breed Sci* 64:300–308
- Yamaguchi N, Yamazaki H, Ohnishi S, Suzuki C, Hagihara S, Miyoshi T, Senda M (2014c) Methods for selection of soybeans tolerant to seed cracking under chilling temperatures. *Breed Sci* 64:103–108
- Yamaguchi N, Kurosaki H, Ishimoto M, Kawasaki M, Senda M, Miyoshi T (2015) Early-maturing and chilling-tolerant soybean lines derived from crosses between Japanese and Polish cultivars. *Plant Prod Sci* 18:234–239
- Yamaguchi N, Ohnishi S, Miyoshi T (2018) Screening for chilling-tolerant soybeans at the flowering stage using a seed yield- and maturity-based evaluation method. *Crop Sci* 58:312–320
- Yamanaka N, Ninomiya S, Hoshi M, Tsubokura Y, Yano M, Nagamura Y et al (2001) An informative linkage map of soybean reveals QTLs for flowering time, leaflet morphology and regions of segregation distortion. *DNA Res* 8:61–72
- Yamanaka N, Morishita M, Mori T, Lemos NG, Hossain MdM, Akamatsu H et al (2015) Multiple *Rpp*-gene pyramiding confers resistance to Asian soybean rust isolates that are virulent on each of the pyramided genes. *Trop Plant Pathol* 40:283–290
- Yamashita Y, Tazawa A, Minami M (2012) Development of a method to evaluate the field resistance of soybean to *Phytophthora sojae*. *Jpn J Crop Sci* 81:183–189
- Yamashita Y, Takeuchi T, Ohnishi S, Sasaki J, Tazawa A (2013) Fine mapping of the major *Soybean dwarf virus* resistance

- gene *Rsdv1* of the soybean cultivar ‘Wilis’. *Breed Sci* 63:417–422
- Yan T, Di S, Rodas FR, Torrico TR, Murai Y, Iwashita T et al (2014) Allelic variation of soybean flower color gene *W4* encoding dihydroflavonol 4-reductase 2. *BMC Plant Biol* 14:58
- Yano R, Takagi K, Takada Y, Mukaiyama K, Tsukamoto C, Sayama T et al (2017) Metabolic switching of astringent and beneficial triterpenoid saponins in soybean is achieved by a loss-of-function mutation in cytochrome P450 72A69. *Plant J* 89:527–539
- Yoshikawa T, Okumoto Y, Ogata D, Sayama T, Teraishi M, Terai M et al (2010) Transgressive segregation of isoflavone contents under the control of four QTLs in a cross between distantly related soybean varieties. *Breed Sci* 60:243–254
- Yu N, Lee TG, Rosa DP, Hudson M, Diers BW (2016) Impact of *Rhg1* copy number, type, and interaction with *Rhg4* on resistance to *Heterodera glycines* in soybean. *Theor Appl Genet* 129:2403–2412
- Zhai H, Lu S, Wang Y, Chen X, Ren H, Yang J et al (2014) Allelic variation at four major maturity *E* genes and transcriptional abundance of the *E1* gene are associated with flowering time and maturity of soybean cultivars. *PLoS ONE* 9:e97636
- Zhang B, Chen P, Florez-Palacios SL, Shi A, Hou A, Ishibashi T (2010) Seed quality attributes of food-grade soybeans from U.S. and Asia. *Euphytica* 173:387–396
- Zhao C, Takashima R, Zhu J, Xu M, Sato M, Watanabe S et al (2016) A recessive allele for delayed flowering at the soybean maturity locus *E9* is a leaky allele of *FT2a*, a *FLOWERING LOCUS T* ortholog. *BMC Plant Biol* 16:20
- Zhou Z, Jiang Y, Wang Z, Gou Z, Lyu J, Li W et al (2015) Resequencing 302 wild and cultivated accessions identifies genes related to domestication and improvement in soybean. *Nat Biotechnol* 33:408–414

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.